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Efectos sobre la biodiversidad de distintos manejos en un gradiente de usos y hábitats

Antonio José Carpio Camargo

TESIS DOCTORAL

TITULO: *Efectos sobre la biodiversidad de distintos manejos en un gradiente de usos y hábitats*

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TÍTULO DE LA TESIS:

Efectos sobre la biodiversidad de distintos manejos en un gradiente de usos y hábitats

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INFORME RAZONADO DEL/DE LOS DIRECTOR/ES DE LA TESIS

El documento presentado por el doctorando D. Antonio José Carpio Camargo, y que lleva por título "Efectos sobre la biodiversidad de distintos manejos en un gradiente de usos y hábitats" corresponde a su trabajo de tesis doctoral. Éste trabajo se ha enfocado en el estudio de algunos de los principales poblemos que amenazan la pérdida de biodiversidad (intensificación agrícola, introducción de especies exóticas, sobreabundancia de ungulados), y conducidos todos ellos a través de una línea común como son las cubiertas vegetales. Los principales eventos analizados fueron: el papel del olivar y las cubiertas vegetales sobre las comunidades de reptiles, y la depredación de nidos presentado en los capítulos I y II; el impacto de los herbívoros sobre estas cubiertas y los efectos en cascada que provocan sobre el resto del ecosistema en el capítulo III; y el role de las especies exóticas, con especial atención al factor antrópico.

El presente trabajo supone una aportación importante a los campos de la Ecología y la Agricultura sostenible, contribuyendo a mejorar el conocimiento sobre el efecto que los diferentes usos y manejos del suelo tienen sobre la biodiversidad. Ésta tesis se presenta en formato de Tesis Internacional constituida por un conjunto de quince trabajos, de los cuales catorce están publicados por el doctorando, como primer autor, en revistas incluidas en el Journal Citation Report (JCR). El doctorando cumple con los requisitos académicos y científicos exigidos para la defensa de la tesis y para poder optar al grado de Doctor en Biología con mención Internacional. Para ello el doctorando ha realizado una estancia de investigación de tres meses y quince días en la Universidad de Gävle (Suecia). Así mismo, varios de los artículos que comprende la presente tesis han sido publicados en revistas de elevado Factor de Impacto en sus áreas. Finalmente el doctorando presenta otros trabajos publicados, durante su doctorado.

Por todo ello, se autoriza la presentación de la tesis doctoral.

Córdoba, 15 de Abril de 2017

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INFORME SOBRE APORTACIONES DERIVADAS DE LA TESIS DOCTORAL Y FACTOR DE IMPACTO DE LAS REVISTAS CIENTÍFICAS (JOURNAL CITATION REPORTS)

Publicaciones en revistas científicas (Capítulos de la Tesis)

1- **Carpio, A.J.,** Oteros, J., Tortosa, F.S., Guerrero-Casado, J. (2016). Land use and biodiversity patterns of the herpetofauna: the role of olive groves. Acta Oecologica. 70, 103–111. DOI 10.1016/j.actao.2015.12.007. (Capítulo 1.1 de la Tesis).

Factor de Impacto: 1.42. Posición de la revista en relación a su categoría específica: 97/150; tercer cuartil (Q3), segundo tercil (T2).

2- **Carpio, A.J.,** Cabrera, M., Tortosa, F.S. (2015). Evaluation of methods for estimating species richness and abundance of reptiles in olive groves. Herpetological Conservation and Biology. 10(1), 54–63. (Capítulo 1.2 de la Tesis).

Factor de Impacto: 0.768. Posición de la revista en relación a su categoría específica: 107/161; tercer cuartil (Q3), segundo tercil (T2).

3- **Carpio, A.J.,** Castro, J., Mingo, V., Tortosa, F.S. (2017). Herbaceous cover enhances the squamate reptile community in woody crops. Journal for Nature Conservation. 37, 31–38 DOI 10.1016/j.jnc.2017.02.009. (Capítulo 1.3 de la Tesis).

Factor de Impacto: 2.22. Posición de la revista en relación a su categoría específica: 13/49; segundo cuartil (Q2), primer tercil (T1).

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A mis padres Diego y Carmen, por su apoyo incondicional

A mis abuelos y mi hermano Diego

«La ignorancia engendra más confianza de la que con frecuencia engendra el conocimiento: son aquellos que saben poco, y no aquellos que saben mucho, los que afirman positivamente que tal o cual problema jamás podrá ser resuelto por las ciencias».

Charles Darwin

«El hombre de hoy usa y abusa de la naturaleza como si hubiera de ser el último inquilino de este desgraciado planeta, como si detrás de él no se anunciara un futuro».

Miguel Delibes

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ÍNDICE GENERAL

RESUMEN

Los distintos manejos a los que se ve sometido el medio ambiente repercuten de forma directa sobre la biodiversidad que esta alberga. Estos manejos varían dependiendo del uso de la tierra, así sea agrícola, cinegético, ganadero, forestal, etc.… y por lo tanto sus efectos sobre el hábitat y las especies que contiene son bastante variables. La presente tesis tiene como objetivo la evaluación y cuantificación de los efectos que distintas prácticas de gestión tienen sobre la biodiversidad en un gradiente de hábitats en el Sur de la Península Ibérica. Para ello este trabajo abarca el estudio tanto de zonas agrícolas (olivar), como de zonas forestales (principalmente cinegéticas) en la provincia de Córdoba (Andalucía, España). Un conocimiento más profundo sobre los principales factores que influyen sobre la biodiversidad es de gran interés no solo a nivel ecológico, sino también económico, dado que muchas especies pueden actuar como control de plagas, bioindicadores, y agronómico, ya que muchos de estos factores (por ejemplo el uso de cubiertas vegetales), pueden minimizar problemas agronómicos como la erosión. Algunas especies, además, son de interés socio-económico, como las especies cinegéticas.

Se han analizado las relaciones que mantienen diferentes factores abióticos: ambientales, paisajísticos (cubiertas vegetales, diversidad paisajística…) y estructura del hábitat (setos, diversidad vegetal…); bióticos: sobreabundancia de herbívoros, introducción de especies exóticas, y antrópicos: tipo de manejo y uso del suelo con la biodiversidad en un gradiente de hábitats. A partir de este enfoque multidisciplinar se han obtenido resultados, con un gran interés científico, una alta aplicabilidad y transferibles a la sociedad, ya que permiten identificar muchos de los problemas actuales que afectan a la pérdida de biodiversidad, a la vez que plantea medidas relativamente sencillas para frenar estas tasas.

En los capítulos I y II, "*Situación actual de la biodiversidad en los distintos tipos de olivares: la herpetofauna como modelo*" y "*Efectos de la simplificación del paisaje sobre la depredación de los nidos*", se analizan los efectos de la intensificación agrícola. En el primer capítulo se plantea la situación actual de la hepertofauna, prestando especial atención al olivar y al efecto que las cubiertas vegetales pueden tener sobre las comunidades de este taxón. En el segundo capítulo se determina el papel que

la simplificación del paisaje ha tenido sobre la avifauna, a través de la depredación de los nidos. Este capítulo abarca diversos procesos ecológicos como la hiperdepración, la densidad de nidificación, y la relación entre éstos, la simplificación del hábitat y la depredación de nidos.

En el capítulo III "*Efectos de conejos y ungulados sobre las cubiertas herbáceas y sus consecuencias sobre el ecosistema",* se ha estudiado en primer lugar el papel del conejo en el establecimiento de las cubiertas vegetales en cultivos leñosos, planteando alternativas con especies no palatables como *Anthemis arvensis*. Además se ha estudiado la cascada de efectos que provoca la abundancia de ungulados sobre el ecosistema. El capítulo abarca (i) las alteraciones de las comunidades vegetales y artrópodos, (ii) los efectos negativos sobre las especies de caza menor (conejo y perdiz) producidas a través de diversos mecanismos, como las disponibilidad de alimento y refugio, la alteración de la estructura del hábitat y la depredación de nidos en el caso de la perdiz, y (iii) el propio efecto negativo de la sobreabundancia sobre la propia población del ungulado.

Finalmente, en el capítulo IV *"Interacciones ecológicas entres especies nativas y exóticas"*, se analiza tanto el papel de la caza en la introducción de especies exóticas, como los principales factores antrópicos, abióticos y bióticos que influyen en su introducción. Este capítulo pone de manifiesto el papel del ser humano en la introducción de especies exóticas, y el potencial conflicto que existe entre éstas y las especies nativas, principalmente en los espacios protegidos.

Los resultados obtenidos en la presente tesis contribuyen a profundizar en el conocimiento de la respuesta de la biodiversidad a diferentes manejos en un gradiente de hábitats, y especialmente sobre el papel que las cubiertas herbáceas pueden jugar sobre estas tasas de pérdida de biodiversidad. Éstos resultados han sido obtenidos gracias a un enfoque multidisciplinar, intentando abarcar gran parte de los problemas a los que se enfrenta la biodiversidad en la actualidad. Además de identificar los problemas, se plantean soluciones o medidas que pueden ayudar a mitigar estos problemas, lo cual supone una aportación desde un punto de vista de la aplicación de estos resultados para la sociedad.

ABSTRACT

The different managements to which the environment is subjected have a direct impact on the biodiversity. These uses vary from agricultural to hunting, etc; impacting not only the habitat but also the species therein. This thesis aims evaluating and quantifying the effects that different management practices may exert on biodiversity in a habitat gradient in the South of the Iberian Peninsula. To this end, this work covers the study of both agricultural areas (olive groves) and forest areas (mainly hunting estates) in the province of Córdoba (Andalusia, Spain). A deeper understanding of the main factors influencing biodiversity is of great interest not only from an ecological perspective, but also economically. This is because many species can act as pest control, bioindicators, and agronomic, since many of these factors (for example the use of vegetation cover), can minimise agronomic problems such as erosion. In addition, game species have important socio-economic value.

We have analysed the relationships among different abiotic factors: environmental, landscape (vegetation cover, landscape diversity ...) and structure of habitat (hedges, plant diversity ...); biotic factors: overabundance of herbivores, introduction of alien species and anthropic factors: types of management and land use with biodiversity in a habitat gradient. This multidisciplinary approach yielded results of great scientific interest, high applicability and transference to the society since we identified not only the causes related to the loss of biodiversity, but simple measures to reduce these loss rates.

In chapters I and II, "*Current situation of biodiversity in different types of olive groves: herpetofauna as a model*" and "*Effects of landscape simplification on nest predation*", the effects of agricultural intensification are analysed. The first chapter presents the current situation of the hepertofauna, paying special attention to the olive grove and the effect that the vegetation cover may have on the communities of this taxon. Then, in the second chapter, we studied the role that landscape simplification has had on the avifauna through predation of nests. This section covers various ecological processes such as hyperpredation, nesting density, and their relationship with habitat simplification and nest predation.

In chapter III "*Effects of rabbits and ungulates on herbaceous covers and their consequences on the ecosystem*", we focus on the role of the rabbit in the establishment

of vegetal covers by proposing alternatives to *Bromus rubes* such as is *Anthemis arvensis*. In addition, we studied the effects cascade caused by the abundance of ungulates on the ecosystem. The chapter includes (i) the alterations of the plant communities and arthropods, (ii) the negative effects on the small game species (rabbit and partridge) through diverse mechanisms like the availability of food and shelter, the alteration of the structure of the habitat and nest predation in the case of the partridge, and (iii) the negative effect of the overabundance on the own population of the ungulate.

Finally, in chapter IV, entitled "*Ecological interactions between native and exotic species*" we discussed both the role of game in the introduction of exotic species and the main anthropic, abiotic and biotic factors that influence their introduction. This chapter highlights the role of humans in the introduction of alien species, and the potential conflict between these and native species, mainly in protected areas.

The results obtained in this thesis contribute to deepening the knowledge of the response of biodiversity to different management in a habitat gradient, and especially, the role that herbaceous covers may play on biodiversity loss. These results have been obtained using a multidisciplinary approach; covering a plethora of potential causes that affects biodiversity. In addition to the identification of such causes, we propose restoration measures that can help to mitigate biodiversity loss. This practical approach is a relevant contribution to the society.

INTRODUCCIÓN

1. Contexto de la tesis doctoral.

Esta Tesis doctoral aborda, por un lado, el efecto de la intensificación agrícola sobre la biodiversidad, y por otro, cómo algunos sistemas de manejo pueden ayudar a mitigar la pérdida de biodiversidad. Como modelo de estudio, nos centraremos principalmente en olivares del sur de la Península Ibérica y su transición hacia ambientes forestales, prestando especial atención sobre grupos de bioindicadores, como son reptiles, aves o artrópodos. Abordamos además algunos efectos derivados de la cascada de interacciones que se producen cuando alteramos las cubiertas vegetales debido a altas abundancias de ungulados. Con esta tesis, pretendemos mejorar el conocimiento de un problema reciente, como es la intensificación del olivar; así como evaluar los beneficios que puede tener la implantación de cubiertas herbáceas en estos cultivos. Además, en esta tesis se ofrece un enfoque práctico de los problemas que pueden impedir el establecimiento de estas cubiertas, sobre todo en lo relacionado con la presión de herbivoría, y los efectos en cascada que de ésta sobre el ecosistema; ofreciendo soluciones practicas. A lo largo de la introducción, se revisará la situación actual del olivar, los problemas derivados de su intensificación; así como alternativas de manejo para frenar estos problemas, prestando especial atención a las cubiertas herbáceas. Además se revisara brevemente el tema de la sobreabundancia de las especies de caza mayor (jabalí y ciervo), y sus consecuencias sobre el ecosistema.

Como objetivo principal de esta tesis se ha planteado determinar el papel que las cubiertas vegetales pueden desempeñar sobre la biodiversidad en un gradiente de hábitats, a través de un enfoque múltiple y una visión holística; integrando ideas y métodos de varias disciplinas, como la Agroecología, la Zoología y la Botánica. En el capítulo 1, se ha estudiado la biodiversidad actual del olivar y el efecto de las cubiertas sobre ésta a través de un enfoque comparativo. En el capítulo 2, se han analizado los efectos derivados de la simplificación del paisaje en diversos hábitats, mediante el análisis de las tasas de depredación de nidos. En el capítulo 3, se han analizado los efectos de la presión de herbivoría sobre las cubiertas herbáceas y algunas de sus consecuencias en el ecosistema. Finalmente en el capítulo 4, se han tenido en cuenta las interacciones ecológicas entres especies nativas y exóticas (con especial atención al papel de la caza).

2. Intensificación agrícola y el ejemplo del olivar

Bajo el escenario actual de rápido aumento de la población humana, lograr un uso agrícola eficiente y productivo de la tierra mientras se conserva la biodiversidad se ha convertido en un desafío global (Tscharntke et al. 2012). En Europa, la Política Agrícola Común (PAC) impulsó la intensificación de la agricultura, promoviendo la simplificación y especialización de los agro-ecosistemas a través de la disminución de la heterogeneidad del paisaje, el uso creciente de productos químicos por unidad de superficie y el abandono de zonas menos fértiles (Emerson et al. 2016). En este sentido, durante los últimos 50 años, las tierras de cultivo de los países de Europa occidental han experimentado drásticos cambios, principalmente a través de la intensificación de las técnicas de cultivo (Robinson y Sutherland 2002). Esta intensificación viene caracterizada por un incremento en las intervenciones de gestión y los insumos externos, con el objetivo de mejorar el rendimiento agrícola, lo que incluye aumentos en la mecanización, la eliminación de la vegetación natural, la fertilización y un amplio uso de plaguicidas (Kizos y Koulouri 2006; Plieninger et al. 2013).

En general, la intensificación agrícola conlleva asociada una simplificación y homogeneización de los paisajes, lo que conduce a una reducción de las especies presentes en las tierras de cultivo (por ejemplo, Benton et al. 2003; Medan et al. 2011). Esta intensificación se ha considerado el factor que ha tenido un mayor efecto sobre la pérdida de biodiversidad en los agroecosistemas (Sala et al. 2000), comparable en escala con la derivada del cambio climático (Tilman et al. 2001). Por otro lado, el uso intensivo de un número limitado de cultivos ha reducido drásticamente el número de especies de plantas de las que dependen los seres humanos (Abberton et al. 2016).

A partir de este punto es cuando la nueva PAC establece que la sostenibilidad, debe de ser una de las prioridades clave de la agricultura (Pe'er et al. 2014), y que para alcanzar este objetivo, es esencial reducir la erosión de los suelos y potenciar la biodiversidad en tierras de cultivo. En consecuencia, el 30% del pago de las subvenciones está ahora vinculado a una o más de las tres nuevas medidas ecológicas (``greening measures´´) (EC 2013b, artículo 43): a) diversificación de los cultivos, exigiendo que las explotaciones con tierras de cultivo que exceden de las 20 ó 30 hectáreas deban cultivar al menos dos o tres tipos de cultivos, respectivamente; b) el mantenimiento de los pastos permanentes existentes, no superando una pérdida superior al 5% para 2020; y c) la promoción de las «áreas de interés ecológico», exigiendo que las explotaciones con áreas de cultivo de más de 15 ha dediquen el 5% de esas zonas a elementos ecológicamente beneficiosos bien definidos (Pe'er et al. 2016). Tales elementos, incluyen características del paisaje tales como terrazas, lindes, setos o estanques; pero también tierras de barbecho, cultivos de fijación de nitrógeno y cultivos para crear cobertura herbácea (EC 2013; 2014). No obstante, la expansión de la Unión Europea y su mercado común continúan impulsando la intensificación agrícola en Europa (Carvalheiro et al. 2013) a través del aumento del tamaño de las explotaciones o con nuevos estados miembros que muestran un aumento de insumos (Pe'er et al. 2014).

Esta Tesis Doctoral se centra en una zona donde predomina el olivar, que supone un ejemplo claro de la intensificación agrícola sufrida en las últimas décadas (Gómez-Limón et al. 2012). La extensión del olivar amenaza a los agro-ecosistemas tradicionales como los cereales de invierno, los pastizales extensivos o la propia agricultura tradicional del olivar de bajos insumos, ya que el paisaje en mosaico ha sido sustituido por el monocultivo del olivar (Stoate et al. 2009). Este sistema de producción intensiva se caracteriza por el establecimiento de variedades más jóvenes y más productivas, con una mayor densidad de árboles y riego por goteo, junto con un mayor uso de productos agroquímicos (Palomares et al. 2015). Todo esto ha conducido a una reducción de la heterogeneidad del hábitat, mayor contaminación y erosión del suelo, que, a su vez, ha provocado una disminución de la diversidad animal y vegetal (Santos y Cabral 2003).

2.1. Situación actual del olivar

El olivo se empezó a cultivar en Oriente Medio hace unos 6000 años (Kaniewski et al. 2012). Posteriormente, el cultivo se extendió a toda la Cuenca del Mediterráneo. Su distribución se restringe entre los 30º y los 45º de latitud, tanto en el hemisferio norte como en el hemisferio sur, aunque el 95% de la producción mundial de aceite de oliva sigue concentrado en el área mediterránea (COI 2016).

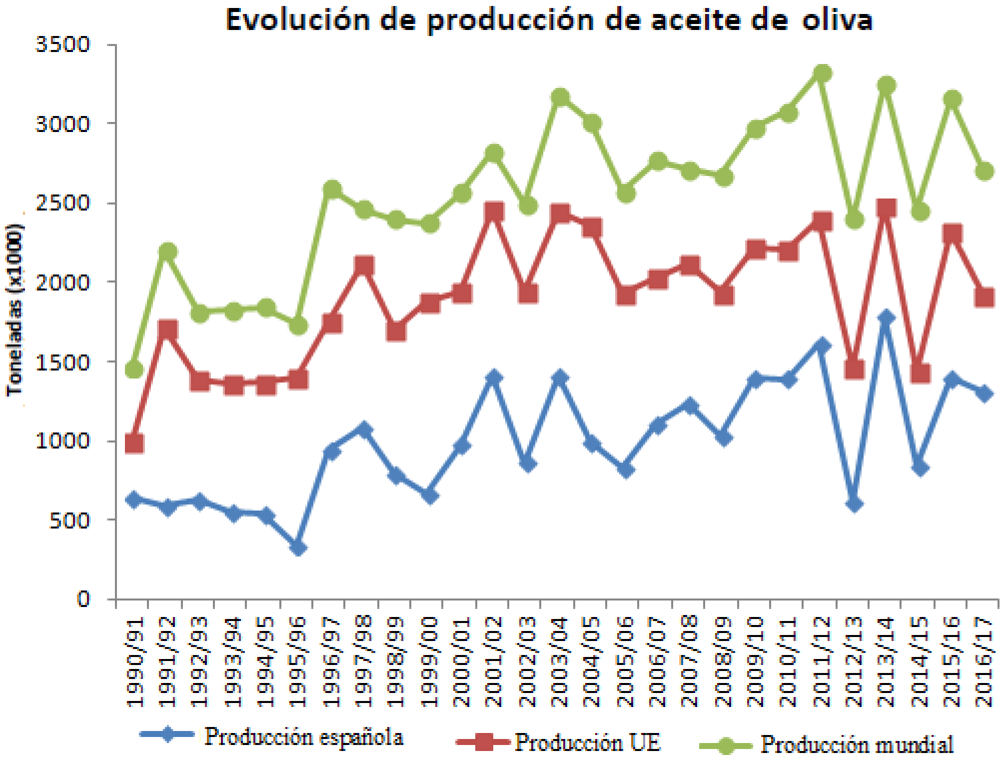


Figura 1. Evolución de la producción de aceite de oliva

En la Figura 1 se observa la evolución de la producción de aceite de oliva durante las últimas décadas (COI 2016). Éste aumento se ha conseguido gracias a la expansión de la superficie de cultivo, así como al desarrollo de estrategias de densificación, intensificación productiva e irrigación, y de mejoras técnicas en las explotaciones. La tendencia creciente en la producción es debido a la mayor actividad exportadora de nuestro país, la cual ha sido favorecida por la incorporación de España al Mercado Común Europeo.

En España se encuentra la mitad de la producción olivícola del mundo, ya que la cantidad de tierra dedicada a los olivares en España aumentó en 300.000 ha entre 1996 y 2008, situándose en la actualidad en 2,4 millones de ha (COI 2013), representado el 3,6% de la superficie en 2012 (CORINE land cover data; http://www.eea.europa.eu). Dentro de este Estado, la principal zona productora de aceite de oliva es Andalucía, representando el olivo el principal cultivo de la región con más de 1,5 millones de ha y el 3% del PIB Andaluz (MAGRAMA 2016). (Figura 2).

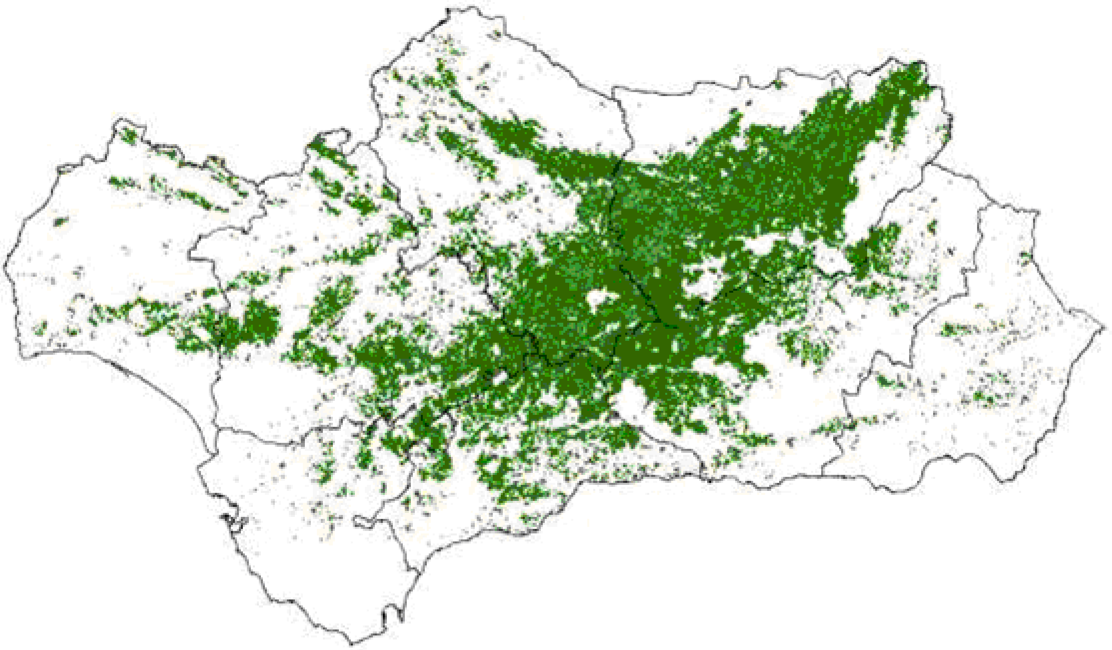


Figura 2. Distribución del olivar en Andalucia (Junta de Andalucia, 2010).

En España, el olivar se ha cultivado tradicionalmente como un sistema no intensivo o de baja densidad arbórea (alrededor de 100 árboles / ha), sin riego y con una cobertura herbácea del suelo que rara vez supera el 25% (Villalobos et al. 2000). Sin embargo, este sistema se ha visto sustituido recientemente (en los últimos 30 años) por un olivar con riego por goteo (hasta 2700m^3/ha/año; Metzidakis et al. 2008), caracterizado por una alta densidad de árboles (300-400 árboles/ha) en olivares intensivos, y (400-1700 árboles/ha) en olivares superintensivos (Cameira et al. 2014). El nuevo sistema está basado en una labranza reducida, altos insumos de pesticidas y fertilizantes, y una mecanización de la cosecha para elevar los rendimientos del olivar (Palomares et al. 2015).

2.2. Sistema de manejos actuales del olivar

Hasta un pasado muy reciente, a partir de los olivos se obtenían otros productos aparte de sus frutos (leña, ramón…). Estos otros usos, hoy prácticamente olvidados, determinaron los esquemas de cultivo que todavía se conservan en muchos olivares (Guzmán Álvarez 2007). Sin embargo, esto evolucionó hacia un marco regular de plantación (separación constante de árboles), con espaciamientos que se han reducido progresivamente desde 12 x 12 m o más, hasta 8 x 8m ó 7 x 7m, y más recientemente en la olivicultura intensiva (7 x 5m, 8 x 6m, etc.), para alcanzar densidades superiores (Guzmán Álvarez et al. 2009). La aparición del olivar superintensivo basado en plantaciones en seto ha supuesto una evolución en los marcos de plantación del olivar. En este nuevo sistema, las alineaciones continuas de pequeños árboles requieren de una agronomía específica, como conseguir setos de 3 o 4 m de altura, obtención de variedades plenamente adaptadas o un enfoque diferente en el control de plagas y enfermedades (Gómez-Calero 2009).

Desde un punto de vista del manejo y el enfoque productivo, los olivares se pueden diferenciar en tres sistemas de producción: agricultura ecológica, producción integrada (ambos certificados) y producción convencional.

- **Olivicultura ecológica**: Esta agricultura, iniciada en la década de los 80, se ha expandido hasta alcanzar unas 50.000ha en el año 2008 (Gómez-Calero 2009). Este sistema de producción se define como un sistema agrario cuyo objetivo es la obtención de alimentos de máxima calidad, respetando el medio ambiente, mediante la utilización óptima de los recursos naturales; excluyendo el empleo de productos químicos de síntesis y procurando un desarrollo agrario sostenible. Incluye la conservación de setos y límites de finca. La normativa de la agricultura ecológica no hace referencia explícita al marco de plantación.
- **Producción integrada:** Este sistema se define como el sistema agrícola de obtención de alimentos, que optimiza los recursos y los mecanismos de producción naturales, asegurando a largo plazo una agricultura sostenible. Incluye métodos de control biológicos, químicos y otras técnicas, que compatibilizan la protección del medio ambiente y la productividad agrícola. La normativa de la producción integrada restringe las labores en parcelas con pendientes iguales o superiores al 10%, obligando a adoptar prácticas de cultivo especiales; como el abancalamiento, cultivo en fajas, cubiertas vegetales vivas o inertes (Garrido et al. 2009). En la producción integrada se recomiendan densidades de entre 200-300 pies/ha (espacio mínimo de 6 m).
- **Producción convencional:** Este sistema incluye todas las actividades agrarias no certificadas en los casos anteriores. Los agricultores y ganaderos, que reciban cualquier ayuda de la PAC están obligados a respetar una serie de normas referidas a la buena gestión del entorno natural, bienestar animal, salud pública. Es lo que se entiende por “condicionalidad” y afecta en la práctica a todo el olivar en Andalucía, incluidos los dos sistemas certificados. La normativa de la condicionalidad limita las labores en recintos con pendientes iguales o superiores al 15%, excepto en los bancales (Gómez-Calero 2009). En cuanto a la densidad de arbolado, la normativa de

condicionalidad derivada de las ayuda de la PAC no hace referencia explícita al marco de plantación.

Otras medidas que dependen de cada tipo de producción son la fertilización (con una lista de productos autorizados para cada tipo de sistema), el riego, el control de enfermedades o plagas, y el manejo y cobertura de suelo. Sin embargo, en esta tesis nos centraremos en el manejo y cobertura del suelo, lo cual es descrito en el apartado 4.1.

2.3. El olivar como agro-ecosistema y su biodiversidad

Este árbol longevo ha formado parte de la identidad económica, social y cultural de los habitantes de la cuenca Mediterránea, y determina su paisaje rural. Incluso ahora, el cultivo del olivo tiene una importancia múltiple para el Mediterráneo. Aunque es un agro-ecosistema, el olivar tradicional se asemejaba al ecosistema mediterráneo natural, y su abandono los transforma en bosques naturalizados de tipo mediterráneo (Loumou y Giourga 2003). Por tanto, estos cultivos constituyen una parte significativa del medio ambiente y la cultura mediterránea. No obstante, su importancia ecológica solo ha sido recientemente admitida. En este sentido, el olivar es un agro-ecosistema multifuncional, cuyas funciones pueden ser metafóricamente concebidas como las cinco líneas de la silueta de una casa (Figura 3). La "casa de las funciones" es una herramienta para evaluar las funciones de los agro-ecosistemas (como lo define Conway 1987). Distinguimos cinco grupos de funciones dentro de este agro-ecosistema: funciones ecológicas, productivas, económicas, sociales y culturales. A cada conjunto de funciones se le puede asignar un lugar específico en esta "casa de las funciones". Sin embargo, Fleskens et al. (2009) muestra que las funciones ecológicas parecen ser las más bajas en el conjunto de indicadores utilizados. Aunque una casa cerrada puede ser construida, ésta es altamente inestable porque la base ecológica es demasiado pequeña. Por tanto, la primera prioridad debe ser la mejora del rendimiento medioambiental.

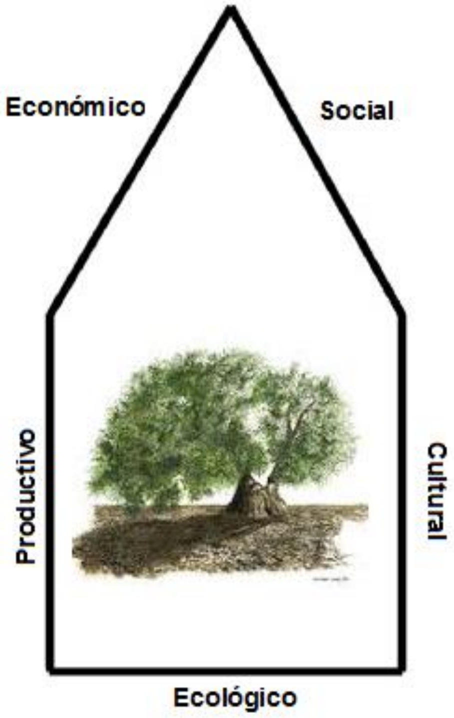


Figura 3. La "casa de las funciones" y sus cinco dimensiones: Fuente: Fleskens et al. 2009.

Estos olivares tradicionales se han caracterizado por una elevada biodiversidad. Por ejemplo, la flora del olivar presenta un excepcional parecido con la flora de los ecosistemas de tipo mediterráneo (Margaris 1980). En consecuencia, estos sistemas, aunque artificiales, a diferencia de lo que existe en otros agro-ecosistemas, son muy similares a los ecosistemas mediterráneos naturales, incluso en su condición funcional (Loumou y Giourga 2003). La existencia de esta rica comunidad herbácea, junto con el refugio que aportan los troncos de los olivos maduros, aseguran las condiciones para la creación de una multitud de hábitats para la fauna (Beaufoy 2001). Esto permite la existencia de una diversa comunidad de artrópodos; por ejemplo, Potts et al. (2006) describió que los olivares gestionados activamente tenían la mayor cantidad de especies de abejas. Santos et al. (2007) determinó que la fauna edáfica estaba dominada por Formicidae, los cuales son importantes agentes en el control de plagas e indicadores biológicos de la condición del suelo en agro-ecosistemas. El gran número de insectos y la generosa flora aseguran la alimentación a un número importante de aves y murciélagos (Davy et al. 2007), lo cual hace al olivar un importante refugio de invierno para las aves del Norte y Centro de Europa (Rey 2011; Castro-Caro et al. 2014a).

3. Problemas derivados de la intensificación del olivar

La continua y creciente intensificación del olivar ha generado una serie de problemas que amenazan su sostenibilidad (Gómez-Calero 2009). Esto ha provocado un desequilibrio entre el valor económico de la producción y el valor ambiental de este agro-ecosistema (Gómez-Limón et al. 2012). Estos problemas básicamente están ocasionados por la intensificación del manejo (riego, laboreo y el uso de agroquímicos), lo cual provoca problemas de erosión, contaminación difusa del agua, sobreexplotación de los recursos hídricos y pérdida de biodiversidad (Fig. 4).

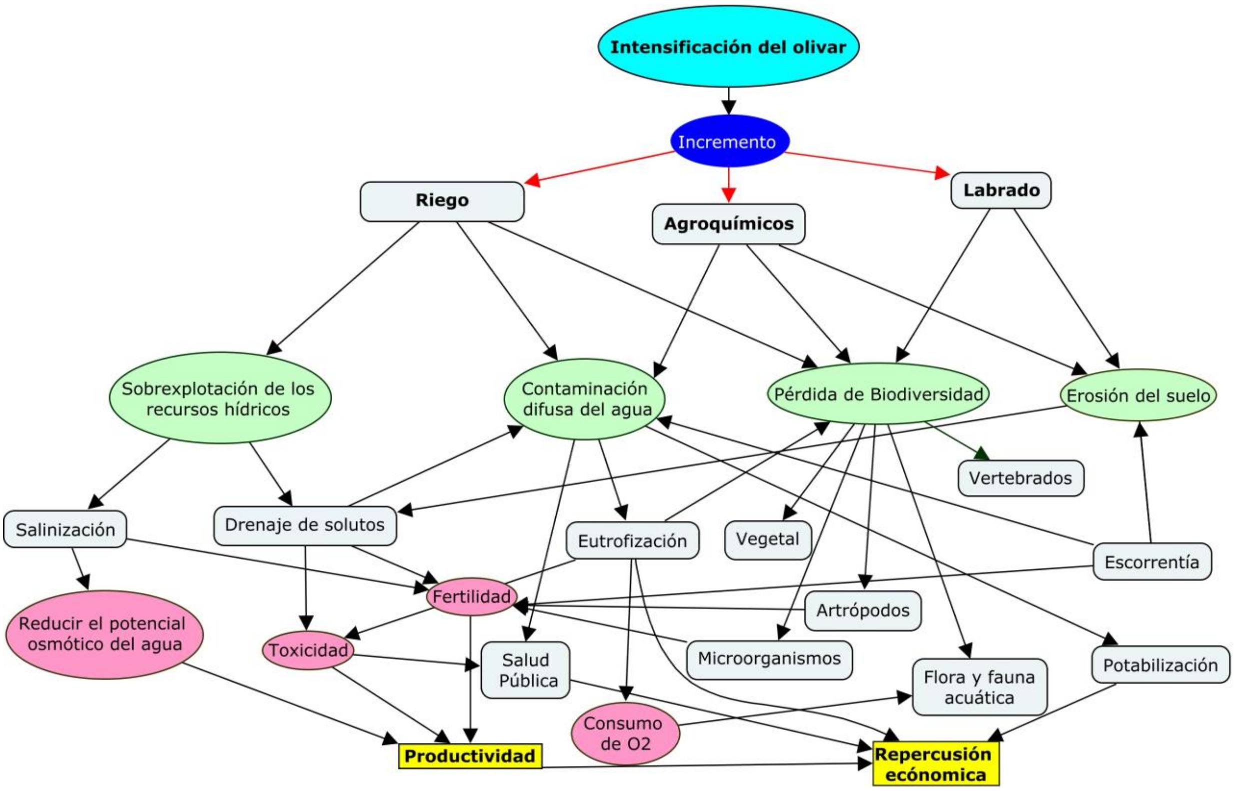


Figura 4. Mapa conceptual de los problemas derivados de la intensificación del olivar. Elaboración propia.

3.1. Erosión del suelo

La erosión es actualmente uno de los principales problemas ambientales en la agricultura mediterránea (Amate et al. 2013). Este problema se ha acentuado con la expansión del olivar en suelos con condiciones desfavorables para la producción agrícola, agravado por una gestión inadecuada en lo que se referido a la eliminación sistemática de la cobertura vegetal (Gómez-Limón et al. 2012). Esto explica por qué, a pesar de la tendencia reciente hacia nuevas plantaciones más intensivas en zonas de valle, la mayoría de los olivares de Andalucía son de secano y plantados en zonas inclinadas (Gómez et al. 2009a). El 31% de la superficie de olivar de Andalucía se encuentra en pendientes superiores al 15%; el 38% de la superficie se encuentra en pendientes moderadas, en un rango de 7-15%; el resto en pendientes inferiores al 7%. Sólo el 16% de la superficie de olivar de Andalucía se encuentra en pendientes inferiores al 5% (CAP 2003). Datos de la CAP (2008) muestran que el 52,7% de la superficie andaluza tiene una tasa de erosión de más de 12 tn/ha/año.

Esta tasa de erosión está influenciada por el tipo de manejo al que se ve sometido el cultivo. Por ejemplo, Gómez et al. (2009a) compararon las tasas de pérdida de suelo bajo tres diferentes sistemas de manejo (labranza convencional, no-labranza con uso de herbicida y cubiertas vegetales). Estos autores encontraron mayores tasas de pérdida de suelo en olivares no labrados, donde la eliminación de la cubierta se realizaba mediante la aplicación de herbicidas (7tn/ha/año); seguido por la labranza convencional (3tn/ha/año) y, finalmente, por los que mantenían una cubierta vegetal (0,8 tn/ha/año). Aunque otros autores (e.g. Kairis et al. 2013) han encontrado tasas aún mayores en los olivares labrados (13,6 a 39,2 tn/ha/año).

3.2. Pérdida de biodiversidad

Como se ha mencionado en el punto 2.3, el olivar tradicional se caracteriza por albergar una rica y diversa flora y fauna. Sin embargo, la reciente intensificación del olivar ha llevado asociada un drástico declive de esta biodiversidad. Allen et al. (2006) muestra como esta intensificación ha conducido a una degradación de las comunidades vegetales, produciendo una homogeneización de la cubierta herbácea, debido principalmente, a las labores de labranza (Cohen et al. 2015). Simões et al. (2014) muestra como los olivares, donde la eliminación de la cubierta vegetal se realiza mediante siega mecánica, albergan un promedio de 28 especies vegetales más que aquellos con labranza. Esta labor de labranza combinada con la aplicación de pesticidas y fertilizantes, también reducen significativamente la abundancia artrópodos en los olivares (Sánchez-Moreno et al. 2015; Özden y Hodgson 2016). Además, afecta de forma directa (a través de los agroquímicos) o indirecta (ausencia de refugio o alimento) a otros grupos taxonómicos de vertebrados como aves, anfibios o reptiles (García-Munoz et al. 2011; Solomou y Sfougaris 2015; Carpio et al. 2016a).

3.3. Otros problemas derivados:

La intensificación de los olivares tradicionales tiene consecuencias ambientales negativas más allá de una disminución de la biodiversidad y un aumento del riesgo de erosión, ya que da lugar a otros como: la sobreexplotación de los recursos hídricos, la contaminación de las aguas e importantes cambios en el paisaje mediterráneo tradicional (Duarte et al. 2008; Gómez-Limón et al. 2012).

- **Sobreexplotación de los recursos hídricos**: Actualmente hay más de 500.000 ha de olivares de regadío, que representan el 35,3% de la superficie andaluza del olivar. Aunque los olivos tienen bajas necesidades de agua y los sistemas de riego por goteo son altamente eficientes, la presión total ejercida sobre los recursos hídricos ha sido significativa, ya que este cultivo consume actualmente cerca del 22% del consumo total de agua en la Cuenca del Guadalquivir. Como resultado, la satisfacción de la demanda de agua en Andalucía ha sido puesta en riesgo y una amplia gama de acuíferos y masas de agua superficiales están ahora sobreexplotados.
- **Contaminación difusa del agua:** La calidad del agua que fluye a través de los olivares se ha visto mermada como consecuencia del uso de productos químicos, incluyendo herbicidas y fertilizantes.
- **Cambios en el paisaje mediterráneo tradicional:** El abandono o la intensificación del olivar ha supuesto un detrimento del paisaje tradicional mediterráneo, caracterizado por un mosaico de olivos, vides y cereales, en beneficio de un monocultivo de olivar intensivo (Duarte et al. 2008).

4. Alternativas de manejo para frenar estos problemas

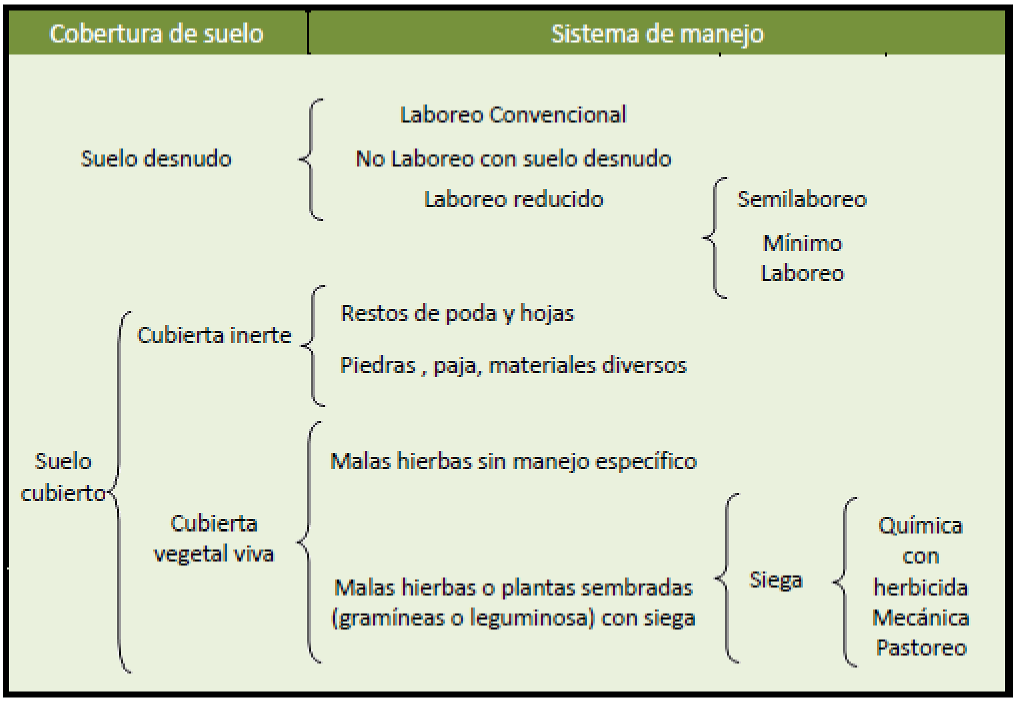
Tradicionalmente el manejo del suelo ha consistido en la eliminación de la cubierta vegetal para evitar la competencia hídrica con el olivo. Esto permite controlar la competencia e incrementar la producción, a la vez que produce una reducción de la materia orgánica de los suelos, y una degradación y erosión acelerada de los mismos (suelos desnudos, Tabla 1). Sin embargo, en 2013, la Unión Europea promulgó en la nueva (PAC) destinar para 2014-2020 casi el 40% del presupuesto en influir hacia una gestión más ``verde´´ en la mitad de su superficie de cultivo (Pe'er et al. 2014).

Esta gestión incluye tres "medidas de ecologización": a) la diversificación de los cultivos, exigiendo que las explotaciones de más de 20 ó 30 hectáreas cultiven al menos dos o tres cultivos, respectivamente; b) mantenimiento de pastos permanentes existentes; y la promoción de las «áreas de interés ecológico», requiriendo que las fincas con áreas cultivables de más de 15 hectáreas destinen el 5% de esas áreas a elementos ecológicamente beneficiosos definidos por la Comisión Europea. Tales elementos incluyen características del paisaje tales como terrazas, setos o estanques, pero también tierras en barbecho, cultivos que fijan nitrógeno, y "cultivos de captura y cubierta verde" (Pe’er et al. 2016).

4.1. Medidas de conservación del suelo

Estos elementos definidos en la nueva PAC, incluyen medidas de conservación del suelo, como las cubiertas inertes y/o las cubiertas vegetales vivas (Tabla 1):

Tabla 1. Principales sistemas de manejo del suelo en el olivar (Gómez-Calero 2009).



Cobertura de suelo		Sistema de manejo		
Suelo desnudo		Laboreo Convencional		
		No Laboreo con suelo desnudo		
		Laboreo reducido	Semilaboreo Mínimo Laboreo	
Suelo cubierto	Cubierta inerte	Restos de poda y hojas		
		Piedras , paja, materiales diversos		
	Cubierta vegetal viva	Malas hierbas sin manejo específico		
		Malas hierbas o plantas sembradas (gramíneas o leguminosa) con siega	Siega	Química con herbicida Mecánica Pastoreo

- **Cubiertas inertes:** En aquellas zonas donde se han propuesto técnicas de no laboreo, eliminando la vegetación, pero proporcionado un acolchado que protege el suelo y aporta materia orgánica mediante los restos de poda antes mencionados o las hojas (Tabla 1). Éstas también pueden incluir otros materiales como paja, piedras, etc.
- **Cubiertas vegetales vivas:** Este sistema mantiene cubiertas las calles de la plantación, aunque sólo desde otoño hasta principios de primavera (durante el período de máxima lluvia y erosión). Esta cobertura vegetal,

constituida por flora espontáneo o por algún cultivo sembrado expresamente para cubrir el suelo y aportar materia orgánica, debe ser controlada en verano para evitar la competencia hídrica (Gómez et al. 2009a; Simões et al. 2014). Los métodos de control incluyen las siegas, desbrozados, pastoreo o tratamientos con herbicidas. La normativa de condicionalidad derivada de la PAC, establece estas y otras medidas con el fin de: evitar la erosión, conservar la materia orgánica y evitar la compactación de los suelos.

Estas cubiertas vegetales también benefician a la biodiversidad a diferentes niveles, ya que proporcionan alimento, refugio, complejidad estructural, lo que finalmente se traduce en un aumento de nichos. Estudios previos han mostrado cómo estas cubiertas albergan comunidades de aves, microbios, polinizadores y artrópodos con una mayor riqueza de especies que cultivos con labranza tradicional (Saunders et al. 2013; Castro-Caro et al. 2014a, b; McDaniel et al. 2014).

Además, como consecuencia de la falta de alimento natural en los cultivos por la aplicación de los herbicidas, varias especies de mamíferos (como el conejo, jabalí y el corzo), se han visto forzadas a alimentarse de los cultivos para cubrir sus necesidades (Herrero et al. 2006; Guerrero-Casado et al. 2015). Esta situación ha provocado importantes daños en cultivos en diversas zonas, generando importantes pérdidas económicas. Dos trabajos previos (Barrio et al. 2010a; Guerrero-Casado et al. 2015) demostraron como los daños a los cultivos por conejo estaban condicionados por la cantidad de alimento disponible, siendo mucho mayor el daño causado en zonas con escasa disponibilidad de alimento.

4.2. Heterogeneidad paisajística y elementos estructurales

Las medidas mencionadas en la PAC, también incluyen todos aquellos elementos o características del paisaje que incrementen la complejidad estructural, tales como terrazas, bosques islas, setos, lindes, arroyos o estanques (Pe’er et al. 2016).

Sin embargo, la intensificación agrícola ha eliminado la mayoría de los setos entre los campos (Figura 5), y los presentes son pequeños, a menudo indetectables en el paisaje (Rey 2011). Estos elementos son componentes importantes de los paisajes agrícolas (Manning et al. 2006), aumentando la heterogeneidad del hábitat y los recursos dentro de estos sistemas (Fischer et al. 2005). Los efectos secundarios de los setos o pequeños remanentes de vegetación natural sobre la biodiversidad han sido reportados en algunos estudios (Benton et al. 2003; Feehan et al. 2005; Castro-Caro et al. 2015).

Figura 5. Foto aérea mostrando olivares con (izquierda) y sin (derecha) restos de vegetación natural entre las distintas parcelas de cultivo. Fuente: Google Earth.

Estos elementos lineales (setos, arroyos y lindes) también actúan como corredores, facilitando la dispersión a mayores distancias a través de las diferentes teselas de la matriz (Hinsley y Bellamy 2000; Benton et al. 2003). La importancia de estos pequeños hábitats residuales (por ejemplo árboles dispersos) tienen una influencia enorme en el mantenimiento de la biodiversidad (Berg 2002, Fischer et al. 2005).

5. Problemas para el establecimiento de las cubiertas vegetales

Tanto en el caso de las cubiertas vegetales de los agro-ecosistemas como en el caso de los pastizales naturales de los sistemas agroforestales, su implementación, desarrollo o conservación pueden tener una serie de problemas (Carpio et al. 2015a; Guerrero-Casado et al. 2015). En este apartado, nos centraremos en el problema del exceso de herbivoría, lo que es particularmente grave en el Mediterráneo (Zalidis et al. 2002; Kairis et al. 2015; Sales-Baptista et al. 2016).

5.1. Consumo de las cubiertas por parte de los herbívoros

En esta tesis pretendemos evaluar también el efecto de los herbívoros sobre la comunidad herbácea en una serie de gradientes de hábitats que van desde sistemas agrícolas intensivos hasta zonas forestales naturales. En este sentido los efectos que la herbivoría y sus problemas asociados pueden tener en cada uno de estos hábitats cambian en función del uso y manejo al que están sometidos (Reidsma et al. 2006).

- **Sistemas agrícolas**: En los sistemas agrícolas los problemas derivados de la herbivoría excesiva están vinculados principalmente con daños al cultivo o a la propia cubierta vegetal (ya sean naturales o sembradas), asociados con un empobrecimiento de las comunidades de plantas (Barrio et al. 2013; Guerrero et al. 2015). En este contexto, Barrio et al. (2011) evaluó si la provisión de cubiertas sembradas podrían ser un medio para reducir el daño causado sobre los viñedos, concluyendo que la cubierta herbácea sólo limitó parcialmente los daños causado por conejos. Sin embargo, estos mismo autores (Barrio et al. 2010a), demostraron que el aporte extra de alimento a los conejos redujo significativamente el daño causado, lo que sugiere que la falta de alimento por el deterioro de las cubiertas provoca, al menos en parte, los daños a los cultivos.

- **Sistemas forestales:** En este tipo de hábitats encontramos otra serie de problemas asociados a los pastos naturales, causada principalmente por la sobreabundancia de ungulados. El pastoreo ha sido una de las causas más antiguas e importantes de la heterogeneidad en los paisajes mediterráneos (San Miguel-Ayanz et al. 2010). Su papel ecológico ha sido tan extenso, diversificado y profundo, que gran parte de su patrimonio biológico y cultural actual (incluyendo muchos tipos de hábitat de pastizales de la Red Natura 2000) depende de la extensa gestión de los herbívoros. Sin embargo, las densidades actuales están alterando la biodiversidad y composición de las comunidades de plantas, ya sea por incremento en los niveles de nitrógeno (Carpio et al. 2015a), o por el sobrepastoreo (Fernández-Olalla et al. 2015) (Figura 6). Esto ha originado que las tierras dedicadas al pastoreo sean el tipo de uso de tierra más degradado en el mundo, particularmente en las zonas áridas y semiáridas, como resultado de actividades humanas impropias como el sobrepastoreo junto con la sequía (Papanastasis 2009).

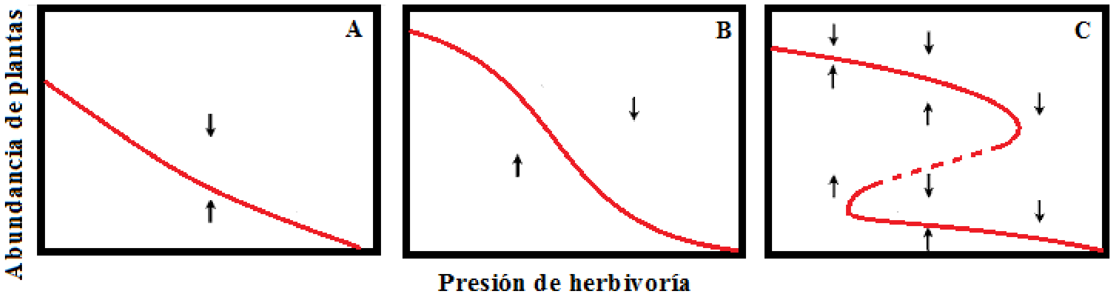


Figura 6. Tres relaciones hipotéticas entre la abundancia de una planta forrajera y la presión de

herbivoría de ungulados. (A) Los herbívoros tienen efectos sólo modestos y monótonos sobre la población. (B) Existe un umbral reversible más allá del cual, la abundancia de la planta cae precipitadamente. (C) La explotación más allá de un determinado umbral causa una disminución no lineal que no es simplemente reversible. Las flechas indican cambios dinámicos en varios puntos. Modificado de Côté et al. (2004).

5.2. Consecuencias sobre el resto del ecosistema

Según Caughley (1981), la sobreabundancia para una determinada especie se produce cuando (a) este hecho afecta al bienestar humano, (b) al estado corporal de la especie sobreabundante, (c) provoca una reducción en la densidad de una especie con valor económico o estético, o (d) causa disfunciones en el ecosistema. En este punto, los efectos densodependientes de la sobreabundancia afectan a la propia eficacia reproductiva y condición corporal de la especie sobreabundante (Stewart et al. 2005). Otros estudios han remarcado los efectos negativos que el exceso de pastoreo puede tener sobre otros animales silvestres, la vegetación y la dinámica del suelo (Augustine y DeCalesta 2003). Otras muchas consecuencias ecológicas de la sobreabundancia han sido tratadas en una revisión de Côté et al. (2004). En este sentido, el efecto que una especie particular de ungulado tiene en un ecosistema depende de su alimentación y del grado y tipo de alteración física que provoca (Latham 1999). Por ejemplo, el impacto del jabalí provoca severos daños a los cultivos, reduciendo además la abundancia y riqueza de plantas y animales (Massei y Genov 2004; Bueno et al. 2010; Barrios-García y Ballari 2012). Además, provoca importantes daños económicos, no solo por daños a cultivo, sino por la propagación de enfermedades al ganado y las personas y las colisiones con vehículos (Gortázar et al. 2006; Lagos et al. 2012). Además, el número de jabalís parece aumentar en muchos países europeos y su impacto también está aumentando (Massei et al. 2015), lo que hace previsible un incremento de los conflictos entre jabalíes y humanos (Delibes-Mateos 2015).

Una parte importante de esta tesis trata de abarcar esta cascada de efectos que la sobreabundancia de ungulados puede generar sobre los ecosistemas (Côté et al. 2004). Estos efectos van desde los niveles más básicos, como son la alteración de los ciclos de nutrientes (Gass y Binkley 2011), cambios en la comunidad de microorganismos y artrópodos del suelo (Carpio et al. 2014a; Peschel 2014); hasta los niveles superiores del ecosistema, como cambios en la composición de especies de flora y fauna (Côté et al. 2004; Carpio et al. 2014b, 2015a).

5.3. El problema añadido de los herbívoros y otras especies exóticas.

Las invasiones biológicas están consideradas como una de las cinco principales presiones que impulsan la pérdida y, en última instancia, la extinción de especies nativas (Roy et al. 2012). Las especies exóticas pueden afectar a los ecosistemas que invaden en diversos grados (Hobbs et al. 2006), causando sustanciales costos económicos y de salud para las sociedades humanas (Pejchar y Mooney 2009). Pero también, causando problemas ambientales como la sustitución progresiva y la eliminación de especies nativas a través de la depredación, la hibridación, la introducción de enfermedades, la alteración del hábitat y la competencia por los recursos o el espacio (Gurevitch y Padilla 2004).

En este sentido, los herbívoros y, más concretamente, los ungulados no son una excepción (Spear y Chown 2009). De hecho, de las especies de ungulados introducidas en Long (2003), cuyas razones de introducción están bien documentadas, la mayoría se introdujeron para la caza deportiva o para la alimentación (Carpio et al. 2016b). Como en el caso de otras especies no autóctonas, los herbívoros alteran el hábitat y el funcionamiento de los ecosistemas, compitiendo con las especies indígenas (Wardle et al. 2001). Sin embargo, las especies cinegéticas no indígenas también constituyen la base de una actividad económica sustancial (Clout y Russell 2007), cuyas introducciones son promovidas por los propietarios de fincas (Castley et al. 2001). Los impactos potencialmente negativos de las especies cinegéticas no indígenas sobre la biodiversidad y su importancia social y económica han llevado a conflictos de intereses en relación con su gestión (Spear y Chown 2009).

OBJETIVOS

El **objetivo principal** de esta Tesis Doctoral es la caracterización y evaluación de los efectos que distintos manejos del hábitat, tanto en ambientes agrícolas como forestales, tienen sobre la biodiversidad, usando las cubiertas vegetales (naturales y cultivadas) como modelo gestión a través de un gradiente de usos y hábitats.

Objetivos específicos:

1. Evaluar de forma teórica a gran escala el impacto de diferentes regímenes de gestión de olivares sobre la biodiversidad de anfibios y reptiles en Andalucía.
2. Establecer el papel que las cubiertas vegetales pueden desempeñar como un medio para mantener la biodiversidad de distintos grupos taxonómicos en los olivares.
3. Caracterizar y evaluar los efectos que la simplificación del paisaje tienen sobre la depredación de nidos a través de un gradiente de usos y hábitats.
4. Identificar el papel que la alta abundancia de herbívoros tiene sobre las cubiertas herbáceas (naturales y cultivadas) en un rango de hábitats (agrícolas y forestales).
5. Evaluar las consecuencias e impactos que genera la sobreabundancia de ungulados sobre los distintos eslabones de la cadena trófica.
6. Revisar las interacciones ecológicas entres especies nativas y exóticas, con especial atención al papel de la caza como fuente de especies exóticas.

ESTRUCTURA DE LA TESIS DOCTORAL

Capítulo 1. Situación actual de la biodiversidad en los distintos tipos de olivares: la herpetofauna como modelo.

Capítulo 1.1. Uso de la tierra y patrones de biodiversidad de la herpetofauna: El papel de los olivares.

Land use and biodiversity patterns of the herpetofauna: The role of olive groves. Acta Oecol 70, 103-111.

Capítulo 1.2. Evaluación de métodos para estimar la riqueza de especies y abundancia de reptiles en los olivares.

Evaluation of methods for estimating species richness and abundance of reptiles in olive groves. Herpetol Conserv and Biol 10(1), 54-63.

Capítulo 1.3. Las cubiertas herbáceas mejoran la comunidad de reptiles en los cultivos leñosos.

Herbaceous cover enhances the squamate reptile community in woody crops. J Nat Conserv. 37, 31-38.

Capítulo 2. Efectos de la simplificación del paisaje sobre la depredación de los nidos.

Capítulo 2.1. La abundancia de conejos influye en la depredación de nidos de aves en olivares Mediterráneos.

Rabbit abundance influences predation on bird nests in Mediterranean olive orchards. Acta Ornithol 50(2), 171-179.

Capítulo 2.2. La influencia de la densidad de nidificación en la depredación en olivares depende de las características del hábitat.

The influence of nest density on nest predation in olive groves depends on habitat features. Ardeola 63(2), 237-250.

Capítulo 2.3. Efecto de la depredación por jabalíes sobre nidos de aves en diferentes hábitats de Suecia.

Effects of wild boar predation on nests of wading birds in various Swedish habitats. Eur J Wildl Res 62(4), 423-430.

Capítulo 3. Efectos de conejos y ungulados sobre las cubiertas herbáceas y sus consecuencias sobre el ecosistema.

Capitulo 3.1. Evaluación de una especie no palatable (*Anthemis arvensis* L.) como cultivo de cobertura alternativo en olivares bajo alta presión de pastoreo por conejos.

Evaluation of an unpalatable species (Anthemis arvensis L.) as an alternative cover crop in olive groves under high grazing pressure by rabbits. Agric. Ecosyst. Environ. In Press.

Capítulo 3.2. Efectos de la sobreabundancia de ungulados silvestres sobre pastizales naturales en el sur de España.

Effects of the overabundance of wild ungulates on natural grassland in Southern Spain. Agroforest Syst 89(4), 637-644.

Capítulo 3.3. Efecto de la densidad de ungulados silvestres sobre los invertebrados en un ecosistema Mediterráneo.

Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem. Anim Biodivers Conserv 37(2), 115-125.

Capítulo 3.4. Depredación de nidos simulados de perdiz roja en fincas de caza mayor del centro-sur de España.

Predation of simulated red-legged partridge nests in big game estates from South Central Spain. Eur J Wildl Res 60(2), 391-394.

Capítulo 3.5. Factores que afectan a la abundancia de la perdiz roja *Alectoris rufa* en cotos de caza mayor*:* implicaciones para la gestión *y* conservación.

Factors affecting red-legged partridge Alectoris rufa abundance on big-game hunting estates: implications for management and conservation. Ardeola 62(2), 283-298.

Capítulo 3.6. La alta abundancia de ungulados silvestres en una región mediterránea: ¿es esto compatible con el conejo europeo?.

The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit?. Wildlife Biol 20(3), 161-166.

Capítulo 3.7. Interpretación del nitrógeno fecal como indicador no invasivo de la calidad de la dieta y la condición corporal en un contexto de alta densidad de ungulados.

Interpreting faecal nitrogen as a non-invasive indicator of diet quality and body condition in contexts of high ungulate density. Eur J Wildl Res 61(4), 557-562.

Capítulo 4. Interacciones ecológicas entres especies nativas y exóticas.

Capítulo 4.1. Papel de la caza en la introducción de especies en Europa.

Hunting as a source of alien species: a European review. Biological Invasions, 1-15.

Capítulo 4.2. Una evaluación de las zonas de conflicto entre la riqueza de especies de vertebrados exóticas y nativas.

An assessment of conflict areas between alien and native species richness of terrestrial vertebrates on a macro-ecological scale in a Mediterranean hotspot. Animal Conservation.

Capítulo 5. Síntesis y conclusiones

CAPÍTULO 1

Situación actual de la biodiversidad en los distintos tipos de olivares: la herpetofauna como modelo

Capítulo 1.1

Uso de la tierra y patrones de biodiversidad de la herpetofauna: El papel de los olivares

Carpio, A. J., Oteros, J., Tortosa, F. S., Guerrero-Casado, J. (2016). **Land use and biodiversity patterns of the herpetofauna: The role of olive groves**. *Acta Oecologica*, *70*, 103-111.

Resumen

La intensificación de la agricultura tiene consecuencias ambientales significativas. Esta intensificación conlleva la simplificación y homogeneización del paisaje, lo que conduce a fuertes impactos negativos a nivel de ecosistemas, incluyendo la disminución de la biodiversidad animal. El propósito de este estudio fue evaluar el efecto de los diferentes usos de la tierra en los patrones de biodiversidad de reptiles y anfibios a escala regional mediante el análisis de una gran base de datos sobre la presencia de anfibios y reptiles en Andalucía (sur de España). Se aplicaron las técnicas de SIG y el Análisis Factorial del Nicho Ecológico (ENFA) para evaluar si el hábitat era adecuado para cada especie de reptil y anfibio, cuando se excluyeron las variables de uso de la tierra. La incongruencia entre la riqueza potencial de especies y la observada se correlacionó con los principales tipos de uso del suelo en Andalucía. Nuestros resultados mostraron que los olivares de regadío y de secano se asociaron con un déficit de biodiversidad de anfibios y reptiles respectivamente, mientras que los bosques y pastizales naturales, junto con las áreas de cultivos más heterogéneos, fueron más adecuados. Un análisis de agrupamiento mostró que las especies generalistas estaban relacionadas con los olivares, mientras que las especies raras y especializadas estaban relacionadas con usos de la tierra relacionados con la vegetación natural. En resumen, nuestros resultados indican que las grandes áreas cubiertas por olivares albergan menos diversidad de anfibios y reptiles, lo que sugiere que se deben llevar a cabo esquemas agroambientales para promover la riqueza de especies en estos cultivos.

Abstract

The intensification of agriculture has significant environmental consequences. This intensification entails the simplification and homogenisation of the landscape, which leads to strong negative impacts at ecosystem level, including declines in animal biodiversity. The purpose of this study was to assess the effect of different land uses on reptilian and amphibian biodiversity patterns at a regional scale by analysing a large database on the presence of amphibians and reptiles in Andalusia (southern Spain). GIS techniques and the Ecological-Niche Factor Analysis (ENFA) were applied in order to assess whether the habitat was suitable for each reptilian and amphibian species, when the land use variables were excluded. The incongruence between the potential and the observed species richness was then correlated with the main types of land use in Andalusia. Our results showed that irrigated and unirrigated olive groves were associated with a biodiversity deficit of amphibians and reptiles respectively, whereas natural forests and pastures, along with more heterogeneous crops areas, were more suitable. A clustering analysis showed that generalist species were related to olive groves whereas rare and specialist species were related to land uses related to natural vegetation. In summary, our results indicate that large areas covered by olives groves harbour less amphibian and reptilian diversity, thus suggesting that agro-environmental schemes should be carried to promote the species richness in these crops.

Introduction

Agriculture intensification is characterised by an increase in management intervention and external inputs with the intention of enhancing agricultural yield, which includes increases in mechanisation, the removal of natural vegetation, fertilisation, and the wide use of pesticides (Kizos and Koulouri 2006; Plieninger et al. 2013). As a general rule, agricultural intensification entails the simplification and homogenisation of landscapes, which lead to an overall decline in farmland biodiversity (e.g. McLaughlin and Mineau 1995; Benton et al. 2003; Medan et al. 2011), thus being considered the factor to have had the largest effect on the loss of biodiversity in agroecosystems (Sala et al. 2000).

In the Mediterranean region, which is considered to be one of the 25 "biodiversity hot spots" in the world (Myers et al. 2000), agricultural intensification has been common since the 1950s (Matson et al. 1997). The olive tree (*Olea europaea* L.) is one of the main crops in this area (Sokos et al. 2013). Half the world's olive production is located in Spain, and the amount of land given over to olive orchards in Spain increased by 300,000 ha between 1996 and 2008 (COI 2013). This intensive olive-producing agriculture threatens traditional agro-ecosystems such as winter cereals, extensively grazed pastures and low-input olive farming, since the traditional mosaic landscape has been replaced with intensive olive monocultures (Beaufoy 2001; Stoate et al. 2001, 2009). This intensive olive system is characterised by the establishment of younger and more productive varieties with a higher tree density and drip irrigation, along with an increased use of agrochemical products (Palomares et al. 2015), which have lead to a reduction in habitat heterogeneity, higher pollution and soil erosion, which have in turn decreased animal and plant diversity (Santos and Cabral 2003; Siebert 2004; Metzidakis et al. 2008).

Solutions to the negative impact of farm intensification are complex. Green *et al*. (2005) proposed two alternatives: wildlife-friendly farming (which boosts densities of wild populations on farmland but may decrease agricultural yields) and land sparing (which minimises the increasing demand for farmland by yield). The authors concluded that high-yield farming may allow more species to persist. However, the conclusions reached by Green *et al.* (2005) were based on birds since no other taxa permit such a detailed and comprehensive analysis. The only taxa to have been reasonably well studied are birds and mammals, and many management decisions are made on the basis of their ecological needs (Stoate et al. 2009; Robledano et al. 2010).

Reptiles and amphibians are recognised as being extremely sensitive to local habitat changes (Anadón et al. 2006; Castellano and Valone 2006) owing to their ecological and physiological constraints (such as temperature or water), low dispersal capacity and small home ranges (Huey 1982), and it is therefore supposed that both groups will be more prone to the risks associated with agricultural intensification than other vertebrate taxa (White et al. 1997). Indeed, Fryday *et al.* (2012) identified 155 papers related to amphibians in agricultural habitats, but none of them were focused on olive groves (but see García Muñoz et al. 2010a, 2013), and the same is true in the case of reptiles (but see Atauri and Lucio 2001). The Iberian Peninsula is one of the Mediterranean areas richest with regards to herpetofauna, and is the home to a considerable number of endemic reptilian and amphibian species (Barbosa et al. 2012; Sillero et al. 2014) that play an important role in the trophic web (Martín and López 2002). The southern areas of the Iberian Peninsula have a higher genetic diversity than those in the north since the area acted as a refuge during last glacial period (Gómez and Lunt 2007). Despite the vast area occupied by olives groves (1.5 million hectares in Andalusia), little is known about the effect of olive groves on the biodiversity pattern of reptiles and amphibians at large scales.

The principal goal of this study was therefore to evaluate the impact of olive groves on amphibian and reptilian biodiversity in Andalusia. We achieved this objective by employing GIS techniques and specific niche requirements to assess whether the habitat was suitable for each reptile and amphibian species in a UTM-grid of 10 x 10 km through the use of Ecological-Niche Factor Analysis (ENFA). Since most new olive orchards are farmed using an intensive irrigated system, the second objective was to identify the impacts of different olive grove management regimes on amphibian and reptilian communities. We expected that reptile and amphibians biodiversity patterns would be modulated by both climatic and land-use variables, and we hypothesized a herpetological biodiversity deficit in those areas with larger surface covered by olive groves.

Materials and Methods

Study area

Andalusia is a large territory in the south of Spain covering 87,268 km^2. It is characterised by a Mediterranean climate, with oceanic features in the western area and arid features in the eastern area. The Andalusia relief is generally orientated in a SW-NE direction, and exceeds 3,000 meters above sea level in Sierra Nevada. Average annual temperature varies over a wide range, due mainly to altitude, from 9-10 °C in mountain enclaves to 18-20 °C in some areas along the Mediterranean coast, while precipitation ranges from a low of 250 mm on the eastern coast of Almeria to 2000 mm in Grazalema (Pita 2003). Andalusia is the largest olive (*Olea europaea* L.) oil producing region in the world, and this production is concentrated in the central-eastern area of Andalusia (Figure 1). In Spain, olive trees have traditionally been cultivated in non-intensive or low tree-density orchards (around 100 trees/ha^{-1}) with no irrigation and with a ground cover (herbaceous vegetation) that rarely exceeds 25% (Villalobos et al. 2000). Drip irrigation has recently (in the last 30 years) been established in intensive orchards characterised by a high tree-density (300–400 trees ha^{-1}) and in super-intensive orchards characterised by a very high tree-density (400–1700 trees ha^{-1}) (Cameira et al. 2014), in which reduced tillage, high inputs of pesticides and fertilisers and mechanical harvesting are used in order to push up olive yields (Palomares et al. 2015).

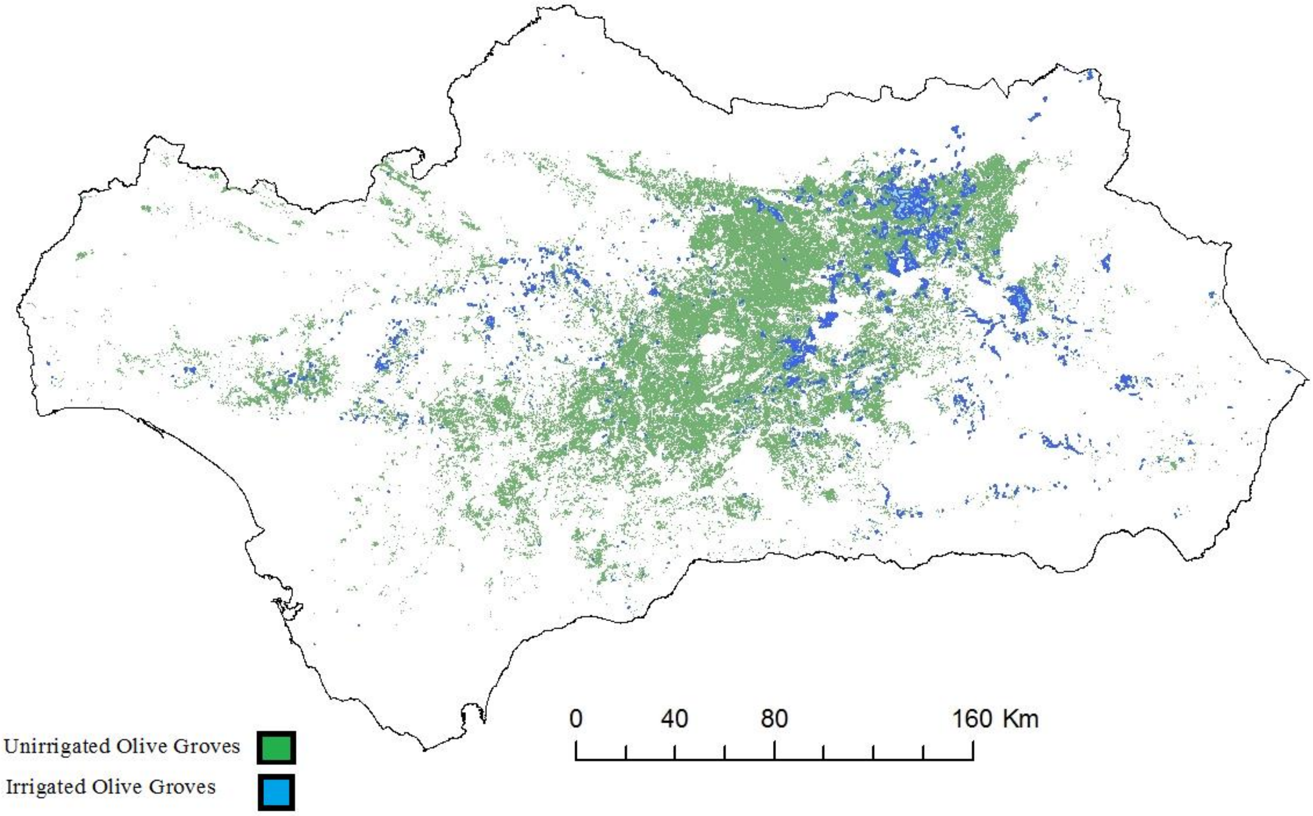


Figure 1. Map of olive crop distribution in Andalusia.

Environmental data

The land use data were compiled using the ``Map of land uses and vegetation cover of Andalusia 2007, scale 1: 25.000´´ (MUCVA, 2007), and were clustered according to study aim (olive groves) and study groups (Appendix 1). The eco-geographical variables (EGVs), which included climatic, geological and topographic variables, were obtained from different sources. The climate data were compiled from a number of databases and are available at the WorldClim website (http://www.worldclim.org/bioclim); altitude data were acquired from the Digital Elevation Model of Andalusia; while geological data were provided by the Spanish Geological and Mining Institute (http://www.igme.es/) (Appendix 2). All these variables were standardised by using ArcMap 9.3 to apply two procedures using: 1) the medium value of each climatic and topographic variable was calculated for each territorial unit; and 2) the percentage of the total area occupied by each type of geological and land use variable within each 10 km square in relation to the total area of the square, thus allowing us to derive an independent variable for each type of EGV. Multicollinearity among these environmental predictors may result in adverse effects in the modelling process, and collinear variables were therefore excluded using the variance inflation factor (VIF), in which 3 was considered to be the threshold cut-off value (Zuur et al. 2010).

The aforementioned objectives were achieved by following five steps: 1) The calculation of Observed Species Richness (OSR), which was carried out separately for amphibians and reptiles in the study area, and 2) GIS techniques and environmental niche modelling to evaluate the suitability of the habitat for each reptilian and amphibian species (excluding the land use variables), which were followed by an estimation of Potential Species Richness (PSR); 3) The calculation of the Subtracted Species Richness (SSR), defined as the difference between OSR and PSR; 4) The influence of land use on the SSR was evaluated using multiple regression; 5) Finally, we assessed how the species are associated to the different land uses by using a cluster analysis.

The data regarding reptilian and amphibian distribution were acquired from the Spanish Vertebrate Atlas (Ministerio de Medio Ambiente 2014), which contains comprehensive information on the distribution of non-domesticated vertebrate (which includes data from 2009-2013). These databases yielded 9668 and 4498 records for reptiles and amphibians, respectively, whose data can be considered as high quality (Martins et al. 2014). With regard to herpetofauna, Andalusia can be considered to have been exhaustively sampled and the associated distribution databases are of a high quality (Martín and Avia 2011).

The spatial resolution of the study was constrained by the data with the coarsest scale (10 x 10 km squares) – the distributional species data (see Moreno-Rueda and Pizarro 2007). This resolution is enough to detect change in biodiversity patterns of amphibians and reptiles (Martins et al. 2014). We analysed 24 of 27 autochthonous reptile species and 15 of 16 autochthonous amphibians which appeared in more than 2% of the UTM grid squares (Appendix 3). We inserted the records concerning reptile and amphibian distribution, represented on the 10 x 10 km UTM grid (990 squares in Andalusia), into a georeferenced database and displayed it using ArcMap 9.3 GIS (ESRI, Redlands, California, USA). The OSR was calculated by means of the addition of all the species present in each 10 x 10 km UTM quadrate (Ribeiro et al. 2009). Taxonomy and nomenclature were checked by using the "Lista Patrón de los anfibios y reptiles de España" (Carretero et al. 2014).

Data analysis

Potential Species Richness (PSR)

As in the work of Ribeiro *et al.* (2009), niche-based models were used to predict the potential geographic distributions of the species based on climatic and geological variables. The EGVs used for the purpose of model distribution (20 climatic, 5 geological and 3 topographic, see Appendix 2) were selected on the basis of their potential significance for the distribution of reptilian and amphibian fauna (Guisan and Hofer 2003; Rodríguez et al. 2005; Moreno-Rueda and Pizarro 2007; Ribeiro et al. 2009; Sillero et al. 2009). The niche-based models were created by selecting a modelling technique that uses presence and background data: the Ecological-Niche Factor Analysis or ENFA (Hirzel et al. 2002). The ENFA was implemented in Biomapper 3.1 software (Hirzel et al. 2004) following the procedures outlined by Hirzel *et al.* (2002).

The resulting habitat suitability grid maps were converted into presence/absence maps using the Receiver Operating Characteristic technique (ROC), as suggested by Hirzel *et al*. (2002). A potential species richness (hereafter PSR) was then calculated by adding up all of the presence/absence maps (Ribeiro et al. 2009).

Subtracted Species Richness (SSR)

The subtracted species richness (SSR) was calculated by applying the formula: SSR = OSR – PSR, which is the keystone variable of this study. Negative values of SSR provides information about the areas in which there are fewer species than expected (deficit of biodiversity), and therefore, species richness is being limited by other factors rather than EGVs, while positive values of SSR (number of observed species superior to the value of potential ones) indicating a possible surplus of biodiversity, suggesting that others factors (such as land use) rather than EGVs are stimulating species richness (for more details, see Ribeiro et al. 2009)

Land use effects on Subtracted Species Richness

The SSR was related to land use variables through the use of a stepwise multiple linear regression. Initial models included all clustered Andalusia land use types, including the four types of olives groves (Appendix 1). Two models were developed, one for each taxonomic group.

Cluster analysis of species according to land uses

In order to observe how the species occurrence was related to different land uses, separate cluster analyses were performed for reptiles and amphibians. This technique allowed the different species to be grouped on the basis of the averaged percentage of each type of land use in each 10km square in which the species was observed.

First, the optimum number of natural groups of species (K) was determined by using a hierarchical clustering analysis; clusters were then generated with a "K-means" conglomerate analysis. Both methods were developed using SPSS version 20 for Windows (SPSS Inc, Chicago IL). A hierarchical clustering analysis was performed using Ward's method, in which information is quantified as the sum of squared distances of each element with regard to the centroid of the cluster to which it belongs. This was done by first calculating the mean vector for all variables and the multivariate centroid for each cluster and then calculating the squared Euclidean distances between each element and the centroid (mean vector) of all the clusters. Finally, the distances for all elements were combined. The "K-means" conglomerate method was used for cluster generation: "k" groups of species were generated on the basis of the affinity to each land use. This clustering method was deemed to be the most appropriate, since it provides a more flexible approach and does not assume any specific distributions of variables (Oteros et al. 2013).

Results

The OSR and PSR species richness values are presented graphically in Fig. 2. A west–east decreasing pattern in the species richness can be observed on the amphibian maps, with maximum species richness in the west of Andalusia and in mountainous areas (which are those areas by the Atlantic and wet areas, respectively), while the reptile maps show that there is lower species richness in the Guadalquivir Valley (an intensively agricultural area), with the highest values being in the extreme west, south and east of Andalucía (located in Doñana National Park, Alcornocales Natural Park and semiarid areas of Almeria).

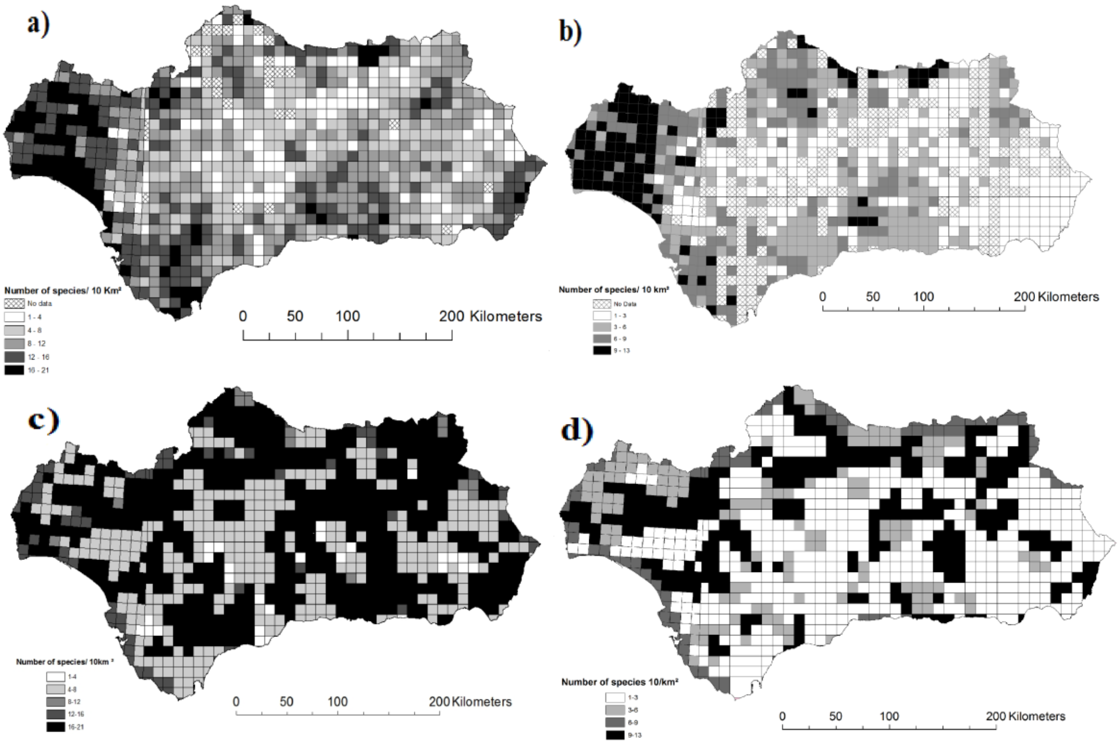


Figure 2. Species Richness maps: a) and b) Observed Species Richness, c) and d) Potential Species Richness for reptiles and amphibians, respectively, derived from the Ecological Niche Factor Analysis (ENFA) models.

Subtracted Species Richness (SSR) ranged from -17 to 14 species for reptiles and -10 to 10 species for amphibians (Fig. 3a and 3b, respectively). Positive values indicate those 10 km squares in which OSR is greater than PSR, thus signifying a surplus of biodiversity. However, negative values appeared in those squares in which the potential distribution models estimated more species than those observed, thus signifying a deficit of biodiversity.

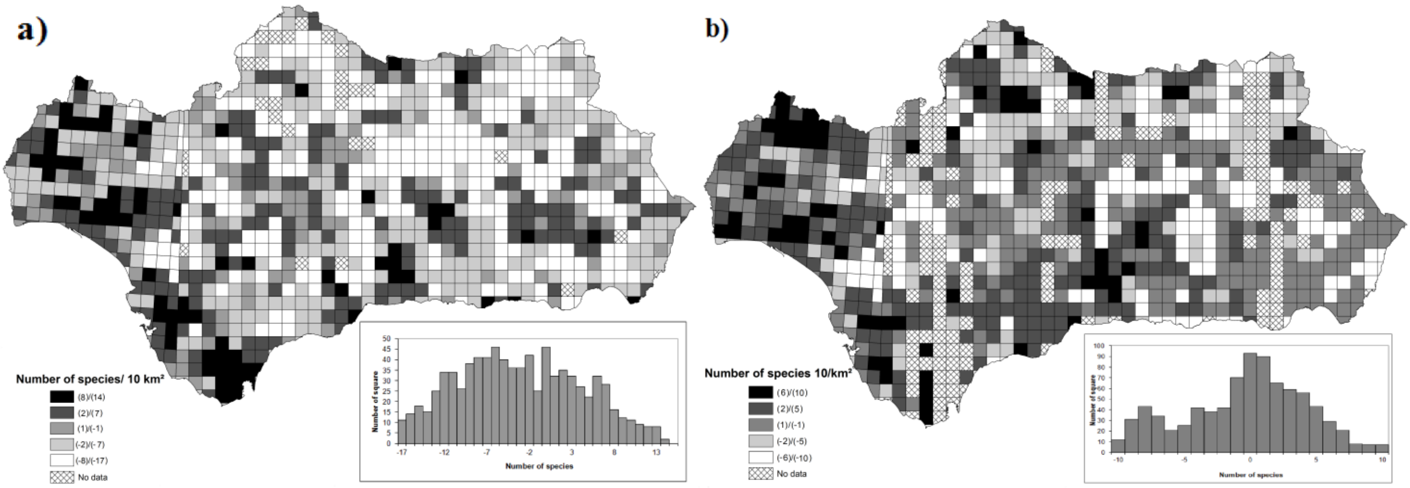


Figure 3. Geographical representation and frequency histogram of the subtraction of Observed Species Richness (Fig. 2a) from Potential Species Richness (Fig. 2c) – Subtracted Species Richness for reptiles (3a) and Observed (Fig 2b) and Potential Species Richness (Fig. 2d) – Subtracted Species Richness for Amphibian (3b). The classification of the grey categories represented on the map was carried out manually according to the distribution of the histograms.

Stepwise multiple linear regression for reptiles species richness revealed a negative relationship between SSR and unirrigated olive groves, while natural pasture and vineyard-olive groves had a positive effect (Table 1). Amphibian species richness had a negative relationship with irrigated olive groves, while natural pasture, forest, heterogeneous agricultural areas and wetlands had a positive effect (Table 1).

A positive relationship of the SSR with one land use variable indicates that a 10 km square with high values of SSR (i.e. a surplus of biodiversity) has high percentages of that land use, while a negative relationship signifies that the same 10 km square unites low values of SSR (deficit of biodiversity) and high percentages of land use.

Table 1. Final models derived from Multiple Linear Regression analysis using the Subtracted Species Richness as a dependent variable for land used, including different

types of olive crops. Variables are rated in descending order.

Reptiles		
Independent variable	Standardised coefficient	*P*
Unirrigated Olive Groves	-0.187	<0.001
Natural Pasture	0.139	<0.001
Vineyard-Olive Groves	0.101	<0.01
Amphibian		
Independent variable	Standardised coefficient	*P*
Natural Pastures	0.128	<0.001
Irrigated Olive Groves	-0.117	<0.001
Forest	0.113	<0.01
Heterogeneous Agricultural Areas	0.080	<0.05
Wetlands	0.077	<0.05

The cluster analyses for the 23 species of reptiles and 15 species of amphibians revealed four major clusters for the former and two main clusters for the latter (Fig. 4). In the case of reptiles, the first cluster included 11 species, which are very common species, such as *Natrix maura, Malpololon mospesulanus, Mauremys leprosa* and *Tarentola mauritanica* (with the exception of *Blanus cinereus*, which is an Iberian endemic, although very common), or very generalist species such as *Psammodromus algirus* and *Podarcis hispanica* complex (Segura et al. 2007; Sillero et al. 2009; Godinho et al. 2011; Geniez et al. 2014). The K-means test revealed that group 1 is the most tolerant to crop agriculture (Olive groves and herbaceous crops); the second group, which includes 9 species that are more restricted species (for example *Chalcides bedriagagi*, which is an Iberian endemic, *Natrix natrix*) or habitat specialists such as *Vipera latastei*, is more closely related to natural pastures and other natural areas. Cluster 3 includes only two species which are very scarce: *Chamaeleo chamaeleon* and *Testudo graeca*, and is associated with heterogeneous agricultural areas and wetland, as they have a coastal distribution, while Cluster 4 includes only one endemic species (*Algyroides marchi*), which is related to forest and shrub areas (Sillero et al. 2009) (Fig. 4).The amphibian group, meanwhile, was divided only into 2 clusters. The first cluster includes very common species such as *Bufo calamita*, *Pleurodeles waltl*, *Bufo spinosus* and *Pelophylax perezi*, but also includes Iberian endemics such as *Triturus pygmaeus*, *Pelodytes ibericus*, *Alytes dickhilleni* and *Discoglossus g. jeanneae*, which were associated with scrubland arable land and olives. The second group includes more specialist species with a higher degree of endemism such as *Alytes cisternasii*, *Lissotriton boscai* and *Discoglossus g. galganoi* (Iberian endemic) and other protected species such as *Salamandra salamandra* and *Pelodytes punctatus* (IUCN, 2012), being these species related to woodland and pastures (Fig. 4).

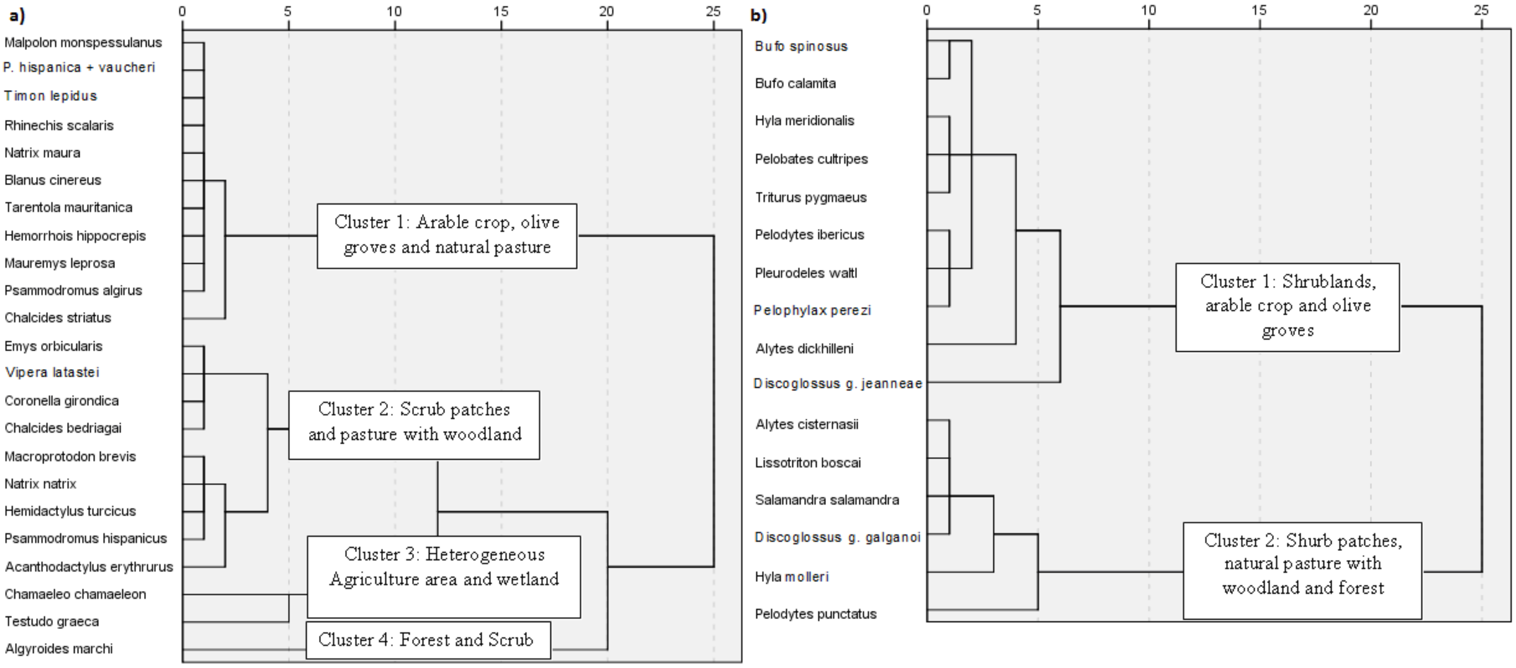


Figure 4. Dendrogram showing four hierarchical clusters of land use types in the case of reptiles (a) and two clusters in the case of amphibians (b). K-means cluster method using ward linkage distance as a measure of similarity.

Discussion

Understanding the ecological determinants of species diversity distribution at large scales and predicting their spread over broad geographical extents are key issues for conservation programmes. However, accurate data related to species distribution covering vast areas is often not available. In this respect, one intrinsic limitation of the methodology employed in this study is the coarse resolution of the distribution data (10x10 km). There is, to date, no alternative source from which to obtain more accurate and balanced data on species distribution in Spain. We deem that 10x10 could be an appropriate resolution with which to test the effect of land use variables on reptile and amphibian biodiversity distribution patterns, since this grain could be enough to sustain viable population of both groups (Martins et al. 2014). Another limitation is the sampling effort throughout the study area (i.e. more effort in protected areas), which could affect the quality of the data regarding presence. However, the sampling effort could be considered as suitable to record presence or absence, being this methodology much more questionable as regards attaining reliable data on species abundance. Despite this, our results still provide a realistic assessment of the effect of land use on regional-scale patterns of reptiles and amphibian species richness.

Previous works have suggested that current agricultural areas are often not optimal habitats for amphibians and reptiles (e.g. Loman and Lardner 2006, 2009; Ribeiro et al. 2009), since both groups are particularly prone to being harmed by agricultural activities (Dürr et al. 1999), such as the use of pesticides (Brühl et al. 2013), and that these habitats may even act as ecological traps (Rotem et al. 2013). Our results have shown that the intensive olive tree monoculture may be the main threat to the amphibians and reptiles in the study area in terms of habitat requirements on a larger scale. There are various threats to wildlife in areas in which intensive olive cultivation takes place that could explain the low values of amphibian and reptile biodiversity in these crops. The scarcity of natural vegetation cover and refuge, along with constant ploughing that keeps the ground bare throughout the year (Rey et al. 2011), the lack of natural prey, the thermal quality of the habitat, and a higher vulnerability to predators as a result of habitat simplification may, meanwhile, be considered as threats to herpetological fauna. These circumstances reduce the habitat heterogeneity, decrease refuges and the availability of food, and even natural migration corridors, which negatively affect both reptiles and amphibians (Atauri and Lucio 2001).

Amphibians were more negatively affected by irrigated olive groves, probably as a consequence of a higher use of pesticides (e.g. copper sulphate or ammonium nitrate) in this kind of crop (Brühl et al. 2013), which may affect their development (see García-Muñoz et al. 2009, 2010b), as might the alteration of wetlands in intensive olive tree monocultures (García-Muñoz et al. 2010a, 2010b, 2011a, 2011b; Ferreira and Beja 2013). On these intensive farms, irrigation is commonly carried out by means of local drip irrigation networks, through which agrochemicals tend to be applied (Metzidakis et al. 2008). It is known that amphibians absorb many toxic substances through the epithelium (García-Muñoz et al. 2009), and it is therefore expected that they will be more sensitive to higher agrochemical inputs in the aquatic network. Therefore, the current trend of replacing traditional olive groves by intensive irrigated system clearly appears to be one of the factors responsible for a biodiversity deficit of amphibians at larger scales.

In contrast, reptiles were more negatively affected by unirrigated olive groves, which is consistent with previous studies showing that unirrigated olive groves adversely affect reptilian wildlife (Atauri and Lucio 2001) owing to weed control through tillage, either by a rotary tiller or a cultivator, and also as a result of the wide use of herbicides (Glyphosate and Diuron) (Metzidakis et al. 2008). However, it is also noteworthy that mixed plots of vineyards-Olive groves and heterogeneous agricultural areas had a positive effect on reptiles and amphibians, respectively, which may be owing to higher landscape heterogeneity in those areas with mixed crops than in monoculture landscapes (Moreno-Rueda and Pizarro 2007). These heterogeneous and crop mixed areas, which could be associated to less intensive farms, probably contain patches of natural vegetation and a longer length of hedge providing more food and shelter opportunities for wildlife. Benton *et al.* (2003) suggested that the loss of landscape heterogeneity is the major threat to farmland wildlife, and management solutions that recreate this heterogeneity may therefore be the key to restoring and sustaining biodiversity in agricultural systems. In the light of this consideration, recovering habitat heterogeneity in intensively farmed olive orchards could improve reptilian and amphibian biodiversity. However, more accurate research is needed to evaluate the effect of specific environmental measures, such as grass ground cover or hedges, on fauna diversity in olive orchards.

Natural pasture land use has a positive effect on the richness of both taxa, which coincides with previous studies (e.g. Atauri and Lucio 2001; Estrada et al. 2007, 2008; García-Muñoz et al. 2010a; Godinho et al. 2011), whereas, as we expected, wetlands and forests appear to be positive for amphibians biodiversity (García-Muñoz et al. 2010a, 2013).

Interestingly, the cluster analysis for both reptiles and amphibians revealed two main groups in terms of land use: 1) common generalist species which were related to olive groves and other crops (included in Cluster 1 in both taxa), and 2) specialist or rare species were related to non-agricultural areas (Clusters 2 for amphibians, and clusters 2, 3 and 4 for reptiles; Figure 4). All this evidence suggests than olive groves are mainly inhabited by generalist species with a wide distribution range, harbouring less species with conservation concerns (e.g. endemic and/or specialist), which are associated to areas covered by natural vegetation according to our results.

We conclude that ENFA models, combined with clustering analyses and multiple regressions, have proved to be feasible techniques for large-scale habitat modelling, allowing the identification of the external factors (e.g. land use) that constrain species richness and the species associated with areas with a surplus or deficit as regards biodiversity. In the light of our results, we can therefore deem that olive groves may act as a "huge void" for reptilian and amphibian species richness, and particularly for those less abundant and/or endemic species. What is more, and taking into account that the olive farmland covers 2.5 million ha in Andalusia, this signifies that the overall biodiversity lost could be enormous in absolute terms, and hence that the current tendency in olive grove agricultural systems could be considered as the major large-scale threat to amphibians and reptiles in the Mediterranean region.

Acknowledgements

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Appendix 1

Land use variables used as independent variables in the multiple linear regression.

Original Variable MUCVA 1:25.000 (2007)	Clustered Variables
Road Infrastructures Urbanisations Urban Areas Industrial and Commercial Areas	Urbanised Land
Continental wetlands and water surfaces	Wetland
Annual crops associated with permanent crops Complex cultivation patterns Land principally occupied by agriculture, with significant areas of natural vegetation Agro-forestry areas	Heterogeneous agricultural areas
Unirrigated olive groves Irrigated olive groves Olive groves with vineyards Wild olive groves	Olive
Vineyards Fruit trees and berry plantations	Other permanent crops
Broad-leaved forest Coniferous forest Mixed forest	Forest
Moors and heathland Sclerophyllous vegetation Transitional woodland-shrub	Scrub and/or herbaceous vegetation associations
Unirrigated arable crop Irrigated arable crop	Arable crop
Natural pastures Pasture with woodland (Dehesa)	Natural pastures

Appendix 2

Ecogeographical Variables used to build the Habitat Suitability Models with the Ecological Niche Factor Analysis (ENFA).

Type	Variable	Source	Resolution
Climatic	Annual Mean Temperature Mean Diurnal Range Isothermality Temperature Seasonality Max. Temperature during Warmest Month Min. Temperature during Coldest Month Annual Temperature Range Mean Temperature during Wettest Quarter Mean Temperature during Driest Quarter Mean Temperature during Warmest Quarter Mean Temperature during Coldest Quarter Annual Precipitation Precipitation during Wettest Month Precipitation during Driest Month Precipitation Seasonality Precipitation during Wettest Quarter Precipitation during Driest Quarter Precipitation during Warmest Quarter Precipitation during Coldest Quarter Potential Evapotranspiration	Wordclim – Global climate data	1x1 Km (raster)
Geological	Alfisol Aridisol Entisol Inceptisol Vertisol	http://www.igme.es/	1:50.000 (vectorial)
Altitude	Digital Elevation Model Slope	Digital elevation model of Andalusia	20x20 m (raster)

Appendix 3

Autochthonous reptile species in Andalusia (Southern Spain) and percentage of 10x10 km squares with recorded presence. * Species excluded from the analysis, in the case of both the OSR and the PSR, owing to their sparse distribution in Andalusia (>2%).

Reptile’s species name	% Squares	Reptile’s species name	% Squares
Emys orbicularis	14.45	*Psammodromus hispanicus*	36
Mauremys leprosa	56	*Timon lepidus*	75
Testudo graeca	2.3	*Lacerta schreiberi**	0.2
Blanus cinereus	69	*Chamaeleo chamaeleon*	13
Chalcides bedriagai	26	*Coronella austriaca**	0.6
Chalcides striatus	24	*Coronella girondica*	28
Hemidactylus turcicus	36	*Hemorrhois hippocrepis*	60
Tarentola mauritanica	85	*Macroprotodon brevis*	32
Acanthodactylus erythrurus	28	*Malpolon monspessulanus*	68
Algyroides marchi	2	*Natrix maura*	79
*Podarcis carbonelli **	0.3	*Natrix natrix*	20
Podarcis hispanica	71	*Rhinechis scalaris*	59
Podarcis vaucheri	4.14	*Vipera latastei*	18
Psammodromus algirus	76		

Amphibian’s species name	% Squares	Amphibian’s species name	% Squares
Alytes cisternasii	20.9	*Pelobates cultripes*	25.25
Alytes dickhilleni	9.29	*Pelodytes ibericus*	27.77
Bufo calamita	60.2	*Pelodytes punctatus**	1.21
Bufo spinosus	56.16	*Pelophylax perezi*	80.9
Discoglossus g. galganoi	16.66	*Lissotriton boscai*	13.03
Discoglossus g. jeanneae	21.01	*Pleurodeles waltl*	36.06
Hyla molleri	2.82	*Salamandra salamandra*	27.47
Hyla meridionalis	37.07	*Triturus pygmaeus*	18.38

Capítulo 1.2

Evaluación de métodos para estimar la riqueza de especies y abundancia de reptiles en los olivares

Carpio, A.J., Cabrera, M., Tortosa, F.S. (2015). **Evaluation of methods for estimating species richness and abundance of reptiles in olive groves.** *Herpetological Conservation and Biology*, *10(1),* 54-63.

Resumen

El Mediterráneo tiene una gran diversidad de herpetofauna, que sigue siendo poco estudiada. Los olivares son uno de los principales agroecosistemas de la región mediterránea, pero la eficacia de los diferentes métodos de estima aún no ha sido probada. Por lo tanto, se comparó la efectividad de los transectos y vallas de deriva para muestrear reptiles terrestres en olivares viejos y jóvenes. Se observaron 857 individuos, representando 10 especies (entre mayo y julio de 2014). Se detectaron 10 especies (820 individuos) con transectos y cinco especies (37 individuos) utilizando las vallas de deriva. El transecto fue más eficiente para determinar la diversidad de especies y la abundancia de reptiles en olivares jóvenes y viejos, pero los valores registrados fueron mayores en olivares viejos que en los jóvenes para ambas variables de respuesta. Finalmente se registraron características del hábitat (tronco o suelo) donde se observó el animal durante los transectos. Recomendamos el uso de transectos para la evaluación de la biodiversidad en olivares, donde los reptiles pasan la mayor parte del tiempo en los troncos y evitan el suelo.

Abstract

The Mediterranean has a high diversity of herpetofauna, which continues to be understudied. Olive groves are one of the primary agroecosystems in the Mediterranean region but the effectiveness of different survey methods has yet to be tested. Therefore, we compared the effectiveness of transects and drift fences to sample terrestrial reptiles in old vs. young olive groves. We observed 857 individuals, representing 10 species (between May and July 2014). We detected 10 species (820 individuals) with transects and five species (37 individuals) using drift fences. The transect was more efficient for determining species diversity and abundance of reptiles in both young and old olive groves, but the recorded values were higher in old olives than in the young ones for both response variables. Finally we recorded habitat features (trunks or ground) during transects where the animal was observed. We recommend the use of transect for biodiversity assessment in olive groves, where reptiles spend most of their time on trunks and avoid the ground.

Introduction

Many reptile and amphibian populations are declining as a result of climate change, habitat loss, invasive species, disease, or agriculture intensification (Stuart et al. 2004; Foley et al. 2005). These taxa are little studied in the Mediterranean, and the status of many species is unknown (Martín and Lopez 2002; Stoate 2009) including many endemic species in the Iberian Peninsula (Corbett 1989). The Iberian Peninsula has been identified as a biodiversity hotpot (Myers et al. 2000) especially herpetofauna (Loureiro et al. 2008; García-Muñoz et al. 2010a). However, due to the agricultural practices of the region, biodiversity loss is a conservation concern (Reidsma et al. 2006).

Olive (*Olea europaea*) groves are one example of agricultural intensification, and are one of the primary agroecosystems in the Mediterranean (Sokos et al. 2013). These groves are an important economical resource (Oteros et al. 2014). However, very few studies have been conducted to evaluate the impact of olive groves on reptile and amphibian biodiversity. Indeed, Fryday and Thompson (2012) identified 155 published manuscripts that associate herpetofauna from European countries with agricultural habitats, but none focused on olive groves (but see Atauri and Lucio 2001; García Muñoz et al. 2010a, 2013). Although dehesas (i.e., oak woodland pastures) and pasture lands have been extensively sampled (Martín and Lopez 2002; Godinho et al. 2011; Rotem et al. 2013), very little information is available regarding diversity and abundance of reptiles in olive groves or how to sample them.

Ecological studies, including monitoring and biodiversity inventories, need survey methods that permit the most efficient and comprehensive completion of study objectives (Hutchens and DePerno 2009). However, most studies of herpetofaunal species richness use only two or three sampling methodologies, which limit the reliability of estimates (Bailey et al. 2004; Hutchens and DePerno 2009). In the case of reptiles, the most widely employed techniques include drift fence arrays (with pitfall and/or funnel traps), transects, and coverboards (Willson and Gibbons 2009). The effectiveness of these methods for determining abundance and species richness varies among studies (Hutchens and DePerno 2009; Sung et al. 2011). Capture rates in coverboards and drift fences have been demonstrated to be quite high (Ribeiro-Junior et al. 2008), and these methods are common in North American studies (Hampton 2007; Hutchens and DePerno 2009), while transect are commonly used by researchers in other regions (e.g., Africa; Rodel and Ernst 2004).

Studies evaluating herpetofaunal sampling methods are common in North America (Hamptom 2007; Hutchens and DePerno 2009), South America (Ribeiro-Junior et al. 2008), Africa (Rodel and Ernst 2004), Australia (Spence-Bailey et al. 2010), and Southeast Asia (Sung et al. 2011). However, only a few studies compare their effectiveness in Mediterranean regions. Our objectives were to compare the effectiveness of two commonly used reptile survey methods (drift fences and transect) by evaluating capture rates and observed species richness in old and young olives groves to provide managers with guidance when choosing survey methods for future studies in woody crops.

Materials and Methods

Study area

We conducted the study within Andalusia (37º30'–37º58'N, 4º17'–4º56'W; between 159–369 m above mean sea level) located in the South of the Iberian Peninsula (Fig. 1). We selected 14 study sites in a representative range of olive groves (irrigated, unirrigated, with cover vegetation vs. bare ground, old and young olive trees). All sites were 20 km apart to ensure independence of the samples. Each site included a plantation of olive groves, which is the leading commercial tree crop in the Mediterranean area (Oteros 2014). Olive groves were 10–100 y old and we separated into young (10–20 y old) and old (90–100 y old) groves for study.

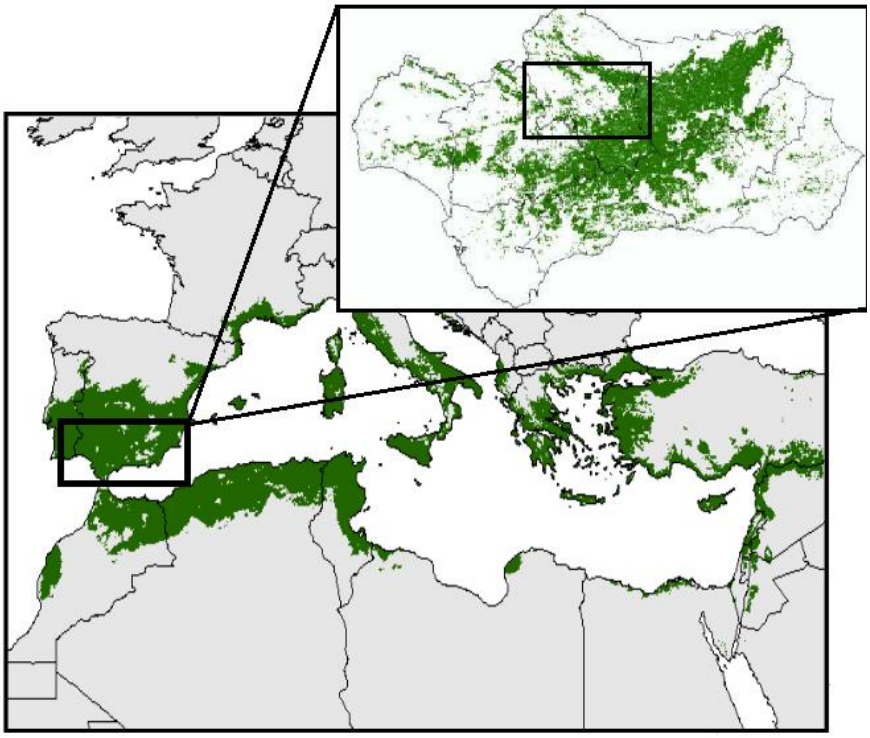

Figure 1. Potential ecological niche of the olive in the Mediterranean basin (Oteros 2014) and the distribution of olive groves in Andalusia showing the study area. (Map taken from Ministry of Agriculture, Fisheries and Rural Development of the Junta de Andalucía 2010).

Reptiles sampling

The Andalusian reptile fauna includes 26 autochthonous species (three chelonians, one amphisbaenian, 13 saurians, and nine ophidians), three of which have an extremely localized distribution with ranges < 2% of total survey area (Ministerio de Medio Ambiente 2014. Spanish Vertebrate Atlas. Ministerio de Media Ambiente). Available from http://www.magrama.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especies-terrestres/inventario-nacional-de-biodiversidad/bdn-ieet-default.aspx. (Accessed 22/05/2014). We conducted all sampling methods from May to July 2014, a period during which reptiles are particularly active because it is their mating season (Martín and Lopez 2002; Godinho et al. 2011). We visited each plot twice (once in May and again in July)

We tested two herpetofaunal survey methods: drift fences and transect. All sampling was > 30 m inside from the edge of the olive grove to avoid edge effect (Sung et al. 2011). We used two transects at each study site for one hour (30 min for each transect) and we spaced these transects ≥ 100 m apart (Hutchens and DePerno 2009). We counted the reptiles observed in each transect in a 10 m-wide belt, 5 m on each side of the survey line. We repeated each line transect census on three days with favorable climate conditions (warm sunny days) between 1100–1300 GMT, when reptiles were most active (Martín and Lopez 2002). We looked for reptiles at potential reptile microhabitats, including under rocks and leaf litter, woody debris, and on tree trunks (Sung et al. 2011). We noted whether the reptile was observed on the ground or on a tree trunk. We completed 168 transect (84 in each census).

Drift fences with pitfall traps and funnel traps of several designs are widely employed in reptile research (Spence-Bailey et al. 2010; Sung et al. 2011; Rotem et al. 2013). We established a drift fence array on each site (n = 14). Each array had seven pitfalls (8 L plastic buckets buried flush with the ground) spaced at 7-m intervals and three double-ended funnel traps, connected by a 50-m drift fence (similar to those of Spence-Bailey et al. 2010). We constructed drift fences by stapling 0.6 m tall transparent plastic sheeting to wooden stakes and burying the bottom (0.1–0.2 m) of the plastic sheeting in the ground to prevent reptiles from crossing underneath (see Sung et al. 2011). To prevent drowning of animals, we drilled 10 mm diameter holes in the bottom of each pitfall bucket for drainage. We constructed funnel traps using 0.3 x 0.4 m aluminium widow screens rolled into cylinders and stapled, and we inserted two wire mesh funnels with 0.04 m diameter openings into both ends of each cylinder. We conducted trapping for four consecutive days in the spring and summer of 2014, resulting in 784 trap-nights. We checked the trap lines once per day and released individuals at the point of capture. We identified all captured animals to species.

Statistical analysis.

We evaluated the capture efficacy among capture techniques by comparing species richness (S) and the number of detections for data collected during May-July 2014. We analyzed the capture rates of both methods measured as captures per trap-hour for drift fences and as capture per hour for transects. We created two Generalized Linear Mixed Models (GzLMM) to compare both methods. The response variables were the number of individuals captured (Model 1) and the number of species (Model 2). We included the method (two levels: drift fences vs. transects), the age of the grove (young vs. old), the date (May and July), and the double interactions between these variables (Date*Method; Date*Olive age; Method*Olive age) and the triple interaction

(Date*Olive age*Method) as explanatory variables in these models. We considered site as a random variable. We used Poisson distribution with a log-link function for both models.

We performed the full arrangement of models (all possible combinations) and model selection by means of a best subset approach using the Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson 2002). We ranked the models generated according to AICc values, in which the model with the lowest AICc is the best. Also, we reported the ΔAICc value to compare the difference between each candidate model and the best model. As a rule, a $\Delta i < 2$ suggests substantial evidence for the model (and thus for the variables included; Burnham and Anderson 2002), signifying that we eventually selected any model with $\Delta i < 2$ with regard to the model with the lowest AICc. We performed all statistical analyses using InfoStat software with $\alpha = 0.05$. Finally, we used a paired Wilcoxon test to assess the differences among the number of reptiles and number of species observed on the ground and on tree trunks (ground vs. tree) in each transect.

Results

We observed 857 individuals (of which 852 were lizards, 4 were snakes and one was worm lizard) representing 10 species. We detected 10 species (820 individuals) with transects and five species (37 individuals) using drift fences for an estimated species richness (S) of 10 (Appendix 1). The most common species detected were *Podarcis hispanica* (50% of records), *Acanthodactylus erythrurus* (28%), *Tarentola mauritanica* (14%), *Psammodromus algirus* (5%) and *Podarcis vaucheri* (1%), while *Lacerta lepida*, *Bladus cinereus*, *Hemorrhois hippocrepis*, *Malpolon monsspesulanus* or *Rhinechis scalaris* represented < 1% of the records.

The final model retained all factors because the triple interaction (Date*Olive age*Method) was significant (Table 1). In both months (May and July) the number of individuals sampled was higher when using transects than when using drift fences (Fig. 2), although with the transects the number of individuals observed was higher in old olive groves (Fig. 2). The best candidate model that explained species richness included method in all models, while only retaining olive age, date, and the interaction between method and date in some of the best candidate models (Table 2). Higher values of species richness were detected using transects compared to the drift fences ($\chi^2 = 67.7$; $P < 0.001$), with a mean (± SE) of 1.8 ± 0.15 species for transect and 0.4 ± 0.08 species for drift fences. We found more reptiles on the trunks than on the ground (Z = -2.69; *P* < 0.01), with a mean of 8.2 ± 2.8 individuals on trunks and 4.3 ± 2.2 individuals on the ground, although no differences were detected for species diversity (Z = -1.27; *P* > 0.05).

Table 1. χ^2, *P*-values and coefficients of the variables included in the best models to explain the number of reptiles (Model 1). The coefficients for the level of fixed factors were calculated using the reference values of 'Drift fence' in the 'Method' variable, 'Young tree' in the 'Olive age' variable and 'July' in the 'Date' variable.

Variables	*Chi-square*	*p-value*	Coefficients± SE
Intercept			0.43±0.56
Date(May)	*9.58*	*<0.01*	May = -1.17±0.55
Olive age (Old)	*1.91*	*n.s.*	Old tree = -0.36±0.87
Method	*918.44*	*<0.0001*	Survey Transect = 2.25±0.23
Date * Olive age	*10.01*	*<0.01*	1.84±0.75
Date * Method	*4.30*	*<0.05*	1.33±0.56
Olive age * Method	*6.95*	*<0.01*	1.37±0.45
Olive age * Method * Date	*4.05*	*<0.05*	-1.49±0.76

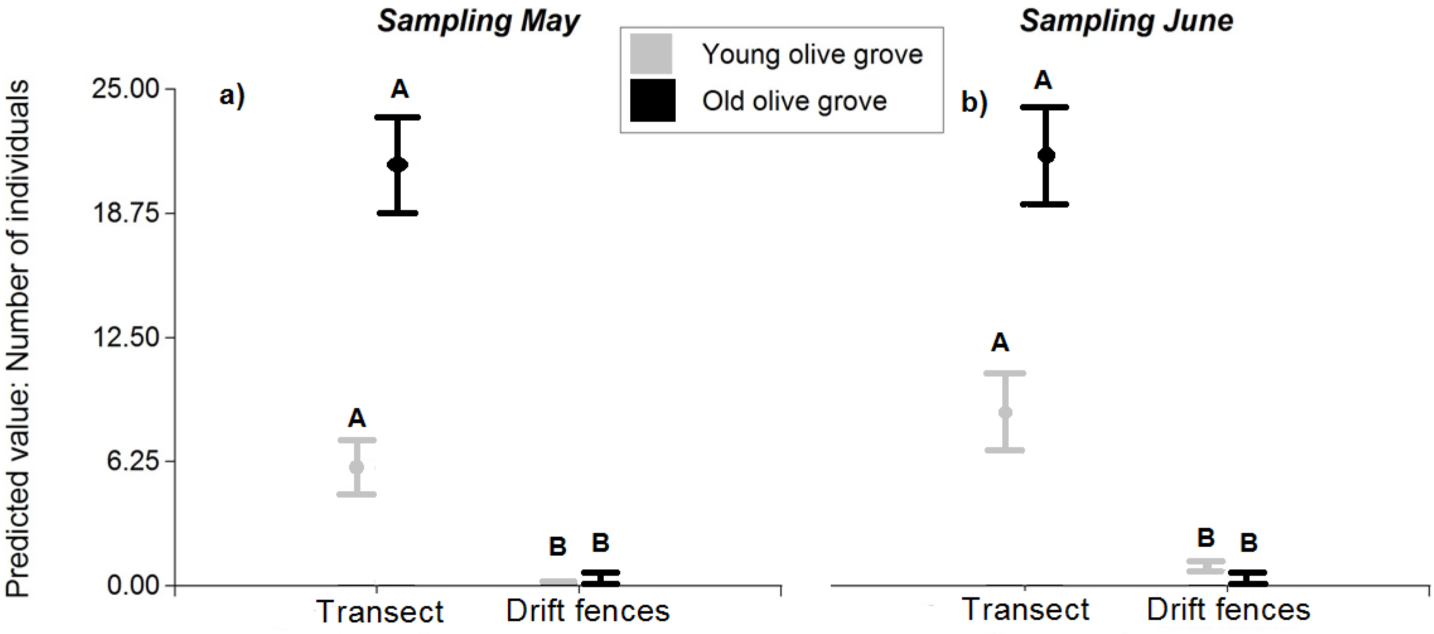

Figure 2. Predicted mean values (± SE) of number of individuals sampled in May (a) and in July (b) 2014 according to the sampling method, partitioned by age of olive

grove (young vs. old). Different capital letters indicate significant differences ($P < 0.05$) between methods.

Table 2. The best candidate models as regards explaining species richness (Model 2). The number of estimated parameters (k), the Akaike information criteria for small sample size (AICc), the difference between each model and the best model (ΔAICc) and the Akaike weight (w_i) are shown.

Candidate model	k	AICc	ΔAICc	w_i
Method	1	110.37	0	0.4
Method + Olive age	2	111.23	0.86	0.26
Method + Date	2	112.00	1.63	0.17
Method + Date + Method* Date	3	112.27	1.9	0.15

Discussion

We found that transects were more effective than drift fences for detecting reptiles regardless of the age of the olive grove. Our results are similar to other studies that indicate that transects are highly effective at sampling herpetofauna species (Rodel and Ernst 2004; Hutchens and DePerno 2009; Sung et al. 2011). These results indicate transects may be a valuable tool for biodiversity assessment in woody crops (such as olive crops). Unfortunately, most studies have used only one methodology (Spence-Bailey et al. 2010; Godinho et al. 2011; Rotem et al. 2013) and comparisons between methods cannot therefore be made (Hutchens and DePerno 2009). Drift fences have been recommended by some researchers because of the ability to reveal the presence of rare species and generate significantly higher captures of common species (Garden et al. 2007; Willson and Gibbson 2009). However, in our study, drift fences were less effective at sampling reptiles than transect surveys. Moreover, the drift fence arrays were expensive to construct, maintain, and operate because traps need to be checked daily, which increasingly is required by Animal Care Committees. Also the materials and manufacturing needed for funnel traps (three per array) contributed to a considerable portion of the total cost for arrays, while transects only requires human effort (Hutchens and DePerno 2009).

One reason that might explain the differences we found between the methods is the territorial behavior of the reptiles at our sites (Haenel et al. 2003.) and the small home range of these species (e.g., 25 m² for *Podarcis muralis* or 86 m² for *Podarcis hispanica*; Verwaijen and Damme 2008), which limits their movement to very specific areas. This might also explain the low rate of capture in drift fences. Most of the reptiles were located on the trunks of olive trees, which likely served as shelter and foraging spots (Kerr et al. 2003). However the significant effect of tree age on the model can be explained because only old tree trunks offers adequate shelter and hunting spots, whereas young trees have homogeneous and smooth trunks lacking the microhabitat needed by lizards for refuge. Kaliontzopoulou *et al.* (2009) described the arboreal behavior of *Podarcis hispanica* with lizards climbing the trunks of oaks to thermoregulate, find food, and escape predators. These authors relate this arboreal behavior to shortages of rocks or stones in the soil in the forests of the oak tree *Quercus suber*, groves of which are similar to that groves of olives. For *Podarcis sicula*, trunks of old olive trees serve as a mechanism of involuntary dispersal both within and outside its natural range (Valdeón et al. 2010; Rivera et al. 2011).

The vertical space in the woody crops used by lizards in olive groves greatly limits the usefulness and effectiveness of drift fences in this broad habitat type. We recommend the use of transect surveys to sample lizards when available time and economic resources are limited in groves of trees. However, only a few snakes were detected by either drift fences with funnel traps (one capture) or along transects (three observations) and therefore we conclude that transects were useful only for detecting lizards. More research into other sampling techniques in these woody crops is needed, and their effectiveness for different taxa should be compared.

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Appendix 1.

Total number of captures of reptile species using different survey methods (drift fences vs. transect) in May and June 2014 in southern Spain.

Group	Species	May		June	
		Drift fences	Transect	Drift fences	Transect
Amphisbaenia	*Blanus cinereus*				1
Lacertilia	*Acanthodactylus erythrurus*	4	68	7	118
	Lacerta lepida		2		3
	Podarcis hispanica	7	97	14	233
	Podarcis vaucheri			2	5
	Psammodromus algirus		29	2	4
	Tarentola mauritanica		49		47
Serpentes	*Hemorrhois*		1	1	

	hippocrepis				
	Malpolon monsspesulanus		1		
	Rhinechis scalaris				1
Unidentified			129		32
Total		11	376	26	444

Capítulo 1.3

Las cubiertas herbáceas mejoran la comunidad de reptiles en los cultivos leñosos

Carpio, A.J., Castro, J., Mingo, V., Tortosa, F.S. (2017). **Herbaceous cover enhances the squamate reptile community in woody crops.** *Journal for Nature Conservation. 37*, 31-38.

Resumen

La intensificación de la agricultura implica la simplificación y homogeneización del paisaje, lo que tiene graves impactos negativos sobre la biodiversidad animal. Las cubiertas herbáceas de los olivares crean parches heterogéneos que difieren de los olivares intensivamente gestionados en cuanto a estructura y composición, lo que puede conducir a una disminución de esta pérdida de biodiversidad. Los reptiles responden rápidamente a los cambios en la vegetación y otros trastornos del hábitat, a pesar de lo cual, estos taxones han recibido muy poca atención con respecto a su vulnerabilidad a los sistemas agrícolas. En este estudio, se investigó la respuesta de un conjunto de reptiles a diferentes sistemas de manejo en olivares. Las comunidades de reptiles se registraron en áreas con tres tipos de sistemas de manejo de olivares: suelo desnudo, cubiertas vegetales naturales y cubiertas vegetales monoespecíficas. Comparamos además la estructura del hábitat y la riqueza de la vegetación en el área de estudio con el fin de verificar si los sistemas de manejo tienen un impacto sobre la frecuencia de ocurrencia y la diversidad de las especies de reptiles dentro de los olivares. La composición de la comunidad de reptiles difería entre los tres sistemas de gestión, aunque esto fue modulado por la edad de los olivos. Nuestros resultados muestran que las comunidades de reptiles fueron más restringidas en áreas de manejo intenso (suelo desnudo) que en aquellas con cultivos de cobertura. Cuando existían cubiertas herbáceas, la cubiertas naturales albergaban una comunidad más diversa. Nuestros datos sugieren que mientras los cultivos de cobertura monospecíficos mejoran la frecuencia de ocurrencia de reptiles, la riqueza de especies no aumenta; Sin embargo, una cobertura vegetal herbácea más heterogénea (que, por ejemplo, contiene más especies y es más similar a la vegetación natural) sería una mejor solución con respecto a la promoción de la diversidad en los conjuntos de reptiles en los paisajes agrícolas. Por último, nuestros resultados pueden utilizarse para mejorar la calidad del hábitat de las comunidades de reptiles en cultivos leñosos similares como viñedos o huertos, en los que comienzan a aplicarse cultivos de cobertura.

Abstract

The intensification of agriculture entails the simplification and homogenisation of the landscape, which has serious negative impacts on animal biodiversity. Herbaceous ground cover in olive groves creates heterogeneous patchworks that differ as regards how intensively farmed olive groves are structured and composed, which may lead to a decrease in this loss of biodiversity. Reptiles rapidly respond to changes in vegetation and other habitat disturbances, in spite of which, this taxa has received very little attention with regard to their vulnerability to agriculture systems. In this study, we investigated the response of a squamate reptile assemblage to different management systems in olive groves. Reptile communities were recorded in areas with three types of olive grove management systems: bare ground; natural cover crop; and, monospecific cover crop. We further compared habitat structure and vegetation richness in the study area in order to verify if management systems have an impact on the frequency of occurrence and diversity of squamate reptiles species within olive groves. The community composition of reptiles differed among the three management systems, although this was modulated by the age of the olive trees. Our results show that the squamate reptile communities were more restricted in areas of intense management (bare ground) than in those with cover crops. When herbaceous covers existed, natural ground cover harboured a more diverse community. Our data suggests that while monospecific cover crops improve the frequency of occurrence of reptiles, species richness does not increase; however, more heterogeneous herbaceous ground cover (which, for instance, contain more species and are more similar to natural vegetation) would be a better solution regarding the promotion of diversity in reptile assemblages in agricultural landscapes. Finally our results may be used to improve the habitat quality of squamate reptile communities in similar woody crops like vineyards or orchards, where cover crops are beginning to be implemented.

Introduction

Understanding the response of species to environmental change is a major goal in predicting its effects on biodiversity (Hooper et al. 2005). The intensification and expansion of modern agriculture is amongst the greatest current threats to worldwide biodiversity (Hole et al. 2005; Stoate et al. 2009). Due to this intensification, Spain has been considered as one of the European regions most vulnerable to biodiversity loss due to agricultural practices (Reidsma et al. 2006). This transformation of large agricultural areas in Mediterranean ecosystems by human activity in recent years has led to an intensive landscape of olive groves that is predominant in southern Spain (Gómez-Limón et al. 2012), while the total area devoted to olive production is still growing. These intensive olive groves are characterised by a tree density of about 250 trees ha^{-1}, yearly fertilisation and pruning, several chemical sprays for pest control, soil tillage once to thrice per year and irrigation of up to 2700m^{3} ha^{-1} yr^{-1} (Metzidakis et al. 2008).

Olive groves have currently reached record levels in terms of area and production, by taking advantage of the European Common Agricultural Policy (CAP) since its establishment in 1980. The main goals of the CAP at the time were the promotion and intensification of olive groves, but due to this recently unsustainable development, the EU has begun to promote the adoption of agri-environment schemes (AES). These schemes aim to mitigate the problems caused by this agricultural intensification process. AES include soil conservation practices in olive groves, such as preventing the incineration of olive-desuckering debris, shredding olive-pruning debris for use as inert soil cover and using cover crops under mower control, to promote biodiversity and to prevent erosion during the rainy season (Rodríguez-Entrena and Arriaza 2013; Michael et al. 2014). One example of AES are herbaceous ground covers, which consist of an inter-tree herbaceous vegetation strip, although it can also extend as a continuous covering across the crop (Paredes et al. 2015), which may be natural and spontaneous or cultivated vegetation (Simões et al. 2014). The use of a cover crop within annual or woody crops has been reported to support more biodiversity than crops of the same species growing in intensive agriculture habitats (Atauri and Lucio 2001; Balouch et al. 2016).

Intensification of olive groves has been reported as being the main cause of regional biodiversity loss in bird populations (Rey 2011; Castro-Caro et al. 2014a). Furthermore, olive groves have been identified as leading cause for diversity loss in amphibians, bats or fish (Davy et al. 2007; García-Muñoz et al. 2010a; García-Muñoz et al. 2013; Matono et al. 2013), along with plant and invertebrate taxa (Cotes et al. 2010; Hevia et al. 2015). However, few studies have explicitly evaluated the effectiveness of AES as regards protecting or increasing the diversity of reptiles (Michael et al., 2014), despite the fact that loss of biodiversity in this taxa should be expected, too (Atauri and Lucio 2001; Carpio et al. 2016a). Moreover, no studies have evaluated the effect of the implementation of ground cover on reptile communities, although the importance of leaf litter (Wanger et al. 2010) and bare ground cover (Michael et al. 2014) have already been highlighted.

The information available on reptiles in agro-ecosystems is truly scarce (Mingo et al. 2016). Additionally, although there has been research concerning the distribution and abundance of faunal groups in different types of elements in agricultural landscapes, most attention has generally been given to natural or semi-natural elements (i.e. small patches of forest and woodland or linear features such as hedgerows or roadside vegetation; Bennett et al. 2006). Fewer studies have examined the use of anthropogenic elements such as orchards, tree plantations or arable land, and how these elements affect reptile assemblages (Bennett et al. 2006).

Reptiles are recognised as being extremely sensitive to local habitat changes (Castellano and Valone 2006) owing to their ecological and physiological constraints (such as temperature), low dispersal capacity, small home ranges (Huey 1982) and territoriality (which is known in multiple lizard species; Böhme 1984). This taxa will therefore be more prone to the risks associated with agricultural intensification than other vertebrate taxa (White et al. 1997; Carpio et al. 2016a). It is for this reason that reptiles may be useful for monitoring the activities of habitat restoration which affect ground cover, woody debris, or foliar canopy cover (Steen et al. 2013; Michael et al. 2014; Bateman et al. 2015). The response of reptiles to native vegetation management in olive groves should, therefore, be of importance to land managers but requires immediate and intense investigation. As the Iberian Peninsula is a hotspot for reptile diversity and one of the Mediterranean areas richest in reptiles (Martín and Lopez 2002), while also the home of a considerable number of endemic reptilian species (Sillero et al. 2014), evaluating how different management systems affect reptile communities could thus be key in order to conserve this rich biodiversity.

Olive groves as agro-ecosystem provide an opportunity to test the effects of herbaceous ground cover on the community of squamate reptiles. The aim of this study was to determine (1) the effects of three management systems (bare ground, natural and cultivated cover crops) on the abundance, richness, diversity and community composition of squamate reptiles, and (2) to determine whether these differences were influenced by the plant community and to assess the effect of management systems on plant richness.

Materials and Methods

Study area

The study was conducted in Andalusia (37º30’–37º58’N, 4º17’–4º56’W, at 159–369 m.a.s.l.), in the South of the Iberian Peninsula (Fig. 1), which it is characterized by a high species richness of reptiles (29 species of squamate reptiles), some of which are endemic. However, the intensification of olive farms (disappearance of vegetable cover, water pollution, high use of insecticide and soil erosion) has caused a decrease in both the number and the diversity of reptile species in olive grove systems (Riesgo and Gallego-Ayala 2015).

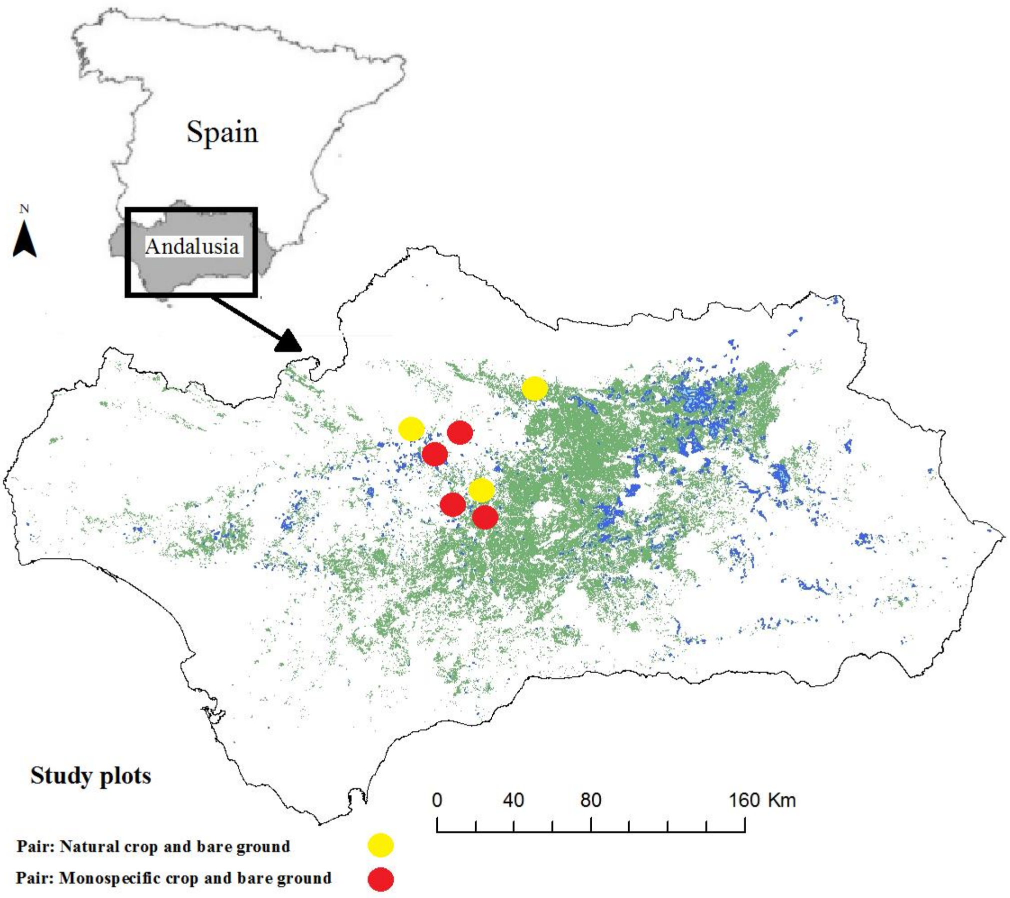

Figure 1. Study plots (coloured points) and the distribution of unirrigated olive groves (green areas) and irrigated olive groves (blue areas) in Andalusia (Spain).

Seven study plots were selected in a representative range of olive groves. Each plot comprised two study sites (an olive grove with herbaceous ground cover –either natural or monospecific– and an olive grove with bare ground; n = 14 study sites; natural cover crop n = 3; monospecific cover crop n = 4). These categories were selected to respond to the questions addressed in this work, where ``bare ground´´ were olive groves without herbaceous vegetation, ``natural cover crop´´ were olive groves with a spontaneous herbaceous cover (multispecific) and ``monospecific cover crop´´ were olive groves with a cultivated herbaceous cover (monospecific). Selected olive groves cover: irrigated and unirrigated; bare ground vs. cover crops; young vs. old trees; and, an altitude between 150-800 m what means that the most common situations are represented. The mean distance between the sampled plots was 21.4 km (SE: 5.6; range: 2.6-62.5 km). The plots were integrated into an olive-dominated landscape, in which agricultural intensification has eliminated most of the natural vegetation (Rey 2011). The mean distance between study sites within a plot was 1.2 km (SE 0.2 range: 0.5-2.4 km). The olive trees were 10–100 y old and were differentiated into young (10–20 y old) and old (90–100 y old) groves for the study. They were of a medium size (3-6 m tall) and their density varied between 7 x 7 m and 10 x 10 m.

Squamate reptiles sampling

We monitored squamate reptiles from May to July in 2014 and 2015, a period during which reptiles are particularly active because of their mating season (Godinho et al. 2011). Each plot was inspected twice per year (once in May and again in July). During each month (sampling season), two line transect census per plot were repeated on three days with favourable climatic conditions (warm sunny days) between 1100–1300 GMT, when the reptiles were most active (Martín and Lopez 2002). The inspection time per transect lasted one hour (30 min for each transect) on each site. This time span was selected based on the literature (eg. Santos and Poquet 2010; Hutchens and DePerno 2009). The transect length was 1-2 km (mean ± E.E. 1.47 ± 0.07 km). Transects were 100 m apart from each other (for more details see Carpio et al. 2015b) and surveys were done in a zigzagging way in order to reduce resightings. The reptiles observed were recorded in each transect, within a 10 m-wide belt (5 m on each side of the survey line), and identified at species level. A total of 336 transects were performed (168 in each year). Species which are less mobiles are harder to detect and less visible according to this method, however the time span was sufficient to detect most present species (Hutchens and DePerno 2009).

Vegetation and landscape indices

Reptiles are very sensitive to habitat structure: some species prefer open areas while others appear under a dense woodland canopy (Santos and Cheylan 2013), and it was for this reason that we assessed vegetation and landscape diversity. The diversity of herbaceous plants (weed) was assessed by creating two linear sampling transects (100 m in length) in two olive rows, in which 10 points (hoop of 0.5 m^2) separated by 10 m were sampled in each row (Guerrero-Casado et al. 2015). All weed species at these sampling points were identified (Appendix 1), and the coverage occupied by all species at a particular point was estimated visually as a proportion of an area, which was always calculated by the same observer (A.J.C.). The mean values of the Shannon diversity index for the weed community and the surface covered by herbaceous vegetation were calculated at study site level per month (April, May and June of 2014 and 2015).

The effect of the surrounding landscape was evaluated by recording two diversity variables at the site level (Martín and Lopez 2002): (i) the Shannon index of the landscape; and, (ii) the edge density of the landscape, which were obtained using FRAGSTATS 4.1 software (McGarigal et al. 2002). Landscape diversity index and edge density were registered in a buffer of approximately 500-m radius around the center of the sampling site. In each buffer, different land cover classes present were recorded (urban land uses, rivers and natural streams, arable crops, olive groves, vineyard, irrigated crops, citrus and dense scrub). Information concerning land cover classes was obtained from aerial photographs (Ortofotografía digital de Andalucía).

Data analysis

As data violated parametric assumptions (homogeneity of variance and normal distribution), a Spearman's correlation test was used to assess the correlation between the explanatory variables (edge density, vegetation richness and landscape diversity index), where variables with rho >0.8 were removed to avoid autocorrelation. Thereby edge density and vegetation richness were not included in the models. A non-parametric test (the Kruskal-Wallis analysis) was used to detect significant differences among the three management systems in terms of landscape diversity index.

In order to determine the relationships between each type of olive grove (bare ground, natural cover crop or monospecific cover crop), with regard to squamate reptiles' richness, diversity and frequency of occurrence (number of observations) generalised linear mixed models (GLMMs) were developed. In all the models, i.e. the frequency of occurrence model (Model 1), the squamate reptile richness model (Model 2) and the squamate reptile diversity model (Model 3), the Shannon index of the landscape was included as covariable, whereas management (3 levels), year (2 levels) olive age (2 levels) and sampling month (2 levels) were added as fixed factors. We also included the interaction between the treatment (ground cover) and the age of the olive tree. The plot (7 levels) was considered as a random factor. Poisson distribution and the log-link function were used with both Model 1 and Model 2, while normal distribution and the identity-link function were used with Model 3. Fisher's least significant difference test (LSD test) for comparisons of the estimated means within a mixed analysis was developed to check differences among the level of categorical variables and to illustrate the interactions. Rather than using criteria based on parsimony to select the 'best model' (which favour precision *vs*. bias), we used the full models. Statistical analyses were performed by employing InfoStats software.

In order to test dissimilarity and differences in species composition among management (natural cover crops, monospecific cover crops and bare ground), year (2 level) and sites (at seven levels: random factor) on which management systems were nested within "sites", we used the permutational multivariate analysis of variance (PERMANOVA). Type III Sum of Squares was used since they are appropriate in the case of an unbalanced design. All the tests were performed with 9999 permutations with the objective of increase the power and precision of analysis (Anderson et al. 2008) of residuals under a reduced model (Anderson and ter Braak 2003). The differences in community structure among the three management systems were then investigated using a posteriori pair-wise test with 9999 permutations. The advantage of the permutation approach is that the resulting test is ‘‘distribution free’’ and not constrained by many of the typical assumptions of parametric statistics (Walters and Coen 2006).

We also conducted a SIMPER analysis (similarity percentages; Clarke 1993) to determinate which species explain the largest proportion of the differences in community composition among managements. In this study, SIMPER was employed to identify those squamate reptile species that were responsible for more than 90% of dissimilarity among management systems. Moreover, we plotted species accumulation curves and rank-abundance diagrams for each management system using the number of species observed (S_{obs}). The analyses were performed using the PRIMER v6 computer programme (Clarke and Gorley 2006), including the PERMANOVA+ add-on package (Anderson et al. 2008).

Results

Habitat structure associated with olive grove type

The Kruskal-Wallis test showed significant differences in landscape diversity index among the three management systems (χ^2=13.51, df=13, p = <0.05), with diversity being higher in natural cover crops when compared to other systems. With regard to the factors that affect the frequency of occurrence of reptiles, Model 1 showed a significant effect of olive grove management, although this was modulated by the age of the olive tree (with the frequency of occurrence being higher in old olive trees), the landscape diversity index and the sampling year, but without effect of sampling month (Table 1). The results showed significant differences between natural and monospecific cover crop vs. bare ground but did not show significant differences between natural vs. monospecific cover crops (Fig. 2). Rather, and with regard to species richness, Model 2 showed a significant effect of olive grove management, the landscape diversity index, and the interaction between management systems and the age of the olive tree (which was higher in the case of old olive trees). The post-hoc test showed significant differences in species richness between bare ground and monospecific cover crops vs. natural cover crops but did not reveal significant differences between monospecific cover crops and bare ground (Fig. 2). Finally, the diversity represented by Model 3 was affected by management systems, sampling year, the landscape diversity index and the interaction between management and the age of the olive trees, showing a less clear separation between the three types of olives groves. The Fisher test showed differences in reptile diversity between natural cover crops and bare ground, while there was an intermediate diversity among monospecific cover crops (Fig 2).

Table 1. F-values and coefficients of the variables included in the mixed models to explain frequency of occurrence (Model 1), species richness (Model 2) and diversity (Model 3). Coefficients for the level of fixed factors were calculated using reference

values of ‘bare ground’ in the variable ‘management’, ‘2014’ in the variable ‘year’, ‘young’ in ‘tree age’ and ‘June’ in ‘sampling month’. (** $p < 0.01$; *** $p < 0.001$).

Frequency of occurrence (model 1)		
Variables	F-value	Coefficient ± E.S.
Intercept	36.6***	13.4 ± 2.86
Management	27.2***	Natural cover crop = 15.6 ± 3.6 Monospecific cover crop = 6.2 ± 1.6
Year	16.2***	2015 = -3.83 ± 0.95
Tree age	9.4**	Old = 1.7 ± 2.56
Sampling month	2.6	May = -1.6 ± 1.02
Landscape diversity index	17.2***	23.63 ± 5.86
Management * Tree age	12.6***	
Species richness (model 2)		
Intercept	15.3***	1.25 ± 0.39
Management	11.5***	Natural cover crop = 2.13 ± 0.64 Monospecific cover crop = 0.27 ± 0.2
Year	1.49	2015 = -0.16 ± 0.12
Tree age	2.17	Old = 1.25 ± 0.6
Sampling month	0.48	May = -0.1 ± 0.13
Landscape diversity index	5.73*	1.33 ± 1.1
Management * Tree age	11.2**	
Reptiles Diversity (model 3)		
Intercept	22.56***	0.14 ± 0.06
Management	6.93**	Natural cover crop = 0.29 ± 0.09 Monospecific cover crop = 0.04 ± 0.04
Year	3.95*	2015 = -0.05 ± 0.02
Tree age	1.8	Old = 0.2 ± 0.08
Sampling month	3.03	May = 0.04 ± 0.02
Landscape diversity index	6.03*	0.27 ± 0.11
Management * Tree age	3.5*	

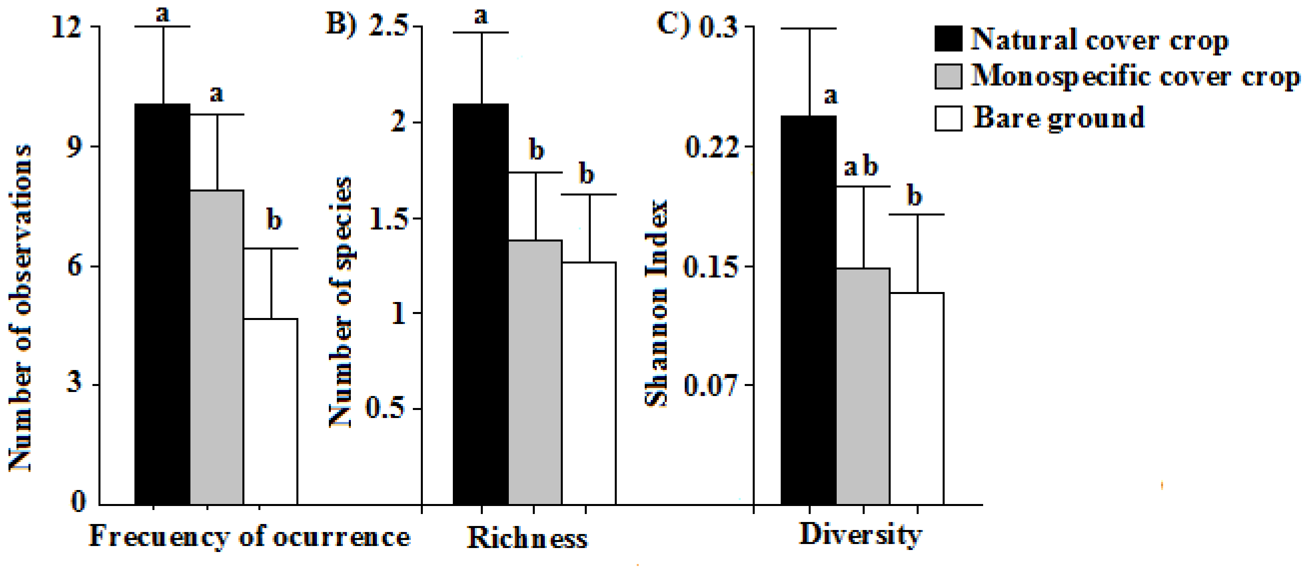

Figure 2. Predicted mean values (±S.E.) of frequency of occurrence (A), species richness (B) and diversity (C) in different olive grove management systems. Lower case letters indicate significant differences ($p < 0.05$) among management according to Fisher LSD tests.

Differences in squamate reptile community

During the study period, we obtained over 1400 records of squamate reptiles representing 10 species, with lizards accounting for the majority of observations (Appendix 2). With regard to the management, 1017 observations belonging to 10 different species were recorded in olive groves with herbaceous ground cover, while 384 observations belonging to 8 species were detected in olive groves with bare ground. Species-accumulation curves indicated that cumulative richness was lower in olive groves with bare ground (Fig. 3). Rank-abundance diagrams showed that the dominant species on bare ground and within monospecific cover crop was *Podarcis hispanica*, while in natural cover crops it was *Acanthodactylus erythrurus* (Fig. 4).

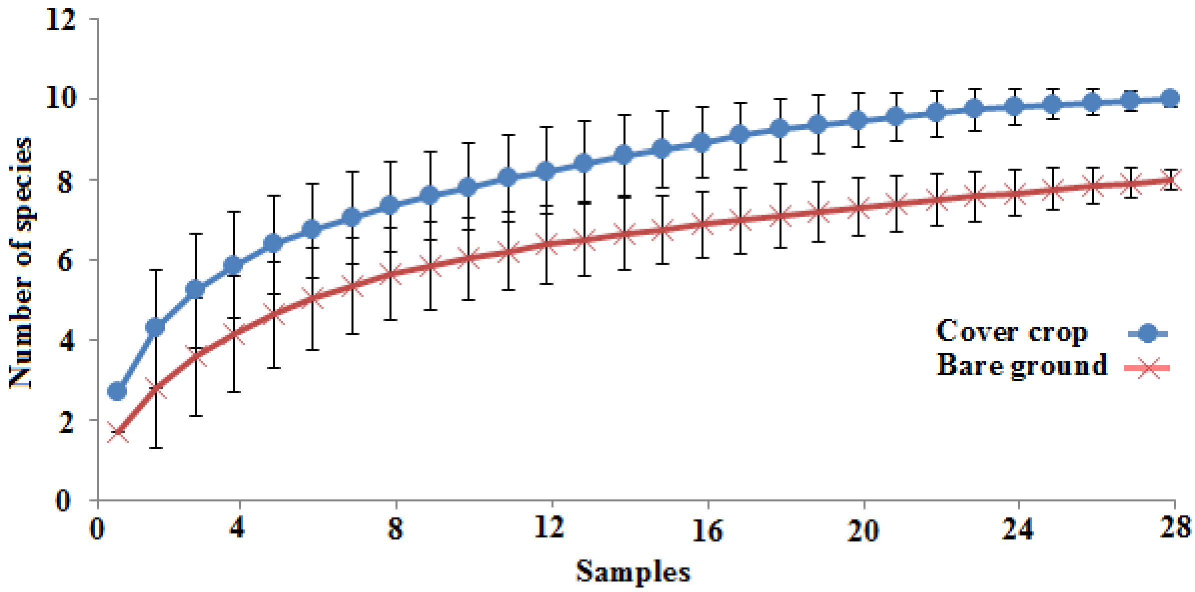

Figure 3. Species-accumulation curves for squamate reptiles identified in two management systems in olive groves

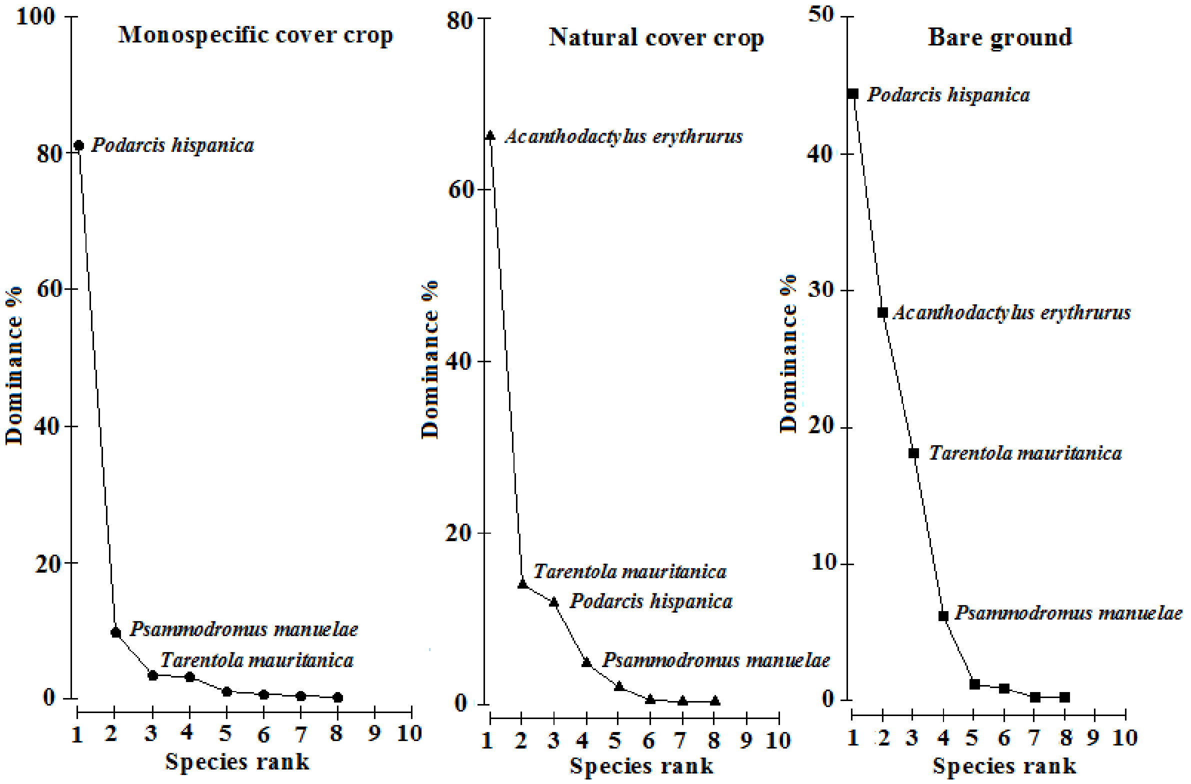

Figure 4. Rank-abundance diagrams of squamate reptile species for each management system.

We found dissimilarities in the reptile communities among management systems (PERMANOVA, $F_{1,\ 56}$ = 6.3, P = 0.001; Table 2), but no significant differences in communities between years (PERMANOVA, $F_{1,\ 56}$ = 2.26, P = 0.14; Table 2). Furthermore, differences among different plots were significant (PERMANOVA, $F_{1,\ 56}$ = 15.4, P = 0.001; Table 2). The results of the pair-wise comparison showed significant differences between all combinations of management systems: natural vs. monospecific cover crops (average similarity 38%); natural cover crops vs. bare ground (average similarity 39%); and, monospecific cover crops vs. bare ground (average similarity 43%).

Table 2. PERMANOVA for number of observations for each species based on management systems, sites and year (multivariate data), and results of the pair-wise test as regards the number of squamate reptiles in each species for each management system (* $p < 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$).

PERMANOVA			
Variable	df	MS	F
Year	1	1539	2.26
Plot	6	9372	15.4***
Treatment (Plot)	7	2502	6.3***
Residuals	41	605	
Total	55		

Pair-wises test		
Management systems	df	*t*
Natural cover crop vs. monospecific cover crop	1	2.31*
Natural cover crop vs. bare ground	1	2.01**
Monospecific cover crop vs. bare ground	1	2.17**

SIMPER indicated a considerable average dissimilarity (76.76%) between olive groves with natural cover crops and bare ground. The difference recorded was mainly owing to a difference in abundance of *Acanthodactylus erythrurus* and *Podarcis hispanica* (Appendix 3). In contrast, the dissimilarity between monospecific cover crops and bare ground was lower, at 72.85%, mainly owing to the contribution of *Podarcis hispanica* and *Psammodromus algirus.* At the same time, the latter's dissimilarity was similar to that found between monospecific cover crops and natural cover crops (72.16%), in which *Podarcis hispanica* and *Acanthodactylus erythrurus* stand out (Appendix 3).

Discussion

Taxonomic responses and changes in diversity according to management system

In this study, for the first time, we investigated reptile assemblages in olive groves, to compare the relative importance of herbaceous ground cover for squamate reptiles in woody crops. Natural cover crops manifested the highest values for all response variables, followed by monospecific cover crops and bare ground management systems, although this was modulated by the age of the olive tree (which was, for all variables, higher for old olive trees). These old trees are characterized by the presence of cavities, which support the importance of tree hollows for reptiles (Gibbons and Lindenmayer 2002), probably because they provide safe shelter against unfavourable weather, predators and human disturbance (Fischer et al. 2010), and how the shortage of hollows can limit their populations (Lindenmayer et al. 2012). These findings support the importance of focusing on improving site scale habitat quality for reptiles, particularly by increasing structural complexity (e.g. a diverse plant community), rather than focusing on cover monocrops (in terms of biodiversity).

Our results show that the frequency of occurrence of reptiles was positively influenced by the presence of vegetation cover, regardless of whether it was monospecific or natural, which is consistent with studies on other crops, such as those of Cunningham *et al.* (2007) or Michael *et al.* (2014) which demonstrated how reptiles respond to replanted vegetation in agricultural landscapes. Sown areas could improve the supply of food (e.g. arthropods; Carpio et al, unpublished data) or provide shelter from predators (Zakkak et al. 2015). Shelters such as burrows, hollows and cavities in the trunks (which depend upon the age of the olive tree) and bushy shrubs have been identified as key habitat resources that lead to an increase in the abundance of individuals (Grillet et al. 2010; Carpio et al. 2015b). The year also had an effect on the frequency of occurrence of reptiles, with a lower frequency of occurrence in 2015, which could be explained by the fact that it was an unusually hot spring (which might limit reptile activity), with an average temperature throughout the study period of 25.8 Cº ± 0.43Cº vs. 23.1Cº ± 0.35Cº in 2014 (t =6.69; p <0.001), especially during the sampling period in July: 29.84Cº ± 0.32ºC in 2015 and 25.68 ± 0.48 in 2014 (t = 8.85; p <0.001).

In terms of species richness, the authors of a previous study performed pair-wise comparisons between conventional and organic farming and they found an average increase of 2.7 times in organic farming in the species abundance of five taxa groups: birds; insects; plants; mammals; and, earthworms for organic farming (see Reidsma et al. 2006). Furthermore, trees within croplands were identified as important structures regarding the presence of agamids (similar to how older olive trees were significant for squamate diversity in our current study; Balouch et al. 2016). Similarly, Smart *et al.* (2005) were able to confirm an increase in abundance rates of lizards within South African rangelands in areas with dense vegetation cover. However, none of these studies directly took into consideration the effects of cover crops on reptiles. In this respect, our results show that management systems have a significant impact on species richness and are dependent on the type of herbaceous ground cover and the age of the olive trees. In contrast to frequency of occurrence, natural cover crops were shown to have greater species richness regarding squamate communities' than monospecific cover crops or bare ground (no difference between them), while also displaying higher plant species richness than both monospecific cover crops (*Bromus rubens* monocrops) and bare ground. These results are in accordance with Qian and Kissling (2010) and Michael *et al.* (2014), which reported that native plant richness positively affects reptile diversity. This result is consequence of the landscape heterogeneity that is created by a combination of patches with natural vegetation and a high plant richness, which enhances the availability of food and shelter for wildlife and maintains natural pest predator populations, hence diminishing the need for pesticides (Nekhay and Arriaza 2009; Bonnet et al. 2012; Paredes et al. 2013; Simes et al. 2014; Pérez-Cembranos and Pérez-Mellado 2015; Bruton et al. 2016). The landscape diversity index and, indirectly, the age of the olive tree also similarly favour the species richness of reptiles by increasing site-scale structural complexity (Atauri and Lucio 2001; Carpio et al. 2015b; Bruton et al. 2016). This is consistent with a study of Bruton *et al.* (2013), which found that, in comparison to site-scale habitat quality, the composition of the surrounding landscape had little influence on reptiles, emphasizing the importance of increasing amount and connectivity of surrounding vegetation of a lesser value, especially in these extremely simplified landscapes.

Reptile community assemblage between management systems

Management system influences species communities. These differences were mainly owing to *P. hispanica,* which appeared to prefer rocky and open patches (Martín and Lopez 2002; Godinho et al. 2011) and seemed less affected by olive grove management. *Podarcis hispanica* was present mainly on bare ground and in monospecific cover crops, while *Acanthodactylus erythrurus* was the most abundant species in natural cover crops, preferring areas with vegetation and low bushes, as well as sandy soils (Martín and Lucio 2002). Another species responsible for dissimilarities in reptile communities was *Psammodromus algirus*, which often moves between vegetation patches and open areas (López and Martín 2013), thus explaining its greater abundance in monospecific covers crops. *Timon lepidus* on the other hand preferred sites with some vegetation cover and where rocks were present (Godinho et al. 2011), thus being more abundant in management systems with natural cover crops. Finally, while *Tarentola mauritanica* was also responsible for differences among management systems, it is more influenced by the age of the tree and the availability of hollows and shelter than by the presence of cover crops (Lisičić et al. 2012). It is further important to note that species occurrences and abundances observed through all management systems were higher for natural and monospecific cover crops, although they only amounted to 3 and 4 sampling sites respectively, while bare ground consisted of 7 sampling sites. This result further strengthens the claim that herbaceous covers do indeed have a great impact on squamate reptile communities.

Conclusion and implications

Mediterranean landscapes are recognised as having high habitat heterogeneity; however, olive orchards are an extremely simplified habitat, which might be an argument in favour of maintaining or establishing these herbaceous ground covers. Our results indicate that the presence of herbaceous ground cover (and particularly natural cover crops) is important as regards enhancing reptile diversity, although this was modulated by the age of the olive trees. Small patches of natural vegetation and other structural elements (such as ditches, hedges, boundaries) within or adjacent to crops play an important role in sustaining biodiversity (Harvey 2007). In this scenario, the maintenance or increasing of habitat heterogeneity with a mosaic of patches with natural cover crops is a major agent regarding the expansion of low-mobility animal groups such as reptiles (Santos and Poquet 2010). Herbaceous ground covers also lead to other benefits, such as soil fertility and the prevention of soil erosion (Gómez et al. 2009a), or pollination enhancement (Tscheulin et al. 2011).

Acknowledgements

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Appendix. 1

List of weed species identified during the fieldwork

Allium ampeloprasum
Amaranthus albus
Amaranthus blitoides
Ammi majus
Anagalis arvensis
Anthemis arvensis
Arenaria hispanica
Aristolochia paucinervis
Asparagus officinalis
Bellardia trixago
Bromus hordeaceus
Bromus madritensis
Bromus rubens
Calendula arvensis
Campanula erinus
Capsella bursa-pastoris
Carduus bourgeanus
Centaurea aspera
Centaurium erythraea
Centranthus calcitrapae
Cerastium glomeratum
Chamaemelum fuscatum
Chenopodium album
Chrysanthemum coronarium
Cnicus benedictus
Convolvulus arvensis
Conyza canadensis
Coronopus squamatum
Crepis capillaris
Crepis vesicaria
Crypsis schoenoides
Cyperus rotundus
Daucus carota
Diplotaxis catholica
Erodium cicutarium
Erodium malacoides
Euphorbia exigua
Fedia cornucopiae
Filago lutescens
Fumaria parviflora
Galium aparine
Galium murale
Galium parisciense
Geranium dissectum
Geranium molle
Geranium rotundifolium
Heliotropium europaeum
Herniaria cinerea
Hirschfeldia incana
Hordeum murinum
Hypochaeris radicata
Lactuca serriola
Lamarckia aurea
Lamium amplexicaule
Lavatera cretica
Leontodon longirostris
Leontodon taraxacoides
Lolium perenne
Lolium rigidum
Malva hispanica
Malva parviflora
Malva sylvestris
Matricaria chamomilla
Medicago polymorpha
Melilotus elegans
Melilotus indicus
Muscari ornithogalum
Ononis mitissima
Phalaris canariensis
Phalaris paradoxa
Picris echioides
Poa annua
Polygonum aviculare
Polypogon monspeliensis
Pulicaria paludosa
Ranunculus parviflorus
Rapistrum rugosum
Reseda phyteuma
Ridolfia segetum
Rumex acetosa
Scorpiurus muricatus
Senecia vulgaris
Silene rubella
Silybum marianum
Sinapis alba
Solanum nigrum
Sonchus asper
Sonchus oleraceus
Sorghum bicolor
Spergularia rubra
Stachys arvensis
Stellaria media
Theligonum cynocrambe
Torilis arvensis
Torilis nodosa
Tragopogon hybridus
Trifolium campestre
Trifolium repens
Trifolium tomentosum
Urospermum picroides
Urtica urens
Vaccaria pyramidata
Veronica arvensis

Appendix 2.

Total number of reptile species identified on the basis of the type of management of the olive grove (cover crop vs. bare ground).

	Management Systems		
Species	**Natural cover crop (n =3)**	**Monospecific cover crop (n=4)**	**Bare groud (n=7)**
Amphisbaenia			
Blanus cinereus	0	2	0
Lacertilia			
Tarentola mauritanica	55	17	58
Acanthodactylus erythrurus	261	16	91
Podarcis hispanica	47	399	142
Timon lepidus	8	3	4
Psammodromus algirus	19	48	20
Podarcis vaucheri	0	5	3
Serpentes			
Hemorrhois hippocrepis	1	0	1
Rhinechis scalaris	2	0	0
Malpolon monspessulanus	1	1	1
Unidentified	53	80	63
Total	447	571	383

Appendix 3

Species responsible for more 90% of dissimilarity among three olive management systems (SIMPER Dissimilarity).

Supplementary Table S3: Species responsible for more 90% dissimilarity between three olive managements systems (SIMPER Dissimilarity).

Natural cover crop *vs* bare ground dissimilarity: 76.8%		
Specie	Contribution (%)	Cumulation (%)
Acanthodactylus erythrurus	35.39	35.39
Podarcis hispanica	25.93	61.32
Tarentola Mauritanica	15.2	76.53
Psammodromus algirus	9.35	85.87
Timon lepidus	8.07	93.95
Monospecific cover crop *vs* bare ground dissimilarity: 72.85%		
Specie	Contribution (%)	Cumulation (%)
Podarcis hispanica	51.06	51.06
Psammodromus algirus	16.34	67.4
Tarentola Mauritanica	12.39	79.8
Acanthodactylus erythrurus	10.38	90.18
Natural cover crop *vs* Monospecific cover crop dissimilarity: 72.16%		
Specie	Contribution (%)	Cumulation (%)
Podarcis hispanica	34.09	34.09
Acanthodactylus erythrurus	27.73	61.83
Tarentola Mauritanica	12.96	74.79
Psammodromus algirus	12.46	87.25
Timon lepidus	6.18	93.43

CAPÍTULO 2

Efectos de la simplificación del paisaje sobre la depredación de los nidos

Capítulo 2.1

La abundancia de conejos influye en la depredación de nidos de aves en olivares Mediterráneos

Carpio, A.J., Tortosa, F.S., Barrio, I.C. (2016). **Rabbit abundance influences predation on bird nests in Mediterranean olive orchards**. *Acta Ornithologica*, *50(2)*, 171-179.

Resumen

En las últimas décadas, la intensificación de las prácticas agrícolas en los olivares, incluido el uso intensivo de agroquímicos, junto con la ausencia de la capa natural de vegetación, ha llevado a una disminución de las comunidades de aves canoras. El aumento de la depredación de los nidos ha sido sugerido como otro factor importante en la disminución de las aves de las tierras de cultivo. La alta abundancia de especies de presas alternativas, como el conejo europeo *Oryctolagus cuniculus*, puede atraer a los depredadores generalistas, lo que puede aumentar las tasas de depredación de los nidos de aves, fenómeno conocido como hiperpredación. En este trabajo se evaluó la depredación artificial de nidos en olivares intensivos, utilizando huevos de codorniz (un huevo de yeso y dos naturales en cada nido) colocados en el suelo (97 nidos) y en los árboles (106 nidos). El 53,7% de los nidos (109 de 203) fueron depredados; 51 de estos nidos tenían al menos un huevo con signos de depredación y en 58 nidos todos los huevos fueron depredados. Los nidos colocados en el suelo (61%) fueron depredados con más frecuencia que los de los árboles (46%). La abundancia de conejos fue identificada como uno de los principales factores que aumentan las probabilidades de que un nido sea depredado. A pesar de las tasas más bajas de depredación de nidos en áreas con baja abundancia de conejos, encontramos una mayor diversidad de depredadores de nidos, como *Mustela nivalis*, *Mustela putorius*, *Martes foina* o *Erinaceus europaeus* en estas áreas. Este estudio sugiere que los esfuerzos de conservación encaminados a aumentar el éxito reproductivo de las aves de las tierras de cultivo deben evitar áreas con gran abundancia de conejos debido al fenómeno de hiperpredación.

Abstract

In recent decades, the intensification of agricultural practices in olive orchards, including intensive use of agrochemicals, along with the absence of natural herb layer, has led to a decline in songbird communities. Increased nest predation has been suggested as another important factor in the decline of farmland birds. High abundances of alternative prey species, such as European rabbits *Oryctolagus cuniculus* may attract generalist predators, which may increase predation rates on bird nests, a phenomenon known as hyperpredation. In this work, we evaluate artificial nest predation in intensively farmed olive orchards, using quail eggs (one plaster and two natural eggs in each nest) placed on the ground (97 nests) and on trees (106 nests). 53.7% of nests (109 out of 203) were predated; 51 of these nests had at least one egg with signs of predation and in 58 nests all eggs were predated. Nests placed on the ground (61%) were predated more frequently than those on trees (46%). Rabbit abundance was identified as one of the main factors increasing the probabilities of a nest being predated. Despite lower rates of nest predation in areas with low rabbit abundance, we found a higher diversity of nest predators, such as *Mustela nivalis, Mustela putorius, Martes foina* or *Erinaceus europaeus* in these areas. This study suggests that conservation efforts aimed at increasing the breeding success of farmland birds should avoid areas with high abundance of rabbits owing to the phenomenon of hyperpredation.

Introduction

A large proportion of European bird species depend on farmland habitats as breeding or wintering areas (see Tucker and Heath 1994; Skorka et al. 2006). As a consequence of agricultural intensification farmland birds have undergone a significant decline in Europe (Preiss et al. 1997; Tryjanowski et al. 2011), due to habitat loss and fragmentation, and increased predation from invasive and generalist predators (Evans 2004; Reif 2013). Few studies have investigated the impacts of agricultural intensification on ground-nesting passerines owing to the difficulty in locating and monitoring their nests in the field, which precludes estimates of their breeding parameters (Weidinger 2001, 2009; Calero-Riestra et al. 2013). Further, the literature on avian life histories is clearly biased towards forest species or populations clustered at north-temperate latitudes (Moreno et al. 2004), whereas little information is available for Mediterranean areas where there are seasonal differences in the availability of food (Stamou et al. 2004) and predation rates (Yanes and Suarez 1995).

In recent decades, agricultural intensification and landscape simplification have dramatically affected the Mediterranean region. Olive groves are one of the predominant crops in this region and play an important role for many resident and migrant bird species (Rey et al. 2011). The intensification of agricultural practices in olive groves, with the intensive use of agrochemicals and the absence of natural herb layer has led to a decline in songbird communities (Castro-Caro et al. 2014a). Intensive management in olive orchards has also produced a simplification of the landscape, with a progressive loss of hedges and remnants of natural vegetation. Predation on adult birds and nests is an important factor in the decline of some farmland birds (Söderström et al. 1998; but see Kujawa and Łęcki 2008). Nest predation rates are generally higher in farmland habitats (Bayne and Hobson 1997; Pita et al. 2009) than in other surrounding habitats such as grassland or forest (Chamberlain et al. 2000), probably as a result of the higher densities and species richness of nest predators (Chalfoun et al. 2002a; Beja et al. 2014). Predation can affect the spatial and temporal dynamics of populations and, therefore, be an important factor in prey population dynamics (Fuller et al. 1995). Changes in landscape characteristics are thought to be one of the key elements concerning increased predation risk (Bodey et al. 2011) owing to a variety of mechanisms. For example, landscape changes can create additional foraging opportunities for predators (Newton 2004), or reduce suitable nesting habitats, making nests more easily detected or disrupting communal defence (Evans 2004). Increases in habitat fragmentation may enhance the accessibility of nests to predators (Marzluff and Neatherlin 2006). In modified landscapes, generalist predators can also be subsidised by anthropogenic food sources, such as rubbish tips or carrion, in modified landscapes (Newton 2004). Such subsidies can increase the potential for predation, as predator populations reach greater densities than those that natural prey would ordinarily sustain (Courchamp et al. 2000). Similarly, when prey species share the same predators, the abundance of one species can negatively affect the other, in a phenomenon known as hyperpredation (Courchamp et al 2000).

The European rabbit *Oryctolagus cuniculus* is a keystone prey in Mediterranean Iberia (Delibes-Mateos et al. 2007), which is sometimes called the “rabbit ecosystem”. Despite a generalized decline of rabbit populations in their native range in Iberia as a result of viral diseases and habitat loss (see a review in Guerrero-Casado et al. 2013a), the species has recovered its abundance in some agricultural landscapes, where the species is considered an emerging pest (Barrio et al. 2010a). Rabbits may negatively interact with many species of birds owing to their common predators. In areas where rabbits have been introduced, their presence has induced the extinction of indigenous prey through the sudden increase of population size of a native or introduced predator (Courchamp et al. 2000). For example, the simultaneous presence of introduced feral cats and rabbits in many island ecosystems represents a threat to small vertebrates endemic to these islands (Smith and Quin 1996). This process, known as hyperpredation, is defined as ‘a restrictive case of apparent competition in which an increased number of primary prey species indirectly induces the decrease of the secondary prey species through the numerical response of predators to the primary prey dynamics’ (Smith and Quin 1996; Courchamp et al. 2000). However, the mechanisms behind hyperpredation include both *apparent competition* (i.e., symmetric indirect interactions of the form: negative—negative) and *apparent predation* (i.e., asymmetric indirect interactions of the form: positive—negative; Bate and Hilker 2012; Moleon et al. 2013). One example of this apparent competition between rabbits and red-legged partridges (*Alectoris rufa*) is shown in the studies of Moleon *et al.* (2008, 2013), who suggested that the decline in rabbit populations may lead to a redirection of predation toward another prey, partridges, thus causing their decline (but see Blanco-Aguiar et al. 2012). However, there are few studies on hyperpredation induced by rabbits within the natural distribution range of the species (Moleon et al. 2008, 2013; Blanco-Aguiar et al. 2012).

A second scenario of apparent predation is that when there is higher rabbit abundance the prey may attract a greater number and diversity of predators (Delibes-Mateos et al. 2007), particularly on a small scale (Guerrero-Casado et al. 2013b). According to Delibes and Hiraldo (1981), in Mediterranean Spain at least 29 different predators, including 17 raptors and 9 carnivores, prey on rabbits. Rabbits are able to maintain their abundance despite a high predation rate owing to their high reproductive rate (Gibb 1990) and can therefore affect the structure of a community by sustaining the density of predators and scavengers (Delibes-Mateos et al. 2007).

In this agricultural context and with a wide range of rabbit densities, we hypothesise that higher rabbit abundance will increase the risk of bird nest predation (apparent predation), since predators are attracted to areas with high densities of alternative prey (Courchamp et al. 2000; Bate and Hilker 2012; Guerrero-Casado et al. 2013b). The alternative hypothesis predicts a higher rate of predation in areas of lower rabbit density (apparent competition), in a similar way to what occurred with the red-legged partridge in other studies (Ontiveros et al. 2005; Moleón et al. 2008, 2013). To evaluate these hypotheses, we conducted an experiment with artificial nests in an olive-grove dominated landscape at seven sites covering a wide range of rabbit abundances.

Material and methods

Study area

The study was conducted in three olive grove areas of Cordoba province, Southern Spain during May–July 2013. We selected 7 study plots, 4 hectares each, based on previously assessed differences in rabbit abundance. Three plots were located north of Villa del Rio (38°00’60”N, 4°16’95”W), 3 plots 5 km to the south (37°58’25”N, 4°17’51"W), and 1 plot was situated in Montilla (37°34’49”N, 4°37’92”W). In the region, olive crops constitute a highly homogeneous landscape in which most of the natural vegetation has been eliminated (Rey 2011). All of the experimental plots were olive orchards with bare soil, little ploughing, and planted using a traditional framework (~ 10×10 m). Olive trees were more than 100 years old and similar in size at the moment of the experiment.

Experiment with artificial nests

The use of artificial nests is a widely used, indirect method to estimate the impact of predation on bird nests (Pärt and Wretenberg 2002; Zannete 2002; Beja et al. 2013; Castro-Caro et al. 2014b). Predators are identified by means of marks on eggs filled with plaster (Yanes et al. 1997).

We used commercial open-cup nests made of natural fibres (8×8 cm). Nests were exposed to the weather for at least 14 days before the experiment to dispel any artificial scent (Zuria et al. 2007). In each nest we placed three quail *Coturnix coturnix* eggs, one of which was emptied and injected with plaster, while the other two were not manipulated (Major 1991; Yanes and Suarez 1997; Willson et al. 2001). A total of 203 nests were placed in the study plots in the field (up to 32 nests per plot when possible; see Table 1), on the ground (97 nests) or on trees (1.5-2 m high, 106 nests). In each plot, nests were placed every 50 m, following a regular grid, alternating between ground and tree locations. Nests were monitored every second day during two weeks, which is the average time of the small bird species' incubation period (Martin 1987), between the last week of May and the first week of July 2013. Latex gloves and specific footwear were used during nest manipulation to prevent the appearance of scents that might be attractive to predators (Whelan et al. 1994). Egg predators were identified based on bite marks on the eggs (Duarte and Vargas 2001), except when eggs had totally disappeared, which may have been due to predation by corvids (Ejsmond 2008). In addition, four automatic cameras (Bushnell Trophy Cam) were placed in each plot, close to nests to identify predators and were moved to another nest when the focal nest was predated. Automatic camera systems have been used extensively to identify potential predator species (Laurance and Grant 1994). Thirty two pictures of predators were obtained and were used to confirm the identification marks appearing on the plaster moulds.

Predation rate in each plot was defined as the proportion of nests predated in each plot, after the two week exposure period. An individual nest was considered predated if any of the eggs was damaged or lost.

Rabbit abundance

Rabbit abundances in the study area are highly variable and depend mainly on social factors and on the availability of appropriate locations for the establishment of warrens (Barrio et al. 2011). We conducted four independent walking transects 500 m long and 2 m wide within each plot, counting the number of latrines per km (Calvete et al. 2006). A latrine was defined as an accumulation of 20 or more pellets on a surface of 20 × 30 cm (Virgos et al. 2003). Latrine abundance and rabbit density estimated by direct observations are highly correlated (Gil-Sanchez et al. 2011) and latrine counts have been commonly used to estimate rabbit abundance in Southern Spain (Guerrero-Casado et al. 2013b). We calculated a Kilometric Abundance Index (KAI) for each plot using the number of rabbit latrines per kilometre of transect.

Landscape variables

Nest predation can be influenced by local factors, such as the presence of hedges, ditches or roads, which increase habitat heterogeneity (Chalfoun et al. 2002b; Whittingham and Evans 2004; Zuria et al. 2007; Castro-Caro et al. 2014b). This effect was accounted for by measuring the distance from each nest to the nearest hedge or ditch, and to the nearest road using ArcGIS 9.3.1 (ESRI Inc, Redlands, CA, USA) (Table 1).

Table 1. Means and 95% CIs of each explanatory variable in each plot. Rabbit abundance was calculated per plot, based on four transects. Distances to hedges/ditches and to roads were calculated for each nest, and averaged per plot (number of nests sampled in each plot is also indicated).

Plot	Nr nests	Rabbit abundance (KAI) (latrine/km)			Distance to hegde/ditch(m)			Distance to road (m)		
		Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
Plot 1	32	51.8	1.0	102.6	117.7	76.9	158.5	119.6	78.2	161.1
Plot 2	28	88.1	1.8	174.4	66.8	42.0	91.5	122.7	77.3	168.2
Plot 3	32	5.8	0.1	11.5	136.2	89.0	183.4	229.3	149.9	308.8
Plot 4	32	1.1	0.0	2.2	788.1	515.0	1061.2	504.9	329.9	679.8
Plot 5	32	30.8	0.6	61.0	138.8	90.7	186.9	410.9	268.5	553.2
Plot 6	24	20.1	0.4	39.8	183.8	110.3	257.3	151.6	90.9	212.3
Plot 7	23	26.4	0.5	52.3	386.8	228.7	544.9	58.6	34.7	82.6

Statistical analyses

Chi^2 tests were used to compare the percentages of nests predated by different groups of predators, for different nest locations (ground or tree nests), in areas with high or low rabbit abundance. Plots with rabbit abundance (KAI values) higher or equal to the median value of KAI across all plots, were classified as having ‘high rabbit abundance’ (4 plots); other plots were classified as ‘low rabbit abundance’ (3 plots).

The relationship between rabbit abundance (KAI) and nest predation at the plot level was assessed using Generalized Linear Models (GLM), where the response variable was the proportion of nests that had been predated out of the total number of nests in each plot. We used a binomial distribution with a logit link, and rabbit abundance at each plot was included as the predictor variable.

To evaluate the factors affecting the probability of predation for each nest, we used Generalised Linear Mixed Models (GLMM), in which ‘plot’ was included as a random effect. In this model, rabbit abundance, nest location (ground or tree), the distance to the nearest road and the distance to the hedge/ditch were included as explanatory variables. The dependent binomial variable used in the model was whether a nest had been partially or totally predated (‘1’; at least one egg had signs of predation) or not (‘0’). We used a binomial distribution function, with a logit-link function. We performed the full arrangement of models (all possible combinations), and model selection was performed through a best subset approach using the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). The generated models were ranked according to AICc values, where the model with the lowest AICc was considered as the best one. We also report the ΔAICc value in order to compare the difference between each candidate model and the best model. Statistical analyses were performed using R 3.1.0 (R Core Team 2014).

Results

Rabbit abundance (KAI) in the study plots ranged from 1.14–88.14 latrines/km (median= 26.43, n = 7 plots). 109 out of the 203 nests showed signs of predation (53.69%); 51 of these had at least one egg with signs of predation, while in 58 nests all eggs were predated. 60 of the predated artificial nests were located on the ground, and 49 were located on trees.

Nineteen species of predators were identified as nest predators and were clustered into 6 groups (Table 2). For 25 nests it was not possible to identify the predator (22.94%, 17 ground nests and 8 tree nests). At high rabbit densities, the most frequent ground nest predators belonged to the carnivore group, accounting for 47.6% of the predated nests (carnivores vs. others, $\chi 2 = 32.6$, df = 1, $p < 0.01$), whereas most of the tree nests were depredated by rodents (95.8% of the depredated nests) (rodent vs. others, $\chi 2 = 124$, df = 1, $p < 0.001$). At low rabbit abundance ground nests suffered similar predation by carnivores, reptiles, birds and rodents (25%), whereas in tree nests the most frequent predators were rodents (83%; rodents vs. others, $\chi 2 = 89$, df = 1, $p < 0.001$) (Fig. 1).

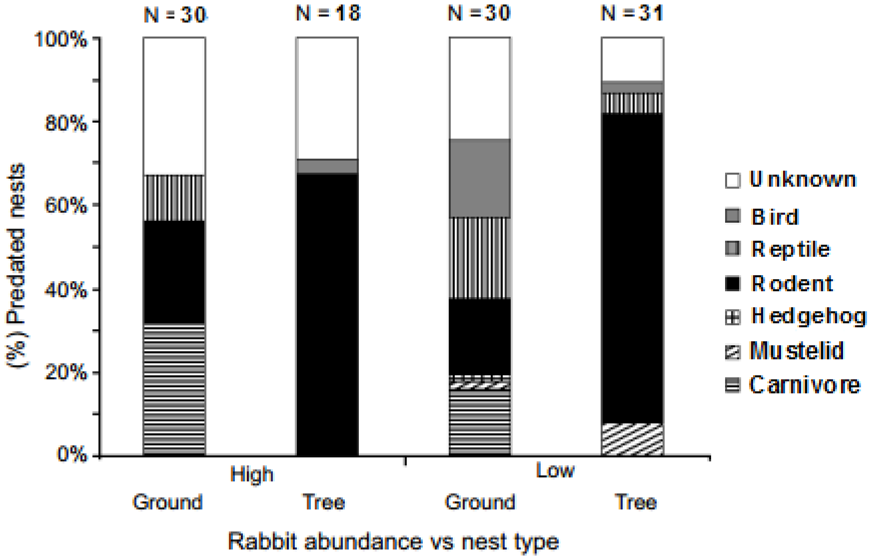

Figure 1. Percentage of nests predated by each predator group, at high and low rabbit abundance and at each nest location (ground vs. tree). Sample sizes are presented above bars.

Table 2. List of predator species detected on artificial nests. 19 species of predators were identified, belonging to 6 groups. Identification of predators was based on pictures, bite marks on artificial eggs or both. Nests were located either on the ground or on trees.

Predator group	Species	Pictures or marks on artificial eggs	Ground	Tree
Carnivores	*Vulpes vulpes*	Both	X	
	Canis familiaris	Both	X	
	Felis catus	Both	X	
	Meles meles	Marks	X	

	Genetta genetta	Both	X	
Rodents	*Rattus norvegicus*	Both	X	X
	Eliomys quercinus	Both	X	X
	Apodemus sylvaticus	Marks	X	X
Reptiles	*Lacerta lepida*	Both	X	
	Rhinechis scalaris	Marks	X	X
	Malpolon monspessulanus	Both	X	
	Hemorrhois hippocrepis	Marks	X	X
Hedgehog	*Erinaceus europaeus*	Both	X	
Corvids	*Pica pica*	Both	X	X
	Cyanopica cyanus	Picture		X
	Corvus corax	Picture	X	
Mustelids	*Mustela nivalis*	Marks	X	X
	Mustela putorius	Marks	X	
	Martes foina	Both	X	X

Nest predation at the plot level was positively associated to rabbit abundance, as measured with latrine counts (GLM, z-value 3.939, p=0.000; Fig. 2). Rabbit abundance explained 55.99% of the variation in nest predation (pseudo-R^2; Zuur et al 2009).

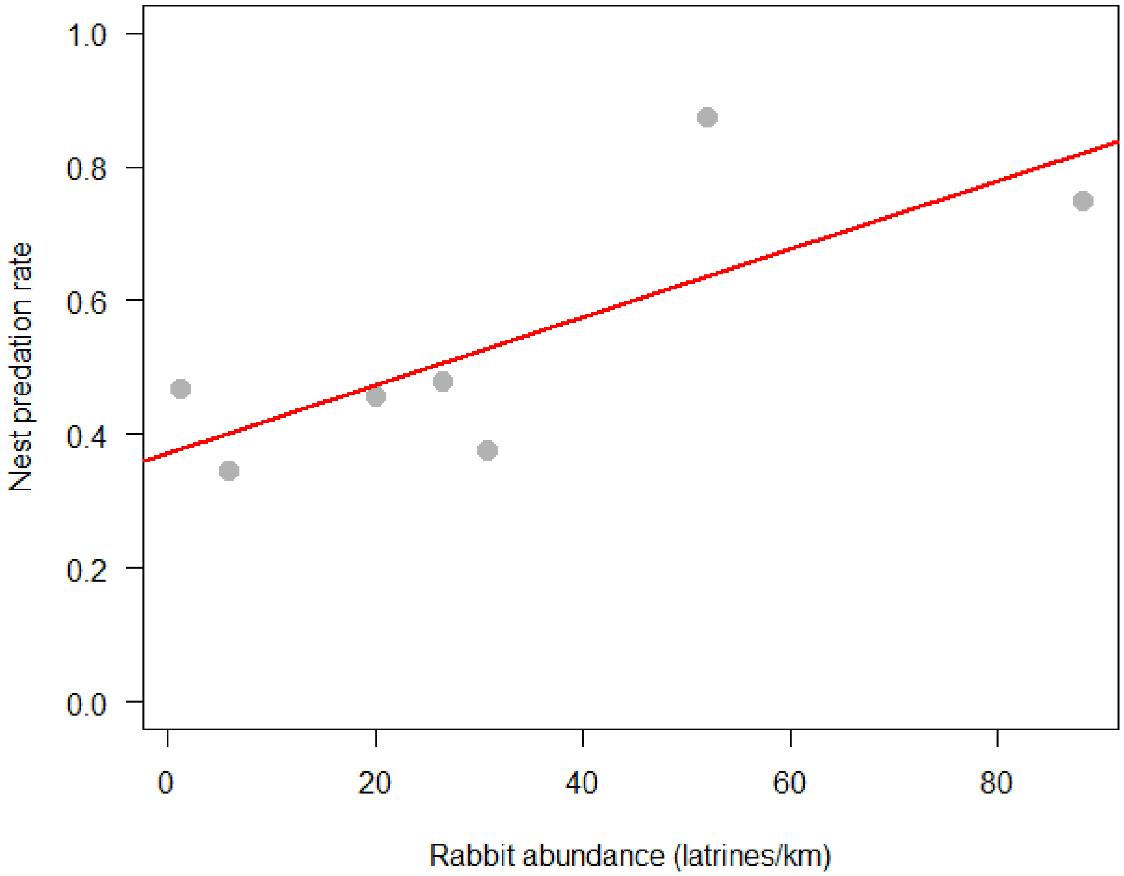

Figure 2. Relationship between nest predation at the plot level (proportion of nests predated in each of the seven study plots) and rabbit abundance, as estimated with latrine counts along transects.

The best candidate model explaining the probability of artificial nest predation included rabbit abundance and nest location (Table 3), where both variables were significant and acted in an additive manner (Table 4). Nests located on trees suffered lower probabilities of predation than ground nests, while the abundance of rabbits showed a positive relationship with nest predation for both nest locations (Fig. 2).

Table 3. Candidate models explaining factors affecting the probability of nest predation. The full model included as predictors rabbit abundance (KAI rabbit), nest location, distance to roads and distance to hedges or ditches. All models include plot as a random factor, and an intercept. The number of model parameters (k), the Akaike information criteria for small sample size (AICc), the difference between each model and the best model (ΔAICc), and Akaike weight are presented.

Candidate models	k	AICc	ΔAICc	Akaike weight
KAI rabbit + Nest location	4	261.8	0.00	0.337

KAI rabbit + Nest location + Distance to road	5	263.0	1.17	0.188
KAI rabbit + Nest location + Distance to hedge-ditch	5	263.7	1.89	0.131
KAI rabbit + Nest location + Distance to hedge-ditch + Distance to road	6	264.5	2.63	0.091
Nest location + Distance to road	4	265.3	3.49	0.059
Nest location	3	265.9	4.03	0.045
KAI rabbit	3	266.4	4.58	0.034
Nest location + Distance to hedge-ditch	4	266.9	5.02	0.027
Nest location + Distance to hedge-ditch + Distance to road	5	267.2	5.31	0.024
KAI rabbit + Distance to road	4	267.4	5.56	0.021
KAI rabbit + Distance to hedge-ditch	4	268.2	6.41	0.014
KAI rabbit + Distance to hedge-ditch + Distance to road	5	268.7	6.88	0.011
Distance to road	3	269.3	7.45	0.008
NULL	2	270.1	8.31	0.005
Distance to hedge-ditch + Distance to road	4	271.2	9.36	0.003
Distance to hedge-ditch	3	271.3	9.42	0.003

Table 4. Best model (AICc criteria, following the guidelines of Burnham and Anderson 2002) for the probability of nest predation. The model includes plot as a random effect. The reference level for the variable 'nest location' is ground nests.

Variable	Estimate ± S.E.	*z-value*	p-value
Intercept	-0.180 ± 0.353	-0.510	0.610
Nest location – tree	-0.787 ± 0.309	-2.546	0.011
KAI rabbit	0.025 ± 0.008	3.028	0.002

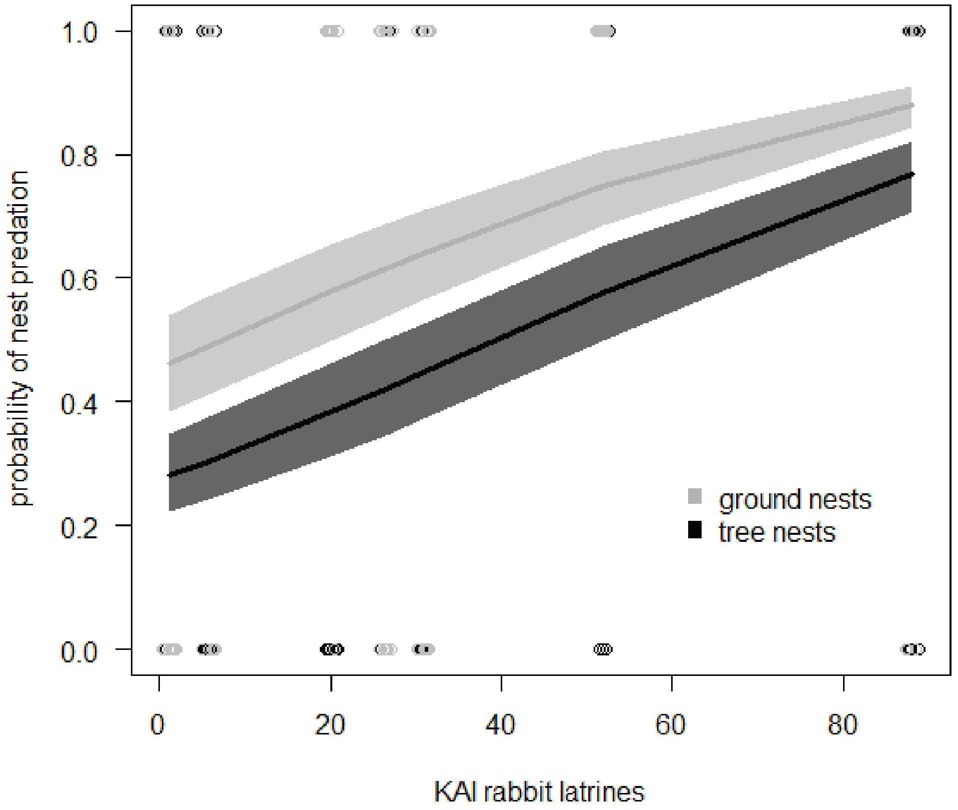

Figure 3. Probability of predation for individual nests on the ground (light grey) or on trees (dark grey), as a function of rabbit abundance (KAI, in latrines/km). Raw values for each nest, either predated (1) or not (0) are also shown, with random noise added to KAI values (horizontal spread) for ease of visualization

Discussion

In this paper, we demonstrate the indirect effects of a main prey species (rabbits) on a secondary prey species (farmland birds), mediated by their common predators. Although only one season was sampled, our results show that the highest abundances of rabbits were related to higher rates of nest predation at the plot level, and to higher probability of nest predation when considering individual nests. These results are consistent with other studies that have noticed that rabbits can attract a greater number of predators (Delibes-Mateos et al. 2007). Interestingly, we found a trend for a higher diversity of predators affecting the experimental nests at lower rabbit abundances. This was true for both ground and tree nests, where we detected twice the number of types of predators at low compared to high rabbit abundances (Fig. 1). This may be due to the presence of opportunistic predators such as foxes or feral dogs and cats when rabbit abundance is high, which adversely affect other predators like lizards (Olsson et al.

2005), mustelids (Hobbs 2001) or other mesopredators (Moseby et al. 2012). The increase in mesopredator abundance is experienced by species in the next lower trophic level in the form of higher predation rates, which can in turn cause songbird populations to decline and can potentially alter the structure of the community (Schmidt 2003). Our results agree with other studies that also show corvids and rodents to be the most active tree nest predators (Castro-Caro et al. 2014b), whereas ground nest predation is mainly perpetrated by mammals (Soderstrom et al. 1998; Vanderwerf 2009), which are also the main predators of rabbits (Delibes-Mateos et al. 2007).

The high predation rates found in this paper agree with previous reports also showing high nest predation in farmland habitats (Bayne and Hobson 1997; Donald et al. 2006). Our results show predation rates on nests placed on the ground that were 20% higher than those on tree nests, similar to what was found by Castro-Caro *et al.* (2014b). This may be due to the extreme simplification of the intensive agricultural landscape, in which the natural vegetation including the herbaceous cover has been almost completely eliminated (Barrio et al. 2013; Castro-Caro et al. 2014a), and this may increase the risk of predation of nests located on the ground (Castro-Caro et al. 2014b). The presence of rabbits may also have a detrimental effect on ground nests owing to the fact that they attract terrestrial predators, mainly mammals, which also have a great impact on the nests placed on the ground (Soderstrom et al. 1998; Schmidt 2003). Some previous studies have reported a relationship between nest predation rate and the distance to roads, hedges or ditches (Soderstrom et al. 1998). However, we did not find any significant effect associated with these variables, which may once again be due to the simplicity of the olive tree orchards in which predators can easily move anywhere on compact, clear and easy-to-walk-on bare ground.

Mediterranean ecosystems have a major importance in conservation biology owing to their high biodiversity (Myers et al. 2000), particularly in the case of birds (Tucker and Heath 1994). We observed a positive relationship between nest predation rate and rabbit abundance. A density-dependent relationship might be caused by the opportunistic nature of certain predators such as Red foxes *Vulpes vulpes* (Delibes-Mateos et al. 2008c), which may negatively affect breeding birds in agroecosystems (but see Kujawa and Łęcki 2008). Agricultural intensification is a major cause of the declines in farmland biodiversity in Europe (Benton et al. 2003). Studies such as those by Donald *et al.* (2001) or Teyssèdre and Couvet (2007) have shown an overall decrease in the diversity of farmland birds as the result of an intensification and expansion of agricultural practices. The high nest predation rates in agroecosystems (Bayne and Hobson 1997; Donald et al. 2006), mean that hyperpredation processes should be considered when designing conservation measures to prevent the excessive nest predation of farmland birds (Courchamp et al. 2000). We suggest that conservation efforts for farmland birds should avoid areas with a potential negative effect owing to the phenomenon of hyperpredation, as may be the case in areas with high rabbit abundance.

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Capítulo 2.2

La influencia de la densidad de nidificación en la depredación en olivares depende de las características del hábitat

Carpio A.J., Castro-Caro, J.C., Tortosa, F.S. (2016). **Influence of nest density on nest predation depends on habitat features.** *Ardeola*, *63(2),* 237-250.

Resumen

La simplificación y homogeneización de los paisajes agrícolas ha llevado a pérdidas dramáticas de la biodiversidad agrícola. Esto incluye las poblaciones de paseriformes, y uno de los mecanismos que puede contribuir a esto sería el aumento de la depredación de nidos. Las cubiertas del suelo son una de las medidas agroambientales, cuyo objetivo es detener la pérdida de biodiversidad mediante la creación de parches de hábitat de alta calidad integrados en un paisaje homogéneo mediante el mantenimiento de la cubierta vegetal herbácea en los cultivos. Sin embargo, aunque estos parches de buena calidad del hábitat son los preferidos por las aves para criar, podrían también atraer a los depredadores, y un incremento de la densidad de nidos en estos pequeños parches podría dar lugar a un aumento de las tasas de depredación. Por ello, hemos realizado experimentos de depredación de nidos con nidos artificiales con el fin de investigar si el efecto de la cobertura del suelo sobre la depredación de nidos es dependiente de la densidad. Los experimentos se llevaron a cabo durante la temporada de cría en 2014, en dos zonas del sur de España. Se han utilizado dos niveles de densidad de nidos, ya sea en olivares con cubierta o con suelo desnudo. Un total de 420 nidos fueron colocados, de los cuales 226 fueron depredados (53.81%). Nuestros resultados mostraron que 1) En olivares con cubierta la depredación de nidos fue dependiente de la densidad de nidos solo al considerar los nidos de los árboles, mientras que no hubo depredación dependiente de la densidad en los olivares con suelo desnudo en nidos de suelo ni de árboles, y 2) los nidos artificiales colocados en el suelo fueron depredados con más frecuencia (65%) que los colocados en los árboles (29%), con independencia de la presencia de cubierta vegetal o el nivel de densidad de nidos. Este estudio sugiere que las variaciones en los patrones de depredación de nidos están determinadas por la composición de especies de depredadores de nidos y sus comportamientos de forrajeo específicos en diferentes paisajes y hábitats, mientras que también pone de relieve la necesidad de implementar medidas agroambientales orientadas a la conservación de aves agrícolas.

Abstract

The simplification and homogenization of agricultural landscapes has led to dramatic losses of farmland biodiversity. This includes passerine populations, and one of the mechanisms that may be contributing toward this may be increased nest predation. Ground covers are agri-environmental measures whose objective is to halt the loss of biodiversity by creating high quality habitat patches embedded in a homogeneous landscape by maintaining herbaceous ground cover within crops. However, although these patches of good habitat quality are preferred by breeding birds, they could also attract predators, and an increased nest density in small habitat patches would thus result in increased predation rates. We have therefore performed nest predation experiments with artificial nests in order to investigate whether the effect of ground cover on nest predation is density dependent. The experiments were carried out during the breeding season in 2014, in two areas of southern Spain. We used two nest density levels in either ground-cover or bare-ground olive orchards. A total of 420 nests were placed, of which 226 were predated (53.81 %). Our results showed that 1) nest predation was density dependent in orchards with ground cover only when considering tree nests, while there was no density-dependent predation in bare-ground orchards in either ground or tree nests, and 2) artificial nests placed on the ground were more frequently predated (65%) than those placed in trees (29%), irrespective of either the presence of vegetation cover or nest density level. This study suggests that variations in patterns of nest predation are determined by the species composition of nest predators and their specific foraging behaviors in different landscapes and habitats, while it also underscores the need to implement agri-environmental measures in order to preserve the targeting of farmland birds.

Introduction

Many farmland songbirds have, in recent decades, undergone population declines in Europe (Donald et al. 2006). The degradation of farmland ecosystems has created an environment, in which prey populations might be more sensitive to predation, i.e., habitat change may interact with predation rates (Evans 2004). Nest predation is the primary cause of nest losses for a wide range of bird species in various habitats and at different geographic locations (Martin 1993; Schmidt and Whelan 1999), and has probably contributed to the decline in passerine populations in landscapes that have been heavily modified by agriculture and other human developments (Bayne and

Hobson 1997; Donovan et al. 1997; Willson et al. 2001; Kentie et al. 2015). For example, in Spain most farmland birds favour fallow fields for nesting; however, the intense use of herbicides or repeated ploughing there suggests that fallow fields are presently a rare habitat type and that the few favorable patches have high nest densities which attract predators and thus expose nests to very high predation rates (Pescador and Peris 2001; Sánchez-Oliver et al. 2014). A typical example is skylarks *Alauda arvensis*, which preferentially nest in set-aside fields, but suffer high nest predation rates owing to high nest densities in this habitat type (Donald 1999; Kuiper et al. 2015). This decoupling of habitat attractiveness from suitability may have led to the development of the 'ecological trap' concept (Battin 2004; Robertson and Hutto 2006).

Gates and Gysel (1978) proposed that increased nest density in small habitat patches results in increased predation rates. Nevertheless, there is a considerable debate as to whether nest predation is density dependent, and some studies report strong evidence for patterns of density dependent nest predation (Gunnarsson and Elmberg 2008), while others report weak density dependence (Clark and Wobeser 1997) or density-independent nest predation (Padysakova et al. 2010; Ringelman et al. 2012, 2014). Density dependent predation requires predators to assess and respond to spatial or temporal heterogeneity in resource (e.g., nest abundance) (Schmidt and Brown 1996). This response may be functional (e.g., an increased foraging time for nests; Holt and Kotler 1987), numerical (e.g., aggregation toward patches of higher nest density: Holt 1977), or psychological (e.g., search image formation, Morgan and Brown 1996). Nevertheless, the effect of predators on nest predation depends on their searching behavior (Cornell 1976), and medium-sized generalist predators (e.g., foxes, feral dogs or corvids) are therefore most likely to exhibit density dependent nest predation because only they have sufficiently large home ranges and daily movements to be able to detect and respond to differences in nest density.

In the Mediterranean Basin, olive orchards are one of the primary agro-ecosystems and they are important wintering and breeding areas for numerous European bird species (Rey 2011). In recent decades, agricultural intensification and other changes in land use have led to significant negative environmental consequences including water pollution, and particularly soil erosion (Gómez et al. 2009a). However, many farmers are now preventing erosion by maintaining (or implementing) vegetation cover within crops, which likely increases and provides structural complexity and resources for foraging birds (Wilson et al. 1999; Vickery et al. 2009). For instance, Castro-Caro *et al.* (2014a) have shown that increased vegetation cover is correlated with increasing abundance and richness of songbirds in the olive groves of southern Spain. In addition, breeding birds select their territories in olive orchards according to the availability of food resources such as seeds and arthropods (Muñoz Cobo et al. 2009). As a result, birds prefer to settle in fields with vegetation cover, and songbird density in these fields can be at least twice as high as that which occurs on bare-ground in conventional olive groves (Muñoz-Cobo et al. 2009; Castro-Caro et al. 2014a). Hence, in these good-quality orchards (olive groves with vegetation cover) nest density is expected to be higher in comparison to that of bare-ground orchards. According to theoretical models (see patch use theory; Stephens and Krebs 1986) the foraging effort of predators may be directed towards those patches with the highest availability of cumulative prey. However, predators' response to heterogeneity in nest abundance may also be influenced by additional ecological variables, such as the abundance and distribution of alternative resources within the environment. For instance, Castro-Caro *et al.* (2014b) have shown that vegetation cover in olive groves enhances breeding success by reducing nest predation because of a greater diversity of either predators or microhabitats (Castro-Caro et al. 2014b), but it is still not known whether the effect of such vegetation cover on nest predation is density dependent.

Since patches of good quality habitat are scattered within a matrix of bare-ground olive monoculture, bird abundance and nest density are expected to be higher in these patches (Castro et al. 2014a). The question of how nest predation might respond to such an increase in nest density therefore arises. In the present study, we asses whether the effect of ground cover on nest predation is density dependent in the olive orchards of southern Spain by using artificial ground and trees nests. Quail eggs have been useful as regards estimating the spatial variation in nest failure risk for ground-nesting passerines (Cortés-Avizanda et al. 2009; Vögeli et al. 2011). The aim of this work is to test how nest abundance affects nest predation rate in two different olive farming practices (bare ground vs ground cover), predicting that nest predation will increase with increasing nest density. We also use previous research into nest predation rates in different habitats and landscapes (Gunnarsson and Elmberg 2008; Ringelman et al. 2014) as a basis to predict that predation rates will be higher in ground than in tree nests.

Material and methods

Study area and study design

The study was conducted in 2014 on five study sites in Southern Spain from mid April to early June, coinciding with the breeding period of the most common nesting species birds in the area (Muñoz-Cobo et al. 2001). Three study sites were located in Villa del Río (37° 58' N, 4° 17' W), while another two were located in Montilla (37° 34' N, 4 ° 37' W), Córdoba province. All sites were embedded in an olive-dominated landscape, in which agricultural intensification has eliminated most of the natural vegetation (Rey 2011). A more detailed description of the study area is provided by Castro-Caro *et al.* (2014b). Two independent plots (between 3.9-6.9 ha) were selected on each site (between 8.4-11.7 ha), one with vegetation cover and the other with bare ground (Table 1). There was a distance of at least 500 m between the plots (average = 960 ± 297 m, range 510-1200 m). In ground cover plots the herbaceous ground cover comprised spontaneous annual species that are adapted to the Mediterranean climate and set their seeds before the summer drought. Cover was present throughout the groves except in the area below tree crowns, which was kept plant-free by the application of contact and systemic herbicides. The amount of ground covered by grass cover varied among plots (ranging 50-75%). Ground cover was not mown or grazed during the experiment. All experimental plots were olive orchards that were managed using conventional olive-grove farming practices and were selected at random, although an effort was made to choose olive groves of the same age and tree density. All of the olive orchards had trees >100 years old at a density of ~ 100 trees/ha, and were subjected to the same pruning schemes. The community of tree-nesters in the olive groves studied was dominated by cardueline finches, and principally the european serin *Serinus serinus*, the european greenfinch *Carduelis chloris* and the common linnet *Carduelis cannabina*, while the ground-nester communities were dominated by crested larks *Galerida cristata* and woodlarks *Lullula arborea* (Muñoz-Cobo et al. 2009; Castro-Caro et al. 2014a).

The assemblage of potential nest predators includes corvids such as common ravens *Corvus corax*, and, in a few plots, azure-winged magpies *Cyanopica cyanus*. No common magpies, *Pica pica*, were found in the area. The most common mammalian carnivores are the red fox *Vulpes vulpes*, feral dogs and cats (Castro-Caro et al. 2014). Small mammals have been reported to be one of the main predator guilds of nests (e.g., rats *Rattus sp.* and garden dormouse *Eliomys quercinus*; Gil-Delgado et al. 2010).

Nest predation experiment

The artificial nests used resembled those of crested larks, which build ground nests, and serins, which build open cup nests on the outer parts of olive tree branches. Both bird species breed in olive agro-ecosystems in Spain; their breeding season extends from March to early June, and two or three broods per year are common. The clutch size for crested larks ranges between three and seven eggs, while it is between two and five for serins. The incubation time is around 13 days for both species (Cramp and Perrins 1994).

A total of 420 nests were placed on the 10 plots on the five study sites, of which 210 (630 eggs) were located on the ground and 210 (630 eggs) were located in trees. We used two densities either on plots with vegetation cover or in bare ground: high nest density (Nº nests/ha ranged from 9.8 to 13.5) or low nest density (Nº nests/ha ranged from 4.6 to 5.9; Table 1). The nests were placed in a 50 x 50 m grid on plots with low nest densities, while in the case of high density the nests were placed in a 30 x 30 m grid. In both cases, the nests were placed in alternating positions (tree and ground nests alternated in the grid nodes, following Ludwig et al. 2012). Ground nests were placed in a small hollow dug in the ground at the border of the tree canopies and were oriented toward the north, while tree nests were fixed to branches at a height of about 2 m and oriented randomly. The nests were exposed to predators for a two-week period and were controlled every three or four days. The first period of exposure took place in the study site of Villa del Río from 18 April to 2 May, the second period was in Montilla from 6 to 20 May and the third period was in Villa del Río again, from 23 May to 6 June. A nest was considered to have been predated if any of the eggs were damaged or lost. The nest predation rate was estimated as the percentage of the nests predated on each plot.

Table 1. Plot size, number of nests per plot, nest density (number of nests per ha) and date of nest exposure in each of the plots on the study sites. High: plot with high nest density; Low: plot with low nest density; VC: plot with vegetation cover; BG: plot with bare ground cover. Date of nest exposure: (1) 18th April – 2nd May; (2) 6th May – 20th May, and (3) 23th May – 6th June.

Study site	Plot	Plot size (ha)	Nº Nests	Nests/ha	Exposure period
Montilla A	High-VC	4.94	52	10.5	6 May to 20 May
	High-BG	4.22	48	11.3	6 May to 20 May

Montilla B	Low-VC	5.93	32	5.4	6 May to 20 May
	Low-BG	4.51	24	5.1	6 May to 20 May
Villa del Río A	High-VC	3.86	52	13.5	18 April to 2 May
	High-BG	5.31	52	9.8	18 April to 2 May
Villa del Río B	High-VC	4.41	48	10.9	23 May to 6 June
	High-BG	4.07	52	12.8	23 May to 6 June
Villa del Río C	Low-VC	6.96	32	4.6	23 May to 6 June
	Low-BG	4.76	28	5.9	23 May to 6 June

Artificial nests were used in order to overcome the extreme difficulty of finding real nests in the study area (Castro-Caro, unpublished data), thereby obtaining sufficiently large sample sizes to test the ecological hypothesis. The use of artificial nests is an indirect method by which to estimate the impact of predation and has been widely used in bird studies (Zannete 2002; Beja et al. 2014). We used commercially available open-cup nests made of hempen braid that were 8 cm in diameter and 5 cm deep. The nests were exposed to the weather for at least 14 days before use in order to dispel any artificial scent (Zuria et al. 2007). In each nest we placed three quail *Coturnix coturnix* eggs, two of which were unmanipulated and the third of which had been emptied and injected with plaster, thus ensuring that the three eggs had the same external appearance (Yanes and Suárez 1997) and that the plaster eggs could be used to identify teeth marks left by the predator (Major et al. 1991; Willson et al. 2001; Carpio et al. 2014c). Latex gloves and clean footwear were used during the placing of the nests in order to prevent scents that might be attractive to predators (Beja et al. 2014). Predators were identified by means of marks on the eggs filled with plaster (Carpio et al. 2014c). In addition, four automatic cameras were placed on each plot to identify predators and were moved to another nest if the nest was predated. Automatic camera systems have been extensively employed to identify potential predator species (Laurance and Grant 1994). Photographic evidence was used to confirm the identification based on marks on the plaster moulds (Herranz et al. 2002); identification was correct in 100% of cases.

Statistical analysis

Predation level of a plot or nests inside each plot may be influenced by the presence of landscape features that promote landscape heterogeneity, such as hedges, ditches or roads (Zuria et al. 2007). To account for these effects we calculated the distance from each nest to the nearest hedge, ditch and road using ArcGIS 9.3. (Cox et al. 2012).

Chi^2 tests were used to compare nest predation by each predator group (rodents, carnivores, reptiles, corvids, mustelids and hedgehod) depending on the nest density (high vs. low), the type of nest (ground vs. tree), and the vegetation cover (ground cover vs. bare ground). The relationships between the level of nest predation and the various experimental factors were evaluated using generalized linear mixed models, in which 'site' was always considered to be a random factor and plots were nested within sites. In this model, nest location (categorical as ground vs. tree), nest density (categorical as high vs. low), vegetation cover (categorical as ground cover vs. bare ground), distance to road and distance to hedge-ditch were included as explanatory variables. The dependent variable used in the model was whether or not each individual nest was predated (totally or partially predated) *vs.* not predated. We used a binomial distribution, with a logit-link function.

Because stepwise selection can have important shortcomings (Whittingham et al. 2006), we further applied a best subset analyses to the GLMM. AICc was used to rank the candidate models, with the best fitting model presenting the smallest AICc. The difference between the obtained AICc value for each model (AICc_i) and the minimum AICc model (AICc_{min}) was calculated (ΔAICc), and the best set of models was obtained by considering the ones with $\Delta\text{AICc} < 10$. Models that differed in AICc by more than 10 were assumed to have no support (Burnham and Anderson 2002), and therefore we initially treated all models with $\Delta\text{AIC} \leq 10$ as candidate ones. Akaike model weights (*wi*) were used to evaluate the most parsimonious model (Burnham and Anderson 2002) (Appendix 1). The assumptions of normality, homogeneity and independence in the residuals were met in the model (Zuur et al. 2009). Statistical analyses were performed using InfoStat software (Balzarini et al. 2001).

Results

Of the 420 nests, 226 were predated (53.81 %). The average number of depredated eggs per nest was 1.35 ± 0.08 (Mean ± S.D.). Nests placed on the ground were more frequently predated (65.23% = 137 nests) than those placed in trees (42.38% = 89 nests).

When we compare the proportion of nest failure due to the different predators, we found that the principal predator of the nests located in trees were rodents (65% of total predation, $Chi^2 = 23.23$, df = 6, $P < 0.001$). In contrast, ground nests showed no differences in relation to the proportion of nest failure by different predators ($Chi^2 = 1.75$, df = 6, $P = 0.107$). With regard to the treatment of vegetation cover, in both cases (ground cover vs. bare ground) rodents proved to be the main predator (27% and 44.5% of nests predated respectively, vs. carnivores 13.6% and 16.7%, corvids 5.1% and 11.1%, lizards 13.6% and 7.4%, hedgehogs 5.1% and 1.9%, mustelids 13.6% and 7.4% and snakes 22% and 11.1%, $Chi^2 = 3.84$, df =6, $P < 0.001$ and $Chi^2 = 4.65$, df = 6, $P < 0.001$). Finally for the treatment of nest density, in both cases (high density vs. low density) significantly more nests were predated by rodents than by others predators groups ($Chi^2 = 24.54$, df = 6, $P < 0,001$ and $Chi^2 = 4.49$, df = 6, $P < 0.001$ respectively). (Figure 1).

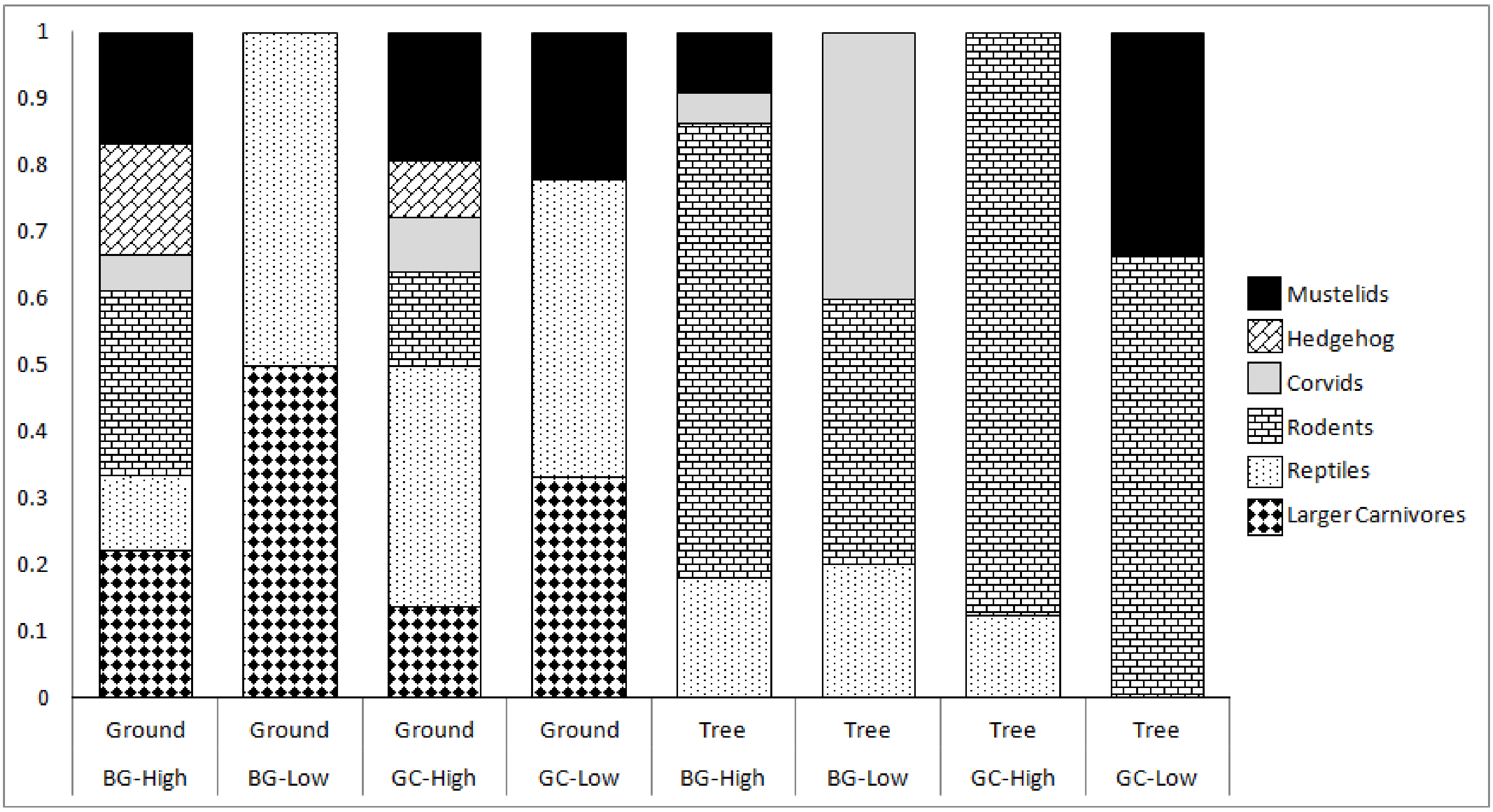

Figure 1. Percentage of nest predation by each predator group for each nest type (Ground vs. Tree), each cover type (GC: Ground cover vs. BG: Bare ground), and each nest density (High vs. Low).

In the analysis of factors influencing predation rates the full model proved to be the best model (although other two models were similar; ΔAIC ≤ 2), in which only nest location, the interaction ``vegetation cover * nest density´´, ``vegetation cover * nest location´´ and triple interactions were significant (Table 2). We found that ground nests were frequently more predated than tree nests. Even if nest density itself was not significant, we found a negative effect on predation rate when interacting with the vegetation cover and nest location. (Figure 2, Table 2). The interaction shows that when there is ground cover, nests in low density are predate more frequently that nests in high density, the difference being much more marked for tree nests, whereas no differences in predation rate between high and low density were found for either ground or tree nests placed in bare ground plots.

Table 2. Best model for nest predation, according the AICc value, following the guidelines of Burnham and Anderson (2002). Coefficients for the fixed factors were calculated using reference values of "bare ground" in the variable "cover vegetation"

“ground” in “nest type”, and “high density” in “nest density”. The SD of the intercepts was “0.34”.

Predated nests				
Variable	*F*	*df*	*P*	Coefficient ± S.E.
Cover vegetation	0.19	1	n.s.	-0.94 ± 0.29
Nest type	96.02	1	<0.001	-2.16 ± 0.24
Nest density	0.85	1	n.s.	0.94 ± 0.6
Distance to road	1.48	1	n.s.	-0.03 ± -0.015
Distance to Hedge - Ditch	3.44	1	0.06	-0.011 ± -0.007
Cover * Nest density	9.14	1	<0.01	
Nest type * Nest density	0.05	1	n.s.	
Cover* Nest type	7.28	1	<0.01	
Cover*Nest type*Nest density	4.21	1	<0.05	

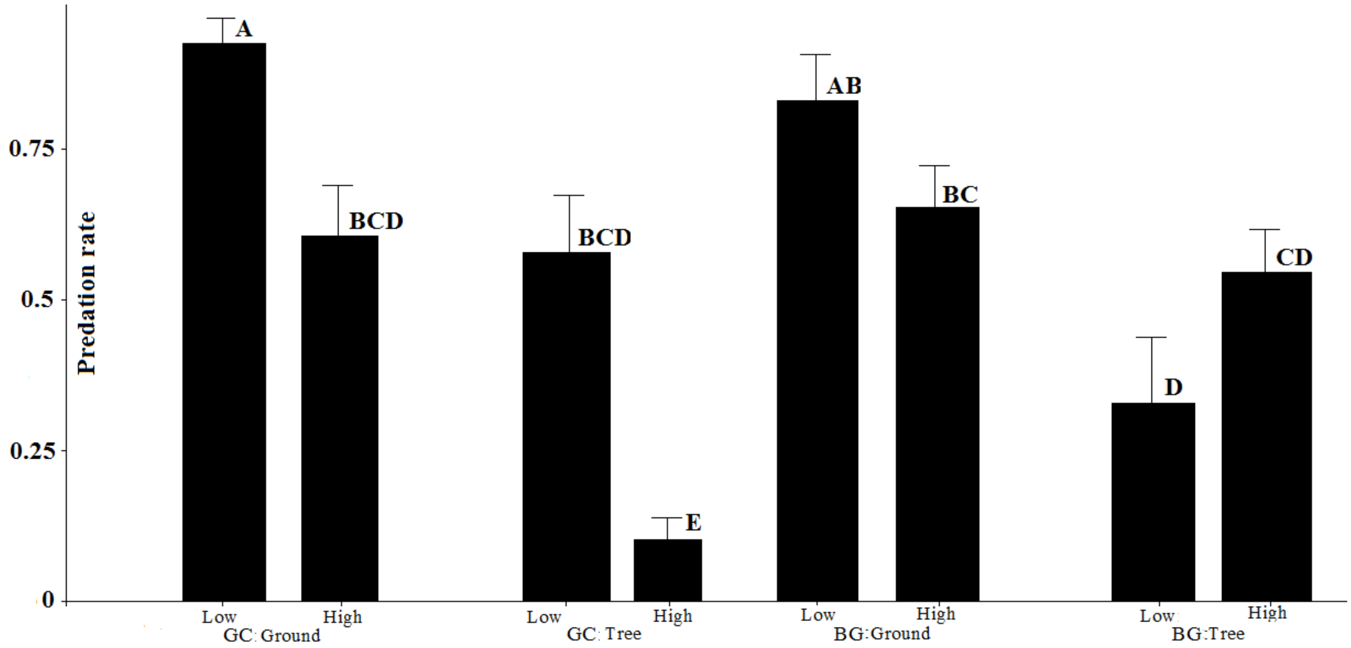

Figure 2. Predation rate (between 0 = not predated and 1 = predated) as a function of the interaction between nest density (Low = low density and High = high density), vegetation cover (GC = Ground cover and BG = Bare ground) and nest type (Ground or Tree). Means with common letter are not significantly different (p> 0.05).

Discussion

Predation rates on artificial nests is likely to be different to that on natural nest in absolute terms (Berry and Lill 2003), but can provide an accurate index of predation risk relative to the factors under investigation (Andrén 1995; Reitsma and Whelan 2000). Our results show that nest predation was not directly affected by nest density or ground cover. However we found significant effects on predation when both factors interact as well as with the triple interaction with nest type. Predation was affected by nest density in olive groves with ground cover (this being particularly marked in tree nests). In contrast, nest predation did not show any relationship with the density on bare-ground in either ground or tree nests. Nevertheless, our results show that this dependence relationship, is inverse; that is, nest predation rates were inversely related to nest density, a result that is contrary to the general assumption that nest predation rates increase with nest density (Gunnarsson and Elmberg 2008). However, behavioral-ecological theory predicts many possible anti-predator benefits to nesting in a group of conspecifics. Ringelman *et al.* (2014) demonstrated that mallard nests with closer nearest neighbours were more likely to be successful. For example, since many nest predators would become satiated after (or even before) consuming the large number of eggs (up to nine) in a single mallard nest (Ackerman et al. 2004), the per capita risk of predation might be diluted by nesting near other ducks. In our study, the main predators in tree nests were rodents (e.g., rats and dormice), which could be satiated after consuming quail eggs (up to two natural eggs per nest). In addition, according to the 'Optimal foraging theory' (Charnov 1976; Stephens and Krebs 1986), the feeding behavior and search for food of different predators depends on the density of a prey type. Predators' food and dietary selection are conditioned by the ease with which they can consume high quality and easy to capture prey, thus implying an increase in nutritional value while reducing the energetic costs of capture and thereby maximizing intake rates (Krebs et al. 1977). The main factors that will influence predators' preference for a type of diet will therefore be the density of each available prey type and the time needed for search and capture these prey (Charnov 1976). If the quantity of one prey type greatly increases in a given habitat, predation does not increase equally, since the time needed to capture each prey will limit search time for predation (or at least in the case of smaller predators) (Charnov 1976; Křivan and Vrkoč 2004).

A greater number of nests will constrain the time needed to prey upon each one, thus decreasing the proportion of predated nests, and increasing the probability of survival of each individual nest thanks to a dilution effect of predation (Ringelman et al. 2014). In our system, the fitness benefits of nesting at higher density appear to outweigh the potential risks. Understanding the foraging methods of predators and the fitness costs and benefits of nest dispersion may not only help us better understand the driving factors that impact on nest success for those species of management concern, but might also provide an explanation for the apparently contradictory patterns of density-dependent nest predation reported among sites (Rigelman et al. 2014).

Artificial nests placed on the ground were more frequently predated than those placed in trees irrespective of either the presence of vegetation cover or nest density level. Overall, this result agrees with established patterns of nest predation noted in literature (e.g., Wilcove 1985; Melampy et al. 1999), which postulates that ground nests have higher rates of predation because of the presumed greater diversity of ground predators (Figure 1). There was a clear difference between ground and tree nest predation. Our results agree with other studies which indicate that the major predation rates in trees correspond to rodents, while those on the ground principally correspond to carnivores (Söderström et al. 1998; Vanderwerf 2009) (Figure 1). Foxes and feral dogs have particularly been reported to exert a significant predatory pressure on some farmland species, particulary ground-nesting birds (Yanes and Suárez 1996; Pita et al. 2009). For these predators, an increased reward frequency probably reinforces search behavior (functional response). After depredating a nest, foxes are likely to employ area-restricted searches in order to locate additional nests (Seymour et al. 2003, 2004), because foxes do not become ‘satiated’ after depredating a single nest. Consequently, both search intensity and the proportion of nests lost as the result of predators should increase with the frequency or density of occupied nest sites (reward rate). Moreover, predators can enhance their search efficiency by specializing in prey types and learning search images (Lewis 1986). However, the lack of density-dependent predation in ground nests may be the result of a lack of response by these predators to differences in the range of nest densities, because the size of their home ranges and daily movements override the two levels of nest dispersion used in this study. In fact, Ringelman *et al.* (2014) reported that some nest predation patterns may result simply from differences in the spatial scale at which nest density was defined. Nevertheless, in spite of the considerable interest in density-dependent bird-nest predation, few studies have examined the spatial scale at which nest clustering naturally emerges (Ringelman et al. 2014).

Finally, we found a marginally significant effect of the distance of nests to structures such as hedgerows or streams, which adversely affected the rate of nest predation (Table 2.) Increased predation was observed in the nests closest to these structures. Some groups of predators, especially mammals, could use hedgerows as corridors and refuges, thus leading to an increase in the risk of the predation of nests closest to these remnants of natural vegetation (Söderström et al. 1998; Salek et al. 2009).

Although we did not survey or measure the nest predation of real nests, similar nest predation rates have been found on real tree-nests (56.60 %) in olive groves in the same area (Castro-Caro et al. in unpublished data) compared to ours (42.38 %), which highlight the suitability of artificial nests in this study.

Currently only a few farmers keep ground cover in olive orchards during the breeding season, which may attract most breeding song birds to the green spots. This may increase nest abundance in the favourable spots, thereby potentially creating an ecological trap due to the higher predator activity in the area (Robertson and Hutto

2006). However our results show that a increase in nest density did not increase predation, even more we found a decrease in predation rate at higher nest density.

In conclusion, herbaceous ground covers may effectively provide structural complexity and resourced for foraging birds (Castro-Caro et al. 2014b). However, they may not always be suitable for nesting birds as in the case that they can act as ecological traps. According to our results nest predation was density-dependent; that is, there were a higher nest predation rates at low density (4 nest/ha) for those nests placed on trees of ground-cover plots. Although we did not survey or measure nest density on real nests, this low density is likely to be closer to the real density of breeding songbird communities in olive groves (Gil-Delgado 1981) than high density we used in this study (11 nests/ha) which suggests that for tree-nesters plots with ground cover may be a sink rather than a source, while underscored the need of studies on predator communities to document the responses to spatial and temporal heterogeneity in resources (e.g. nests) to help design effective measures to promote biodiversity in Mediterranean farmland systems.

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Capítulo 2.3

Efecto de la depredación por jabalíes sobre nidos de aves en diferentes hábitats de Suecia

Carpio, A.J., Hillström, L., Tortosa, F.S. (2016). **Effects of wild boar predation on nests of wading birds in various Swedish habitats.** *European Journal Wildlife Research*, *62(4),* 423-430.

Resumen

En las últimas décadas, el jabalí ha sufrido una expansión en Europa, lo que puede haber afectado negativamente a las poblaciones de aves que anidan en el suelo y en particular a las aves limícolas. El objetivo de este estudio fue evaluar la depredación de nidos de aves limícolas por jabalíes en Suecia, donde esta especie ha estado aumentando desde su reintroducción. Esto se realizó colocando nidos artificiales en siete áreas de estudio diferentes. A continuación se hizo una comparación de las tasas de depredación de los nidos colocados en parcelas de control (áreas en las que no había jabalí, pero si otros depredadores) y parcelas con diferentes abundancias de jabalí. Contrariamente a lo que se esperaba, la proporción de nidos depredados fue significativamente menor en aquellas áreas donde el jabalí estaba presente, con una tasa de depredación del 54%, mientras que la tasa de depredación en las otras parcelas fue del 87.5%. El jabalí fue identificado como el segundo depredador de nidos más importante en las parcelas en las que estuvo presente, representando el 18% de los nidos depredados. El principal predador en ambos tipos de parcelas fue el zorro, que fue responsable del 28% y 38.5% de los nidos depredados en parcelas con y sin jabalí, respectivamente. Curiosamente, la depredación por tejones ocurrió principalmente en áreas donde el jabalí estaba ausente (34.5% de los nidos depredados), mientras que sólo un nido fue depredado por este predador en áreas con jabalí. Sin embargo, no es posible afirmar si la depredación de los tejones fue menor debido a la presencia de jabalí o si esto se debió al hecho de que los tejones no seleccionan esos parches debido a las características del hábitat.

Abstract

The wild boar has, over the past few decades, undergone an expansion in Europe, which may have negatively affected ground-nesting bird populations and particularly those of wading birds. The aim of this study was to evaluate predation on waders' nests by wild boar in Sweden where this species has been increasing since its reintroduction. This was done by placing artificial nests in seven different study areas. A comparison was then made of predation rates of the nests placed on control plots (areas in which no wild boar were present, but other predators were) and plots containing different abundances of wild boar. Contrary to our expectations, the proportion of nests predated was significantly lower in those areas in which wild boar were present, with a predation rate of 54 %, whereas the predation rate was 87.5 % in the others. The wild boar was identified as the second most important nest predator in the plots in which it was present, accounting for 18% of the predated nests. The main predator on both types of plots was the red fox, which was responsible for 28% and 38.5% of the predated nests on plots with/without wild boar, respectively. Interestingly, predation by badgers occurred principally in areas in which the wild boar was absent (34.5% of the predated nests), whereas only one nest was predated by this predator in areas containing wild boar. It is not, however, possible to state whether predation by badgers was lower because of the presence of wild boar or whether this was owing to the fact that badgers do not select those particular patches because of habitat features.

Introduction

The wild boar (*Sus scrofa*) has undergone a remarkable expansion in Europe during recent decades in terms of both population abundance (Acevedo et al. 2014) and distribution range (Massei et al. 2015). This species is currently the most widespread and most abundant wild ungulate in Europe (Apollonio et al. 2010), and is found on all continents except Antarctica. The increase in the abundance of wild boar has led to conflicts such as traffic accidents (Lagos et al. 2012), agriculture damage (Herrero et al. 2006), conservation problems (Bueno et al. 2009; Carpio et al. 2014b, 2014c) and health risks (Gortázar et al. 2007, 2010).

In Sweden, the last recorded observations of wild boar in a natural environment are contained in a diary by King Erik XIV which describes a hunt on the Baltic island of Öland in 1688 (Anonymous 1980). However, this population, despite its subsequent reintroduction in 1723 by order of King Fredrik I, became extinct over 200 years ago (Welander 2000). Nevertheless, the wild boar was re-introduced into Sweden in 1976 when a group escaped from enclosures in which they were being held for hunting and meat production (Thurfjell et al. 2009). The wild boar population has since grown rapidly in the southern and central parts of Sweden and wild boar are once again considered a part of the Swedish fauna (Truvé and Lemel 2003). The wild boar is also expected to recolonise Norway, and the first wild boar was shot 40 km from Oslo in 2013 (Massei et al. 2015).

Hunters are currently feeding wild boar to increase their numbers (Thurfjell et al. 2009), since hunting in Sweden is primarily a leisure activity in which 260,000 hunters participate, and its economic significance is considerable with a value of over 100 million € (Bernes 2011). However, wild boar may have a number of effects on the environment and its flora and fauna (Barrios-García and Ballari 2012; Ballari and Barrios-García 2013). For example, they are known to be an active predator on ground-nesting birds (Carpio et al. 2014c). Sweden has high densities of several wader species that breed in meadows along the coast and/or shores of inland lakes (e.g. Ottvall and Smith 2006; Lindström et al. 2015). The populations and distributions of many species of waders have declined throughout the European continent (Heath et al. 2000; Thorup 2006; Wetlands Internacional 2012), concurrent with the declines and degradation of wetland habitats (International Wader Study Group 2003; Piersma 2007; Ross et al. 2012; Clemens et al. 2014). However, it has also been suggested that increased nest predation may be an additional cause of declines in wader populations (Macdonald and Bolton 2008).

Wading birds have a vast variety of social systems. Nest spacing may vary considerably, since some species are solitary and often territorial (Nethersole-Thompson and Nethersole-Thompson 1986), while others tend to concentrate in large numbers in certain breeding habitats, with the result that large proportions of the populations of certain species reside in relatively few areas (Brown et al. 2001). These colony-living birds pose particular biological and management problems since the loss of a single breeding site can result in the loss of a whole population segment (Hafner 1997; Evans et al. 2016). Colony-breeding species may, nevertheless, increase their survival and reproductive success owing to predation dilution, confusion and satiation effects on predators (Will 1994; Krakauer 1995; Macdonald and Bolton 2008). However, the positive effects of colony-living species against predation depend on the kind of predators. Hogstad (1995) found that Fieldfares *Turdus pilaris* breed in solitarily conditions in a high density of mustelids, whereas avian predators breed in a colonial manner. The review of Akerman et al. (2004) showed a number of studies demonstrating the effects of nest density and nearest-neighbour distance on predation rates and found that the more closely the nests are placed, the more often they were predated by carnivores (such as red foxes, racoons or striped skunks), whereas more isolated nests were more frequently predated by birds.

The aim of this study was to quantify the role of the wild boar as a potential predator on wading birds' nests. We predicted that the predation rate would be higher in nests with a higher density, i.e. those in which colony-living is simulated, than in solitary nests, while controlling for wild boar abundance.

Material and methods

Study area

The study area was located between the counties of Gävleborg, Uppsala, Västmanland and Dalarna in mid Sweden (N 60°16′–60°83′ E 16°88′–17°70′, WGS84) (Figure 1). The landscape consists of a mosaic of different habitat types: a) agricultural land, on which cereals such as wheat (*Triticum aestivum*), rye (*Secale cereale*), oats (*Avena sativa*) and corn (*Zea mays*) are the main crops, but on which some fields are also planted with potatoes *(Solanum tuberosum*) and willow "forests" (*Salix sp.* L.), which are grown for energy production; b) open areas, such as pastures, meadows and areas close to water dominated by the common reed (*Phragmites australis*); c) deciduous forests, which are dominated by birch (*Betula* sp.), and aspen (*Populus tremula*) and others species, such as oak (*Quercus robur*), alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), lime (*Tilia cordata*) and hazel (*Corylus avellana*), and d) mixed coniferous forests that mainly consist of planted stands of Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) of varying ages (approximately 70% of the study area).

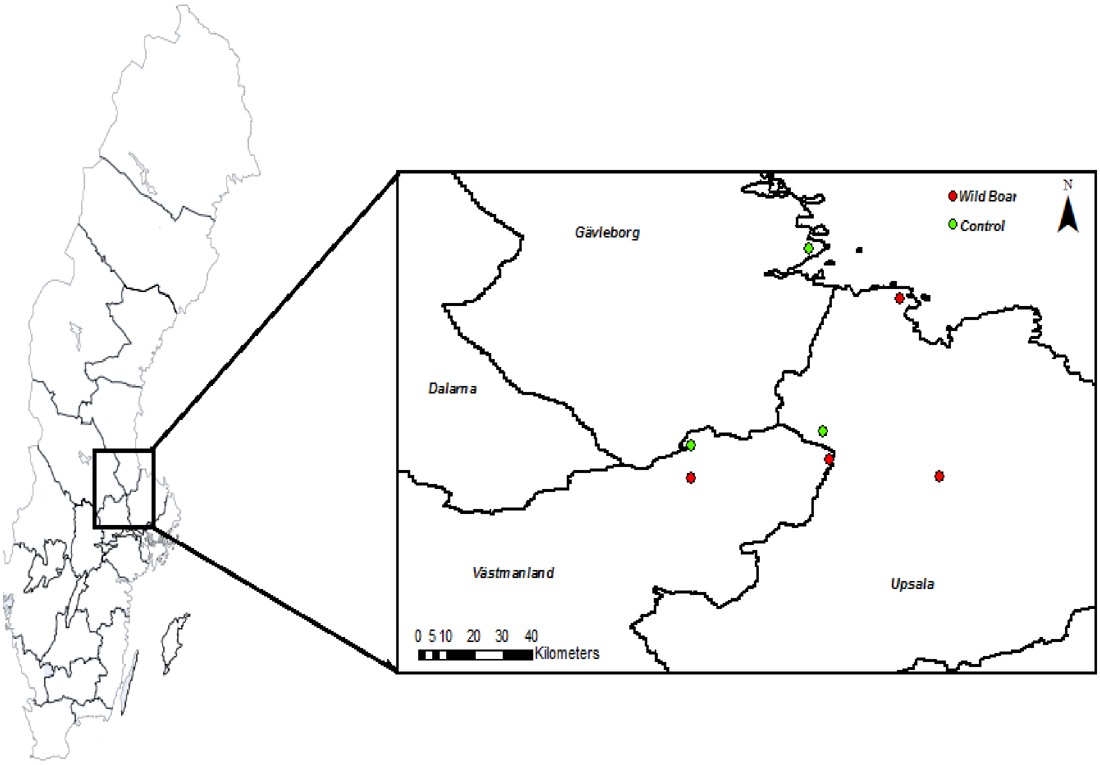

Figure 1. Map of the study area, showing the different plots (with wild boar and controls)

Hunting is practiced in the study area and is recorded by professional game keepers. Wild boar densities are primarily dependent on extensive supplementary feeding and baiting, mostly with sugar beet (*Beta vulgaris*) and other items, including maize and bread, which are used by hunters and landowners at feeding stations surrounding the study area (Thurfjell et al. 2009, Carpio 2015, pers. observ.). The hunting bags in the study area ranged between 0-8.3 wild boar/1000 ha during the 2014/2015 season (www.viltdata.se), which are similar to those found in other studies in southern Sweden (Thurfjell et al. 2009).

The community of wading birds that nest in the study area was composed mostly of Lapwings (*Vanellus vanellus*), Eurasian Curlews (*Numenius arquata*), Green

Sandpipers (*Tringa ochropus*), Wood Sandpipers (*Tringa glareola*), Common Redshanks (*Tringa totanus*), and others species such as Eurasian Woodcocks (*Scolopax rusticola*) and Common Snipes (*Gallinago gallinago*). The assemblage of potential nest predators includes Ravens (*Corvus corax*), Jackdaws (*Corvus moredula*), Common Magpies (*Pica pica*), European Jays (*Garrulus glandarius*) and Hooded crows (*Corvus cornix*) (Andrén 1992), and gulls such as the Black-headed Gull (*Chroicocephalus ridibundus*), the Common Gull (*Larus canus*) or the European herring Gull (*Larus argentatus*) (Göransson 1975). The most common mammalian carnivores are the Red Fox (*Vulpes vulpes*) and the Badger (*Meles meles*). Others potential predators include rodents (e.g. Rats *Rattus* sp.; Neinavaz et al. 2013).

Experimental design

We located a total of 98 artificial nests, 56 of them on the plots on which wild boar abundance was > 0 (n = 4 plots with wild boar) and 42 in the control area in which wild boar abundance was 0 (n = 3 plots without wild boar). We placed eggs in 14 nests per plot between May and June of 2015. Half of the nests on each plot (n = 7 nests) were clustered in the manner of colony-living breeders and the other half were isolated, following a 10 × 10 m grid for colony-living nests and one of 100 x 100 m for solitary nests (Beaver et al. 1980; Nethersole-Thompson and Nethersole-Thompson 1986; Del Hoyo et al. 1996). The nests were placed in a small hollow dug in the ground at the border of the wetland and were exposed to predators for 24 days (which is the most common incubation period for most waders; see supplementary material in Portugal et al. 2014). In each nest, we placed four quail (*Coturnix coturnix*) eggs, two of which were not manipulated and two of which were emptied and injected with plaster (*n* = 392; see Castro et al. 2014b for more information on this method). A nest was considered to have been depredated if any of the eggs were damaged or lost. The nest predation rate was estimated as the percentage of nests depredated in each plot. Egg predators were assigned according to the tooth marks on the plaster eggs (Carpio et al. 2014c). Moreover, automatic cameras were placed at eight nests to identify predators (four cameras at nests in areas with wild boar and four cameras at nests in control areas), according to the recommendations for their use in identifying nest predators (Macdonald and Bolton 2008).

Estimating wild boar, carnivore abundance and percentage of rooting

We estimated the wild boar abundance index by following the protocol of Acevedo *et al.* (2007) based on the frequency of faecal droppings in walked transects. The counts took place in two transects of 4 km in each of the seven plots in April 2015. Each transect count consisted of 40 segments of 100 m in length and 1 m in width, divided into ten sectors of 10 m in length. Sign frequency was defined as the average number of 10-m sectors containing droppings per 100-m transect (Carpio et al. 2014c), and a single average value of wild boar abundance was calculated per estate. This was done using a frequency based indirect index (FBII) which was calculated according to Acevedo *et al.* (2007) using:

$$\text{FBII} = \frac{1}{n}\sum_{i=1}^{n} S_i$$

where S*i* is the number of sign-positive sectors in the *i*th 100-m transect (i.e. S*i* varies between 0 and 10), and *n* is the number of transects considered (i.e. n= 40 for the total analysis).

We also obtained an abundance index by counting carnivore scats in the two 4-km-long transects mentioned above. The percentage of soil rooting by wild boar recorded in the transects was also calculated, in which a fixed bandwidth of 1 m was established and the length of each rooting was scored within this band (Bueno et al. 2010; Carpio et al. 2014b).

The location of transects within each study area was determined using a stratified sampling experimental design, signifying that all of the habitats from each plot studied were represented in the sampling exercise according to their abundance (the habitats with the highest percentage of surface represent a higher proportion of transect). The main habitats in the study area have been considered: deciduous forest, farmland, mixed forest, wetland, natural pastures and coniferous forest (the dominant landscape).

Structure of vegetation

The habitat in which each nest had been placed was classified according to the characteristics of the vegetation as (1) Farmland-wetland (open habitat), (2) Forest (coniferous-deciduous) and (3) edge (ecotone between 1 and 2). The maximum height of the vegetation in a 1-m perimeter around the nest was also measured (Taylor and

Ford 1999). These variables were selected because the habitat and height of the vegetation may affect nest detectability (Rands 1988; Macdonald and Bolton 2008).

Statistical analysis

Chi-squared tests were used to compare the proportion of nests that were predated between treatments. We compared the percentage of rooting in the different habitats (farmland-wetland, edge and forest) using the Kruskal–Wallis test. Spearman's correlation test was used to assess the correlation between the explanatory variables (variables with rho >0.8 were removed).

In order to determine the factors that relate to the survival of artificially simulated wading birds' nests (n = 98), two generalised linear mixed models were constructed (model 1a and 1b), in which the dependent variable was whether the nest was total or partially predated vs. not predated. In model 1a, *treatment* (plots with vs. plot without wild boar), *type of nests* (colony-living vs. isolated nests) and *habitat type* (open, forest and edge) were included as the factors, whereas the abundance of carnivores, and the height of the vegetation in which nests were located, were included as co–variables. In model 1b, we included the same variables but omitted the *treatment* which was, in these models, substituted for wild boar abundance, and therefore included only those plots on which wild boar were present (n = 4). We also included the interaction between the treatment and nest type, treatment and habitat, carnivores and wild boar abundance and habitat. The 'plot' was included as a random factor in both models. We used a binomial distribution with a logit-link function.

A second linear mixed model (normal distribution with an identity link function, model 2) was created to study the relationship between carnivore abundance (dependent variable) and wild boar abundance. Wild boar abundance was included as a factor and 'plot' was included (seven levels) as a random factor.

The selection of models was based on AIC (Burnham and Anderson 2002) by comparing nested models following a backwards procedure (Zuur et al. 2009). The assumptions of normality, homogeneity and independence in the residuals were met in all the models (Zuur et al. 2009). Statistical analyses were performed using InfoStat software. The significant p-value was set at p = 0.05.

Results

The wild boar frequency index in the study area ranged from 0 (control areas) to 0.37, while carnivore abundance ranged from 0 to 6.25 scats/km. The percentage of rooting ranged from 1.5% to 14.5% (on plots with wild boar), but no significant differences were found among habitats (P>0.05 by Kruskal Wallis test) (Fig. 2).

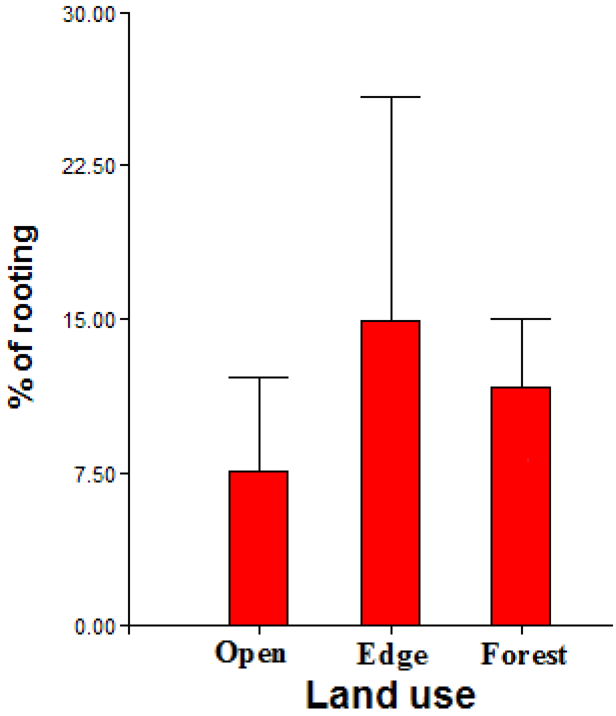

Figure 2. Percentage of rooting by wild boar in open (wetland and farmland), edge and forest (deciduous and coniferous) habitat.

Thirty out of the 98 nests were not predated, 58 were predated and 10 were lost for other reasons (stochastic processes: flooding, agriculture...), signifying that 69.4 % of nests were lost (predation or other causes), which should simulate the extent of the waders' incubation period. The average predation was 8.1 ± 5 nests per plot (mean ± S.D.) and 32.6 ± 20 eggs per plot (mean ± S.D.). Overall, the proportion of predated nests (χ^2=10; d.f. =1; p <0.05) was higher on the control plots (87.5 % of nests) than on the plots with wild boar (54 % of nests) (Fig. 3).

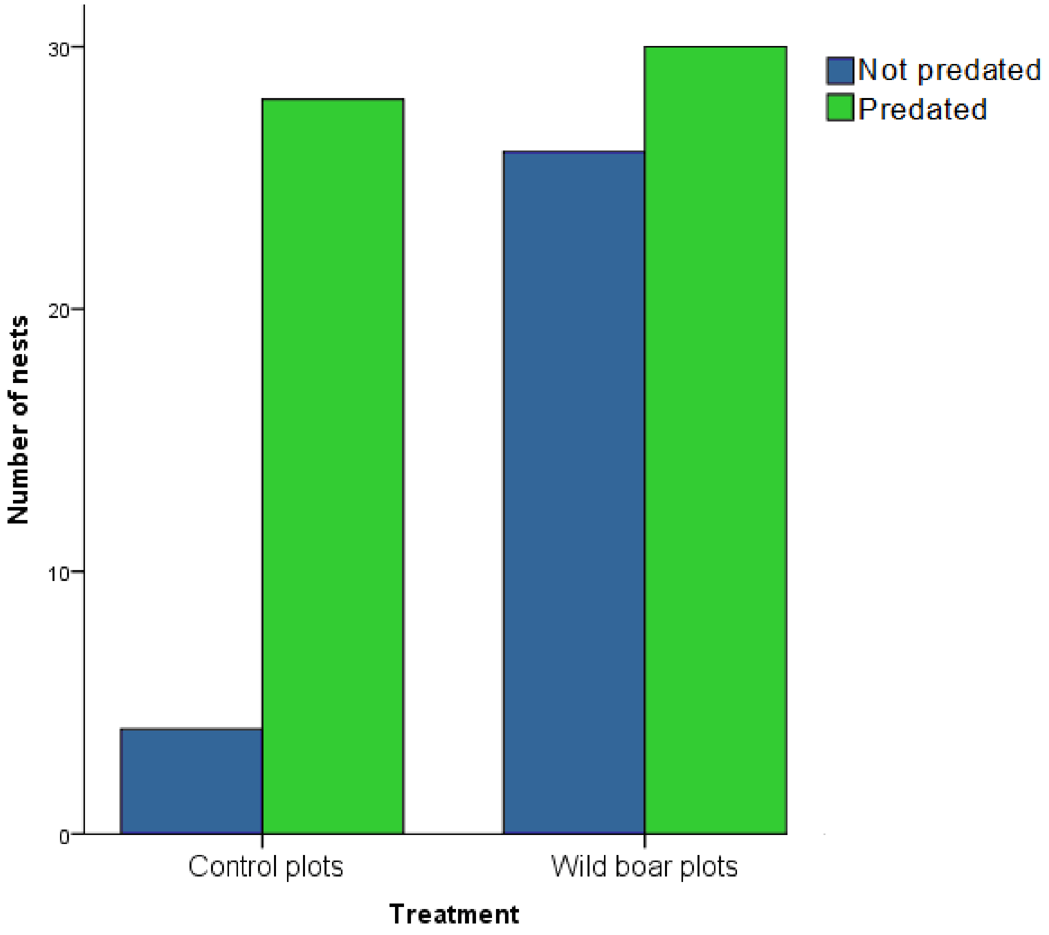

Figure 3. Chi-square test comparing the number of predated nests according to treatment (10 nests were lost owing to flooding in control plots).

In areas with wild boar, the most common nest predator was the red fox, accounting for 28 % of the nests predated, followed by the wild boar, which predated 18 % of the nests (Fig. 4). A different picture of predation was found on the control plots (without wild boar), where more nests was predated by the red fox (38.5 %) and badgers (34.5 %). Of 45 nest predation events identified using nest cameras, 28 occurred on plots without wild boar and 17 in areas with wild boar. In areas with wild boar, 41.17 % of these events were perpetrated by foxes, 29.41% by wild boar, 17.64 % by birds, 5.89% by rodents and 5.89% by mustelids, while in areas without wild boar the predators principally responsible for these events were the red foxes (39.28%) and badgers (35.72%), followed by birds (25%).

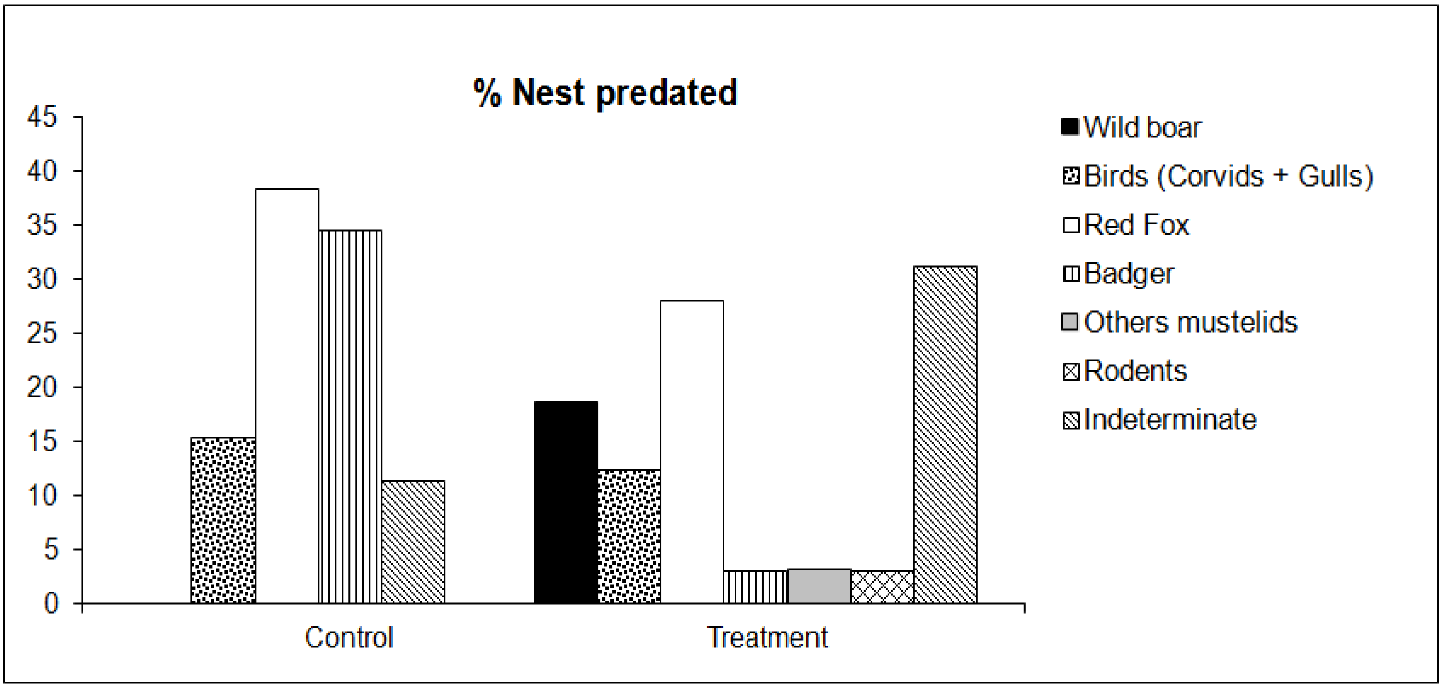

Figure 4. Percentage of nests preyed on by different species according to treatment (control ‘plots without wild boar’ vs. treatment ‘plots with wild boar’).

With regard to the factors affecting nest predation (model 1a and 1b), the percentage of rooting was not included in the models (r>0.8 with density of wild boar; Spearman correlation-test). In model 1a (plots with vs. plot without wild boar), variables such as vegetation height, habitat type or interaction between treatment and type of nests, treatment and habitat and carnivores and wild boar abundances and habitat were excluded according to AIC criterion. The model showed a significant positive relationship between carnivore abundance and nest predation. A significant interaction between treatment (with wild boar and control areas) and nest predation was also found, signifying that the areas without wild boar had higher rate of nest predation than those with wild boar. There were no significant effects as regards either the type of nest or habitat (Table 1, model 1a). In model 1b (wild boar abundance), only wild boar abundance and nest type were retained in the best model. This model revealed a negative relationship between wild boar abundance and nest predation.

With regard to model 2, which concerns carnivore abundance (Table 1, model 2a and 2b), the treatment (plots with or without wild boar) was statistically significant, showing a negative association between carnivore abundance and wild boar presence (model 2a). However, the abundance of wild boar was not associated with the abundance of carnivores (model 2b).

Table 1. *F*, *p* values and coefficients of the variables included in the mixed models to explain nest predation (model 1a and 1b) and carnivore abundance (model 2a and 2b). Df shows the degree of freedom of the numerator. Coefficients for the level of fixed factors were calculated using reference values of 'Control' in the variable 'Treatment', 'Colonial' in the variable 'Type nest'.

Variable	*F*	*df*	*P*	Coefficient ± E.S
Predation nest (model 1a)				
Treatment	4.67	1	<**0.05**	Wild boar = - 4.52. ± 2.24
Type of nests	2.92	1	0.08	Isolated = - 1.19 ± 0.72
Carnivore abundance	5.54	1	<**0.01**	2.51 ± 0.6
Predation nest (model 1b)				
Type of nests	2.1	1	0.14	Isolated = - 1.07 ± 0.76
Wild boar abundance	4.58	1	<**0.05**	-28.45 ± 12.68
Carnivore abundance (model 2a)				
Intercept	19.31	1	<**0.01**	4.42 ± 0.91
Treatment	8.90	1	<**0.05**	Wild boar = -3.20± 1.07
Carnivore abundance (model 2b)				
Intercept	8.31	1	<**0.05**	1.09 ± 0.71
Wild boar abundance	0.07	1	0.8	0.46 ± 0.34

Discussion

Our results show that when the wild boar is present, it is responsible for 18% of the total nest predation, but we cannot state whether predation is lower in wild boar plots owing to the presence wild boar (and its ecological repercussions) or for other reasons that may relate to wild boar absence (e. g. habitat, presence of other carnivores mediated by habitat). Moreover, we found that the predation on artificial wading birds´ nests in the mosaic areas formed by cropland and adjacent boreal forest located in central Sweden was (1) very high in both treatments, (2) associated with wild boar and carnivore abundances, and (3) associated with the type of treatment.

High predation rates on artificial nests

The predation of artificial nests was high in both types of treatments (>50% in all cases). These rates coincide with those of other studies which have reported clutch failure rates of over 50% that are attributable to predation alone (Macdonald and Bolton 2008). However, in our study, the predation rates were different according to the treatment. In the control plots, the average predation rate of nests was 87.5% with a range of 85–100%. However, there was a lower nest predation rate for plots with wild boar, with an average of 54% of the nests being predated (range = 0–92%).

Mammals have a high capacity to explore relatively new habitats and have been identified as the main predators in many studies (Tryjanowski et al. 2002; Macdonald and Bolton 2008; Malpas et al. 2013; Praus et al. 2014). In our study, mammals accounted for 78 % of the known predators, which is similar to the study by Macdonald and Bolton (2008), in which 70% of the known predators were mammals. Other studies investigating the predation on bird nests, some of which also used nest cameras (such as: Sharpe 2006; Bolton et al. 2007; Macdonald and Bolton 2008), obtained similar results, except that the wild boar is not mentioned in these studies. Another study by Malpas *et al.* (2013) found predation rates of 63% by foxes, while 13% of the nests were predated by badgers, which were the two most important mammalian predators in that habitat.

Interestingly, our study found that nest survival rates were higher on plots with wild boar (Fig. 3), which was unexpected, as the wild boar was the second main predator on plots on which it was present, although other aspects of the habitat such as taller vegetation (Laidlaw et al. 2015) or water depth in wetlands (Hoover et al. 2005) may play a role. Other studies (Batary et al. 2014; Carpio et al. 2014c) have also identified the wild boar as one of the main nest predators. For example, Saniga (2002) showed that up to 30% of Capercaillie (*Tetrao urogallus*) nests were lost owing to predation by the wild boar. However, and contrary to what was expected, we found a very low predation rate by badgers on plots with wild boar (only one case), while on the plots without wild boar (controls) the badger was the second most important nest predator (with 34.5% of predated nests). The predation on birds´ nests by the fox similarly decreased from 38 % in the absence to 28 % in the presence of the wild boar. Competition between wild boar and foxes or badgers has been reported by Massei *et al.* (1996), and some studies have also suggested that when food is scarce, wild boar and other animals may compete for resources (Wood and Roark 1980; Massei et al. 1996). However, this competition would not be expected when the wild boar has recently arrived (as is the case of Sweden). Another plausible explanation for the pattern we observed may therefore be that they (foxes and badgers vs wild boar) have different spatial distributions and habitat requirements, (Virgos et al. 2002). Predation therefore varies spatially and according to habitat (regardless of wild boar presence, predation would be higher in areas in which the wild boar is present than in others), which may explain the significant negative relationship between wild boar and carnivore abundances found in this study.

Colony-living vs isolated nests

Previous studies have found an increase in both survival and reproductive success in colonies as their group sizes have increased (Macdonald and Bolton 2008; Evans et al. 2016). Moreover, other studies that compare species which breed both in both solitary and colonial conditions have found reduced predation and increased reproductive success in individuals that have chosen to nest in colonies (Sasvári and Hegyi 1994; Neff et al. 2004). However, others studies have reported a higher predation rate in larger colonies or no effect at all of increased colony size (Brunton 1997; Picman et al. 2002), which may depend on the environmental conditions and the type of predators (Wiklund and Andersson 1994; Brunton 1999). In this study we did not find any effects of nest density on the nest predation rate, which may be owing to the use of artificial nests in our experiment, since there were no adult animals that could defend or deter potential predators (Berg 1996) as the result of the absence of aggressive neighbours in dense nesting (Pratte et al. 2016).

Finally, we did not find any significant landscape effects on nest predation in the case of either habitat characteristics or the variation in the height of the vegetation surrounding the nest. Other studies have found relationships between landscape context and nest predation rates (Huhta et al. 1996; Bayne and Hobson 1997), although the evidence for this effect was not conclusive and could presumably have occurred as the result of the different predator communities present in each habitat (Macdonald and Bolton 2008). We found the same trends in our study, in which nest predation in forests and edges (75% and 70% of nest predated) were higher (although the differences were not significant) than in farmland and open landscapes (60%).

Predation was the principal cause of artificial nest failure, although there were of course also other causes, such as flooding or destruction by agricultural management. Our results suggest that the current levels of predation on waders' nests in many habitats are unsustainably high (similar to other studies reported in Macdonald and Bolton 2008; Malpas et al. 2013; Laidlaw et al. 2015), which suggests that hatching success rates below 50% are likely to be unsustainable for wading birds. Although the wild boar can have significant impacts on different ecosystem components (Barrios-García and Ballari 2012), little is known regarding the ecological impact of its current densities in Sweden and in different ecosystems. Despite the tremendous impact of wild boar on nest predation reported in this and other studies, and contrary to our prediction, our study provides evidence of a negative relationship between the abundance of wild boar and that of other carnivores, which may be owing to differences in spatial distributions and habitat requirements. However, an assessments of the interaction between the wild boar and other predator species, (and particularly badgers) is needed, and new studies using predator-exclusion fencing and natural nests are necessary to provide a more accurate evaluation of the impact of predation on wading bird communities (Malpas et al. 2013; Carpio et al. 2014c).

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CAPÍTULO 3

Efectos de conejos y ungulados sobre las cubiertas herbáceas y sus consecuencias sobre el ecosistema

Capítulo 3.1

Evaluación de una especie no palatable (*Anthemis arvensis*) como cultivo de cobertura alternativo en olivares bajo alta presión de pastoreo por conejos

Carpio, A.J., Soriano, M.A., Guerrero-Casado, J., Prada, L.M., Tortosa F.S., Lora, A., Gómez, J.A.. **Evaluation of an unpalatable species (*Anthemis arvensis* L.) as an alternative cover crop in olive groves under high grazing pressure by rabbits.** *Agriculture, Ecosystems & Enviroments*. In Press.

Resumen

La sostenibilidad es un atributo clave para el futuro del olivar. Los cultivos de cobertura pueden ser considerados como una herramienta eficaz para lograr la sostenibilidad de los olivares al reducir la erosión, mejorar la fertilidad del suelo y aumentar la biodiversidad. Sin embargo, los herbívoros pueden forrajear sobre los cultivos de cobertura cuando los recursos naturales son escasos. En este estudio se evaluó el impacto del forrajeo de los conejos en la implantación de cultivos de cobertura herbácea de dos especies de plantas nativas, una palatable (*Bromus rubens* L.) y otra desagradable (*Anthemis arvensis* L.) en dos olivares con escasa cobertura vegetal en Andalucía, sur de España. Se sembraron ocho parcelas de exclusión de conejos, cerca de otras ocho parcelas no valladas, donde se midieron la biomasa aérea, la altura y la cobertura del suelo por cada especie. Los resultados mostraron que la biomasa, la altura y la cobertura del suelo de *B. rubens* fueron mayores en las áreas de exclusión de conejo (cobertura de suelo: 36,5 ± 3,3%, altura: 30,3 ± 3,9 cm, media durante todo el período de medición y biomasa: 158 ± 36 g/m^2, en Abril) que en las áreas abiertas (cobertura del suelo: 1,9 ± 0,2%, altura: 5,6 ± 0,7 cm, biomasa: ≅0), mientras que *A. arvensis* no mostró diferencias en la biomasa, la altura o la cobertura del suelo entre los dos tratamientos (cobertura del suelo: 11,3 ± 6,3%, altura: 12,2 ± 7,9 cm, media durante todo el período de medición, y biomasa: 49,5 ± 10 g/m2, en abril). Los resultados mostraron además que el daño causado por los conejos fue causado desde las primeras etapas de desarrollo de *B. rubens*, evitando su crecimiento; pese a que el consumo de biomasa de la planta era mínimo, el daño causado fue crítico. Estos hallazgos sugieren que especies desagradables como *A. arvensis* podrían ser una herramienta adecuada para el establecimiento de cultivos de cobertura herbáceos en olivares con altas densidades de conejo, donde otras especies palatables (por ejemplo, *B. rubens*) son consumidas, contribuyendo así a la conservación y mejora del suelo en olivares con suelos ya degradados por la erosión.

Abstract

Sustainability is a key attribute for the future of the olive grove. Cover crops can be considered as an effective tool to achieve sustainability of olive orchards to reduce soil erosion, improve soil fertility and increase biodiversity. However, wild herbivores may forage on cover crops when natural food resources are scarce. In this study we assessed the impact of European rabbit grazing on the implantation of herbaceous cover crops of two native plant species, one palatable (*Bromus rubens* L.) and the other unpalatable (*Anthemis arvensis* L.) in two olive orchards with very scarce vegetation cover in Andalusia, Southern Spain. Eight rabbit exclusion plots, close to eight other unfenced plots, were planted where the aboveground biomass, height and the ground covered by each species were measured. The results showed that the biomass, height and the ground cover by *B. rubens* were higher in the rabbit exclusion areas (ground cover: 36.5±3.3%; height: 30.3±3.9 cm, averaged over the entire measuring period; and biomass: 158±36 g/m^2, in April) than in unfenced areas (ground cover: 1.9±0.2%; height: 5.6±0.7 cm; biomass: ≅0), while *A. arvensis* showed no difference in biomass, height or ground cover between the two treatments (ground cover: 11.3±6.3%; height: 12.2±7.9 cm, averaged over the entire measuring period; and biomass: 49.5±10 g/m^2, in April). The results further showed that the damage by rabbits was caused from the early stages of development of *B. rubens*, which avoid its growth; notwithstanding the plant biomass consumption was minimal, the damage caused was critical. These findings suggest that unpalatable species such as *A. arvensis* could be a suitable tool for establishing herbaceous cover crops in olive groves at high rabbit densities, where other palatable species (e.g., *B. rubens*) are strongly consumed, thus contributing to soil conservation and improvement in olive groves with soils already degraded by erosion.

Introduction

Sustainability is one of the key priorities defined in the new Common Agricultural Policy (CAP), (Pe'er et al., 2014), including goals such as the reduction of soil erosion, improving efficiency in the use of resources and promotion of both plant and animal biodiversity, to ensure long-term provision of ecosystem services (http://ec.europa.eu/agriculture/cap-overview/index_en.htm). Use of cover crops in woody crops has been shown to be effective in reducing soil erosion and increasing biodiversity, so reducing nitrate leaching and runoff and diffuse pesticide pollution, in previous experiments farms (e.g., Fracchiolla et al., 2015 in almond orchards; Gómez et al., 2009a, b in olive groves; Irvin et al., 2016 in vineyards; Malik et al., 2000 in hardwood plantations).

Olive groves are a very significant agricultural ecosystem in the Mediterranean, and Andalusia, the southernmost region of Spain, is the largest olive growing area in the world as it produces more than a third of the world's olive oil (CAPDR, 2016). In this region the olive grove occupies over 1.5 million ha (about 17.5% of the regional surface and 15% of the world's olive area; FAO, 2016; Junta de Andalucía, 2016), shaping the landscape and impacting the regional economy. In recent decades the olive sector has also started an expansion and intensification process (irrigation, and intensive use of fertilizers, pesticides and machinery) in Andalusia, and it has also recurrently been linked to various environmental problems, such as pressure on water resources and biodiversity, diffuse pollution and soil degradation (e.g., Beauffoy, 2001; Scheidel and Krausmann, 2011). Moreover, soil erosion in olive orchards in this region has been repeatedly mentioned as one of the major threats to the sustainability of this crop (e.g., Beauffoy, 2001; Gómez et al., 2014a; Rodríguez-Entrena and Arriaza, 2013), since on-site damage attributed to water erosion entails a reduction in soil fertility and soil water storage, and therefore in the olive orchard productivity, as well as difficulties in the access to and the movement within the orchards due to gully erosion; while the major off-site effects of water erosion involve surface and groundwater contamination by agrochemicals (especially herbicides and fertilizers).

The combination of low ground cover with steep-slope areas on which these olive groves are usually located, together with periodical high-intensity rainfall events that characterise the Mediterranean climate, explains the severe soil erosion problems in many olive growing areas of Andalusia (Milgroom et al., 2007; Soriano et al., 2014). Moreover, these problems have been magnified since farmers' management over recent decades has tended to plough intensively and/or to spray herbicides repeatedly to avoid competition of weeds with olive trees for soil water, thus resulting in severe weed seedbank depletion, in some situations with the virtual loss of the soil seedbank, and in scarce or zero herbaceous vegetation cover in many olive orchards (Barrio et al., 2013; Simões et al., 2014), worsening the situation of these olive orchards against soil erosion (Ball, 1992). In these olive groves, the protection index of vegetation cover against erosion is maximum (Figure 1), leading to the need to implement soil conservation practices, such as adding olive pruning chips to cover the soil (although it represents a significant risk of spreading diseases in olive groves; Koski and Jaconi, 2004; Cohen et al., 2017) or establishing herbaceous cover crops to promote biodiversity and to prevent soil erosion during the rainy season (Michael et al., 2014; Rodríguez-Entrena and Arriaza, 2013).

To tackle the growing problem of soil erosion, public policies under CAP regulations have implemented mandatory requirements (Conditionality) in olive groves located on areas of mean slopes equal or steeper than 15% of maintaining a vegetation cover at least 1-m width in the lanes, and prohibition of inversion tillage (MAPAMA, 2017). Despite this, in many olive-groves, repeated ploughing is still used and combined with an uncontrolled use of herbicides, with negative results on soil and biodiversity conservation. Nevertheless, several studies showed that olive-growing is compatible with the preservation of a certain biodiversity and with a lower soil loss if the management is less intensive (e.g., Ballais et al., 2012; Gómez et al., 2017; Simões et al., 2014) and the landscape complexity is maintained (e.g., Castro-Caro et al., 2014; Cohen et al., 2015).

The use of cover crops in the lanes of olive orchards has shown its beneficial impact on reducing soil erosion (Durán and Rodríguez, 2008; Durán et al., 2009; Francia et al., 2006; Gómez et al., 2009a, b; Gómez et al., 2011), improving soil properties (Gómez et al., 2009c; Moreno et al., 2009) and increased biodiversity (Paredes et al., 2013; Ruano et al., 2004) in experimental farms. However, the establishment of cover crops is not easily adopted by farmers and numerous practical problems still remain when trying to introduce and manage cover crops in commercial farms, particularly in semi-arid areas, due to the risk of competition for soil water with olive trees when cover crop management is inadequate (Gómez et al., 2014b). In addition, overgrazing due to high abundances of European rabbit (*Oryctolagus cuniculus* L.) together with a low availability of alternative natural food resources can prevent the establishment of herbaceous cover crops in olive groves (Guerrero-Casado et al., 2015). This can be particularly acute in the case of using highly palatable species as cover crops, which may not be viable as a result of rabbits grazing (e.g., Alcántara et al., 2011, cruciferous; Ferreira et al., 2015, *Trifolium* spp.; Guerrero-Casado et al., 2015, *Bromus rubens* L.).

The aim of this research was therefore to test the effectiveness of planting cover crops of an unpalatable species (*Anthemis arvensis* L.) *vs.* a palatable species *(Bromus rubens* L.) in a context of high rabbit density and natural food scarcity (olive groves with very low density and diversity of weeds). We hypothesised that under high grazing pressure by rabbits an unpalatable species will cover a larger soil surface.

Material and methods

Study area

Experimental plots were established in olive groves with scarce vegetation cover and serious soil erosion problems located in the south of the province of Cordoba (Andalusia, Southern Spain), (Figure 1), which is characterised by a Mediterranean climate (with an average annual rainfall of 528 mm, a evaporative demand of 1,418 mm, and with a minimum monthly mean temperature of 9.1 ºC in January and maximum of 27.5 °C in July, over a 15-year span). The main characteristic of the Mediterranean climate is a very warm and dry summer (mean maximum temperature of 36 ºC, and accumulated precipitation lower than 50 mm, in the study area). During the cover crops growth cycle (mid-November 2015 to late spring 2016) the rainfall recorded in the experimental plots was 335 mm. The main crops in the study area are olive (*Olea europaea* L.) and vineyard (*Vitis vinifera* L.), and rabbit hunting is a very popular alternative activity in this area as a result of the high densities attained. This herbivore is even considered to be a pest species in the study area owing to the significant crop damage caused in vineyards (Barrio et al., 2012) and young olive groves.

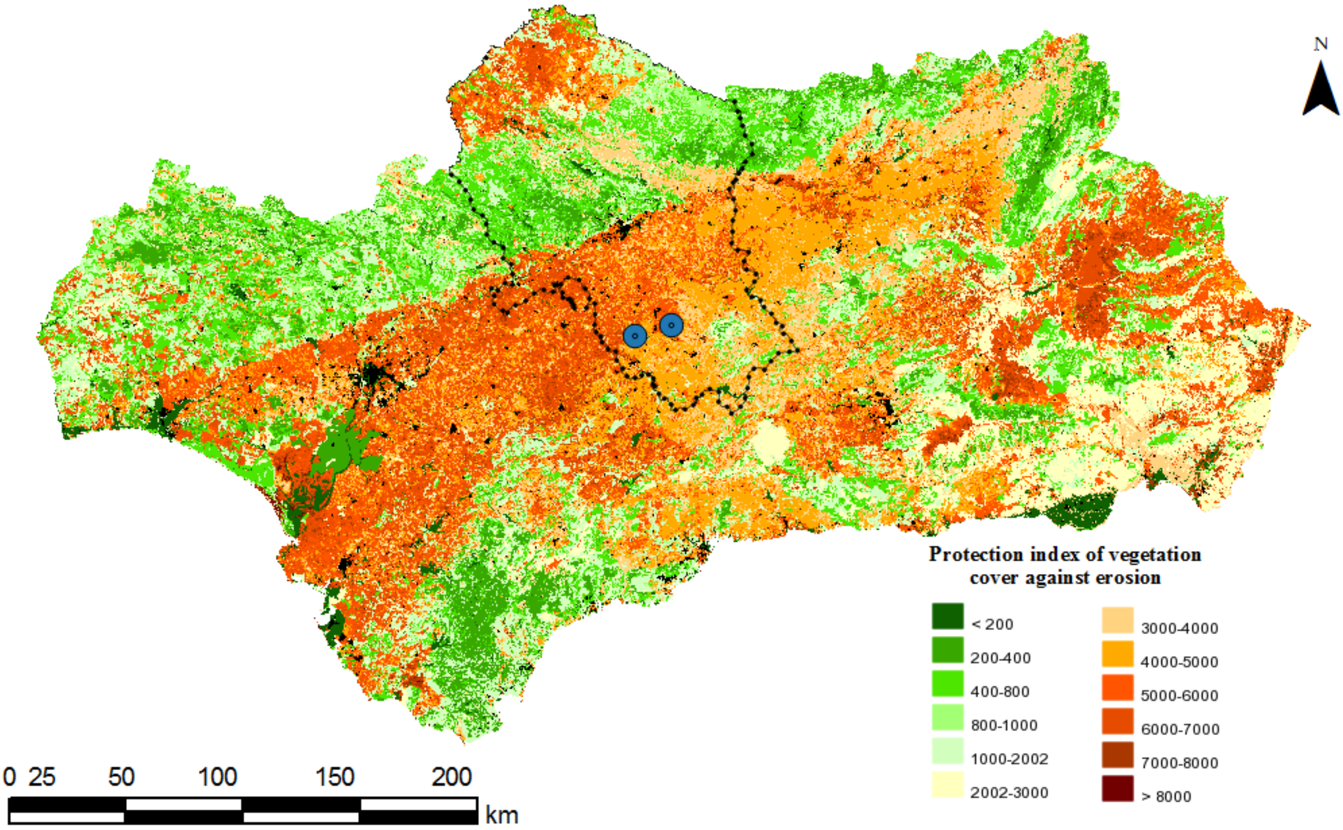

Figure 1. Map of Andalusia (Southern Spain) showing the protection index of vegetation cover against erosion, which was calculated using the land-use map and cover vegetation variation according to the Normalized Difference Vegetation Index (NDVI). Obtained from REDIAM, Junta de Andalucía; http://www.juntadeandalucia.es/medioambiente/site/rediam/menuitem. Experimental plots are represents by blue circles within the province of Cordoba (dash line). The distance between the experimental plots was 8.15 km. High protection index values indicate high soil erosion risk as a result of a scarce vegetation cover.

Experimental design and measurements

We selected two commercial olive orchards (8.15 km apart), with a medium-high density of rabbits and an extremely poor weed community, in which severe damage to cover crops by rabbits has been previously proven (Guerrero-Casado et al., 2015). In each olive orchard, eight elementary plots (4 fenced and 4 unfenced) were established to assess the rabbit damage to cover crops. Rabbit exclusion plots (6 m × 3 m) were fenced 0.5-m below ground and 1-m above ground, while unfenced plots (6 m × 3 m) were only delimited by sticks. Plots were paired (fenced and unfenced plot) and randomly distributed within the each olive orchard. The distance between the two plots of a pair was 5-10 m, and the distance between pairs was higher than 50 m (Figure S1 [supplementary]). The soil type of both olive orchards was Alfisol (Soil Survey Staff, 2014), and the soils had similar silty clay loam textures (Table 1). Soil samples for laboratory analysis were collected at eight random points within experimental plot in each olive orchard, at 0-10 cm depth. The physical/chemical properties of the soil were measured to detect previous differences that might affect the growth of the vegetation cover between both olive orchards.

In each elementary plot were sown two native plant species: *Bromus rubens* (hereafter BR) and *Anthemis arvensis* (hereafter AA), each species occupying half of the plot (3 m × 3 m; Figure S2 [supplementary]). Both species were sown in autumn, November 9, 2015, using a dose of 2.66 g-seed/m^2 for BR and 0.1 g-seed/m^2 for AA (Soriano et al., 2016), and 30 kg N ha^{-1} (as ammonium sulfate, 21% N) was added simultaneously with the seeding. These two species are annual, with a short life-cycle and early maturity, germinating in autumn and wilting in mid-spring, limiting the risk for water competition with the olives trees (Soriano et al., 2016). Both species are also characterised by their short height, which minimises disturbance to farmers in agricultural labours. BR was considered as a palatable species, since in a previous work (Guerrero-Casado et al., 2015) vegetative cover of this species was not established in olive groves owing to rabbit grazing. However, AA was treated as an unpalatable species, because it is highly resistant to predation due to its chemical composition and antimicrobial activity of the essential oils (Riccobono et al., 2017). Both species are easily to establish and have ability to self-seeding and to producing abundant seeds. Therefore, BR would allow a quick soil cover, whereas AA would allow a better soil protection under grazing pressure by rabbits.

Table 1. Mean values and standard deviation (±SD) of physical-chemical properties of soil (in the 0-10 cm depth) in the two studied olive orchards (A and B). Different letters within a row indicate significant differences (Fisher's LSD test; $p<0.05$).

Soil property	Olive orchard		Analytical method
	A	B	
CEC[i] (meq/100g)	27.3 ± 1.2 a	19.1 ± 3.7 b	Ammonium acetate method (photometer)[ii]
Ca exch. (meq/100g)	25.8 ± 0.9 a	16.9 ± 3.6 b	Ammonium acetate method (volumetric)[ii]
Mg exch. (meq/100g)	0.71 ± 0.35 a	1.08 ± 0.80 a	Ammonium acetate method (volumetric)
Na exch. (meq/100g)	0.34 ± 0.03 a	0.32 ± 0.02 a	Ammonium acetate (spectrophotometer)[ii]
K exch. (meq/100g)	0.42 ± 0.07 b	0.81 ± 0.37 a	Ammonium acetate (spectrophotometer)
CO_3^{-2} (%)	41.2 ± 1.5 b	53.5 ± 12.2 a	Gasometric method (Bernard calcimeter)[ii]
$CaCO_3$ (%)	14.9 ± 0.2 b	16.1 ± 1.1 a	Gasometric method[ii]
Organic matter (%)	1.56 ± 0.09 a	1.30 ± 0.34 a	Walkley-Black method[ii]
N Organic (%)	0.10 ± 0.01 a	0.09 ± 0.02 a	Kjeldahl method[ii]
P assimilable (mg kg^{-1})	8.1 ± 2.0 b	12.8 ± 1.0 a	Olsen method[ii]
K assimilable (mg kg^{-1})	189 ± 21 b	343 ± 144 a	Ammonium acetate (flame photometer)[ii]
pH (H_2O)	8.53 ± 0.05 b	8.67 ± 0.08 a	1:2.5 suspension in water
pH (KCl)	7.47 ± 0.03 b	7.67 ± 0.06 a	1:2.5 suspension in KCl
Clay (%)	39.3 ± 1.8 a	30.1 ± 2.6 b	Hydrometer method[iii]
Sand (%)	18.9 ± 1.4 a	18.3 ± 2.3 a	Hydrometer method
Silt (%)	41.8 ± 1.6 b	51.6 ± 2.0 a	Hydrometer method

[i] CEC = Cation exchange capacity

[ii] Page et al. (1982)

[iii] Bouyoucos (1962)

Although perennial herbs could be a more suitable cover crops owing to a higher capacity to regrowth after grazing and that they can cover the ground the whole year, its use as a vegetative cover in the lanes of the olive orchards does not seem entirely advisable since being perennial plants would compete with the olive trees for water during the period of maximum water requirements of the olive grove (warm-dry season), and therefore, only annual herbs withering in mid-spring are suitable in this context. In the case of *A. arvensis*, it is terophyte scapose, with generally low hairiness. Ascending stems, sometimes erect or prostrate, branched (Riccobono et al., 2017). While *B. rubens* is a terophyte that is identified by its pubescent stems, erect, dense inflorescences, and the long awns (12-26 mm) in the florets (Chambers et al., 2016).

We characterized the evolution of the ground cover occupied by BR and AA and their height in monthly measurements from December 15, 2015 to June 10, 2016. The percentage of ground surface covered by both species was calculated through the use of plot surface images, following the methodology developed by Luscier et al. (2006). The height of vegetation was calculated as the average of 10 random points (0.01-m^2) in each elementary plot (Bonham, 2013). Aerial biomass was measured in April, once each species reached its maximum growth, and in June, at BR harvest. Biomass was calculated from sampling areas of 0.25 m^2 of each species in each elementary plot where vegetation was cut. Plant samples were dried in an oven at 70 ºC and the dry weight was converted to g/m^2.

Rabbit abundance was estimated at the olive orchard level by counting the number of latrines per kilometre by walking two transects of 1.5 km in length in each olive grove each month (mean ± SE: 1.62±0.50 km). A latrine was defined as any faecal accumulation having at least 20 pellets over a surface of 20 cm × 30 cm (Virgós et al., 2003). This method has previously been validated in the area (Barrio et al., 2010) and it provides a good approximation of rabbit density at the local scale at least. The counts were performed monthly from December 2015 to June 2016.

Statistical analysis

Four general linear mixed models were applied using the elementary plot as the experimental unit and ground cover and height reached by BR and AA in each elementary plot as the response variables. In these models, ‘treatment’ (fenced and unfenced) and ‘date’ (seven levels) were considered as categorical variables and ‘olive orchard’ (two levels) as random factor. The interaction between ‘treatment’ and ‘date’ was also included in the models in order to evaluate whether the effect of treatment on response variables depended on the date. Assumptions of normality and independence were confirmed and variance structure (varIdent) was added to the models to ensure homogeneity in the residual spread. This allowed the residuals to have different spread across the levels of a categorical variable (in our case, the variance covariate was ‘date’). In addition, Fisher’s LSD post-hoc test within the mixed analysis was applied to check for response differences among different levels of categorical variables and their interaction. InfoStat software was used in all statistical procedures.

With regard to the aboveground biomass, a Wilcoxon paired test was used to check for differences in the biomass dry weight of BR and AA between fenced and unfenced plots (in April, the highest biomass, and June, BR harvest; n=8 pairs per each species each date). This test was also used to compare differences in height and ground cover between BR and AA (separately for fenced and unfenced plots).

One-way analysis of variance of soil properties was performed with olive orchard as factor to test for differences among the two orchards.

Results

Rabbit abundance was higher in olive orchard B (T-test; $p<0.001$) throughout the entire count period (14.2±1.0 *vs.* 23.3±1.7 latrine/km on average), the minimum being recorded in December (11.2 *vs.* 17.1 latrine/km) and the peak in June (24.8 *vs.* 30.2 latrine/km). These values of rabbit abundance are consistent with the medium-high densities of rabbits found in the study area (Barrio et al., 2010). Both soils are alkaline (pH close to 8.5), with a high carbonate content, although with limestone <20%, thus reducing the risk of shift to fixed (non-available) forms for nutrients (Table 1). Although the two soils differ in CEC, exchangeable cations (Ca, K), and P and K assimilable, both soils have sufficient levels of these nutrients (above critical or threshold values albeit in the lower range for P) for soils of this texture and analytical methods used (Delgado et al., 2016). The two soils have similar values of organic matter (OM), higher than the minimum levels for the topsoil in rainfed olive groves recommended by regional authorities (1% OM; Junta de Andalucía, 2008).

Regarding BR models (height and ground cover; Table 2), the treatment effect was significant ($p<0.001$) for both models, since the BR height over the entire measurement period was higher in fenced plots than in unfenced ones (general mean values of 30.3±3.9 cm and 5.6±0.7 cm, respectively) as well as the BR ground cover (average values of 36.5±3.3% in fenced plots and 1.9±0.2% in unfenced plots). However, in AA models the treatment effect was not significant, since the AA height and ground cover were similar throughout the measurement period in fenced (mean values of 12.8±1.5 cm and 11.5±1.4%, respectively) and unfenced plots (average values of 10.5±1.2 cm and 11.0±1.3%, respectively). The date was significant ($p<0.001$) for height and vegetation cover in both BR and AA models, since this variable affects plant growth and plant phenological development. Finally, the interaction between treatment and date only was significant in BR (Table 2). The results showed that significant differences in BR height and ground cover between fenced and unfenced plots appeared in the second month of the study (January), (Figure 2). The average ground cover of BR in fenced plots reached 24% in January (16 times greater than in unfenced plots).

Table 2. Fixed effects (F) of the explanatory variables on height and ground cover of *Bromus rubens* (BR) and *Anthemis arvensis* (AA). df refers to degree of freedom of the numerator; NS not significant; *** p<0.001 (Fisher's LSD test).

Variables	BR				AA			
	Model height		Model ground cover		Model height		Model ground cover	
	df	F	df	F	df	F	df	F
Intercept	1	414.1***	1	122.9***	1	85.6***	1	34.1***
Treatment	1	184.6***	1	89.9***	1	0.22^{NS}	1	2.1^{NS}
Date	6	34.8***	6	8.1***	6	56.4***	6	22.9***
Treatment×Date	6	22.6***	6	8.3***	6	0.97^{NS}	6	2.04^{NS}

Wilcoxon's test showed significant differences (p<0.001) for BR aerial biomass dry weight between fenced and unfenced plots (fenced 158±36 g/m^2; unfenced ≅0; in April), with no significant differences between the two sampling dates (April and June), whereas AA showed similar values (p>0.1) for biomass in both treatments (fenced 56±10 g/m^2; unfenced 43±10 g/m^2; in April). BR reached higher aerial biomass than AA in the fenced plots, whereas the opposite was observed in the unfenced plots (p<0.01). Finally, Wilcoxon's test showed how the height and ground cover of BR were higher than those of AA in the fenced plots (p<0.05 and p<0.001, respectively), while in the unfenced plots AA reached higher values for both response variables (p<0.01 and p<0.001, respectively), (Figure 2).

Maximum ground cover of BR was 70% and 8% in the fenced and unfenced plot, respectively (average values of 56.0±4.8% and 3.8±1.0%, respectively, in mid-April), while the maximum percentage of coverage of AA was 30% in fenced and 35% in unfenced plot (23.6±2.6% and 23.7±4.0%, respectively, in late March). *B. rubens* reached a maximum height of 71 cm in the fenced plot, and 21 cm in unfenced plot (average values of 62.0±3.2 cm and 12.3±2.4 cm, respectively), while *A. arvensis* reached 30 cm and 25 cm in the fenced and unfenced plot, respectively (21.6±2.7 cm and 19.8±1.8 cm, respectively).

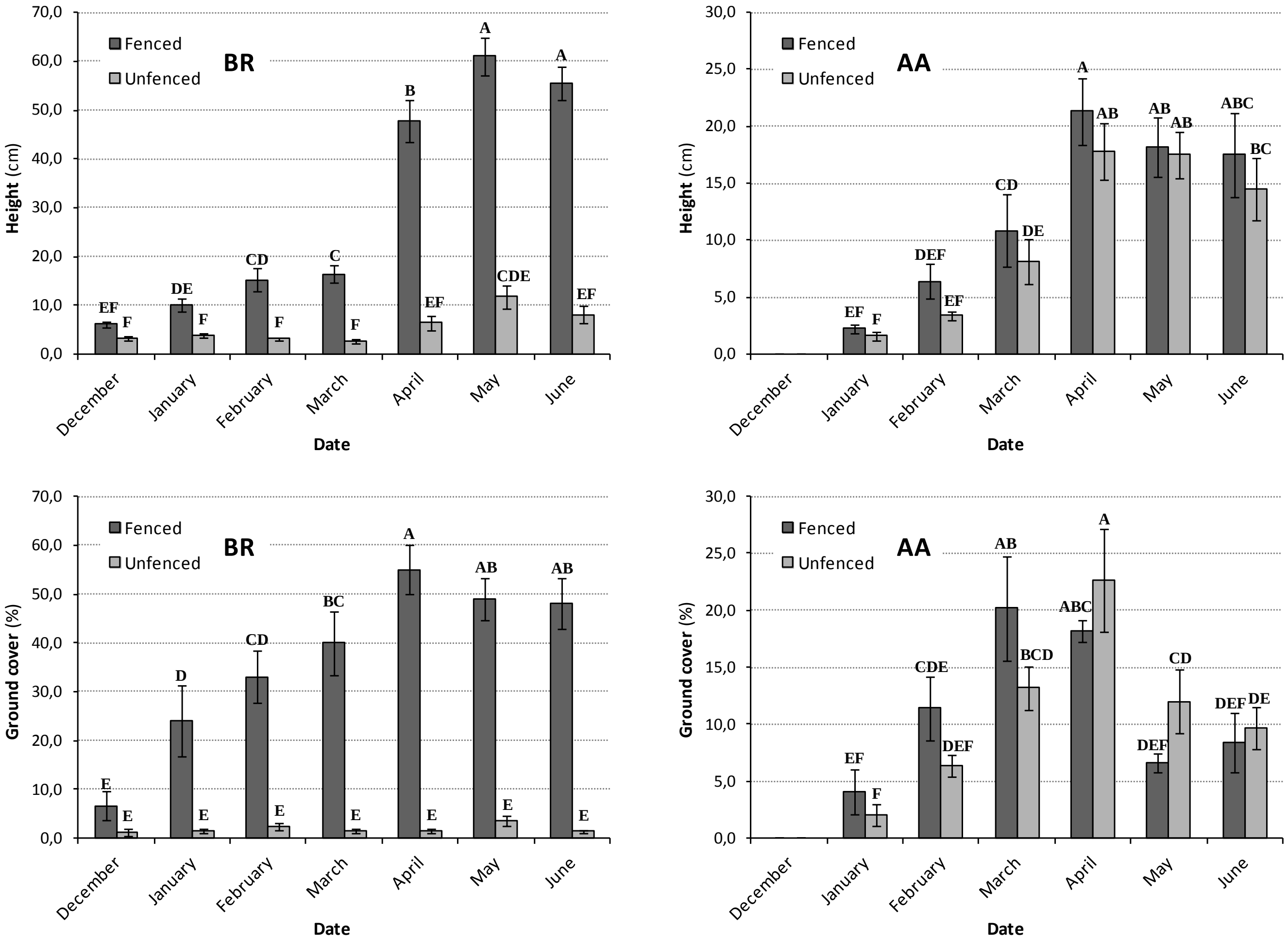

Figure 2. Mean values for height (cm; top) and ground cover (%; bottom) reached by *Bromus rubens* (BR) and *Anthemis arvensis* (AA) for the two treatments (fenced and unfenced plots). The bars indicate the standard error. Different letters indicate significant differences among groups according to Fisher's LSD post-hoc tests ($p<0.05$).

Discussion

Cover crops are known to reduce sediment yields from cropland areas by intercepting the kinetic energy of rainfall and by reducing the amount and velocity of runoff (Dabney et al., 2001). However cover crops become inefficient for agricultural sustainability when they do not reach significant ground cover, estimated in at least 30% during the rainy season (Sarrantonio, 2007), similar to our average values in the case of BR in the both fenced plots but not in the AA plots in which the average values for the season was 11.3%. The growth of AA kept constant in both treatments in spite of the high rabbit abundance. On the other hand, aerial biomass, height and coverage of BR were much higher in the fenced plots. This would indicate, in theory, that rabbit-proof fencing would be an appropriate option to be adopted by olive growers; however, the cost of fencing is prohibitive and the establishment of these fenced would make it difficult to manage the olive groves (tillage, fertilizer application, harvesting, etc.), as well as being ineffective (if rabbit burrows are already established).

Crop damage by rabbit grazing is modulated by rabbit abundance and weed diversity (Barrio et al., 2010; Guerrero-Casado et al., 2015), since a high diversity of weeds provides an alternative food resource to herbaceous cover crops, thus reducing consumption and favouring development and growth. BR was intensively consumed and its height and ground cover were severely limited, as well as biomass production, in the olive groves exposed to medium-high rabbit abundance and low weed diversity. However, we found that rabbits did not consume AA since its height, ground cover and biomass were similar in fenced and unfenced plots throughout its growth cycle (Figure 2). Therefore, the growth of AA was independent of rabbit abundance, even in areas with low density and diversity of natural vegetation, and the height and ground cover of AA were only influenced by the sampling date over the course of its growing season (Figure 2). Regardless of treatment (fenced and unfenced) both coverage and height of this species increased over time, reaching maximum values in early spring, the time in which this species usually reaches its maximum growth in this region (Alcántara et al., 2011; Soriano et al., 2016). In the case of aerial biomass, this was similar both inside and outside of the fenced areas, so that the rabbits did not cause impacts on AA biomass production. Therefore, AA has the potential to be used as a cover crop in areas with low diversity of natural vegetation and high rabbit pressure, since it does not suffer damage in the presence of rabbits. Besides this, AA reaches a short height and has a superficial and highly branched root system, which is beneficial for farmers (Shanks et al., 1995).

However, its growth (<35% of the soil surface was covered) was not enough to reduce soil erosion, since minimum ground cover stands at approximately 30% without slope (Sarrantonio, 2007). Furthermore, the growth of BR was higher than AA in fenced areas (Figure 2), which suggests that BR could cover a larger soil surface in areas with low rabbit grazing pressure, or where there were other food sources, and therefore its use is more recommended under these conditions.

Furthermore, this study coincided in time with a complete life cycle of these annual plants and allowed us to quantify the effect of rabbit grazing on cover crops from the beginning of their implantation. Our results showed that the damage of rabbits on BR was significant from the start of the study, since this annual plant begins to sprout and the first buds appear that will grow over the winter and spring (Serrano et al., 1991). From the first months, the coverage of BR in areas exposed to rabbits was severely reduced, not reaching even 10% coverage and it being always much lower than in fenced areas. In this scenario, the growth of BR was prevented from its early stages of development, because tender buds are preferred by rabbits (Barrio et al., 2013); and therefore, *B. rubens* cannot work as a winter cover crop to reduce runoff and soil erosion and improve soil fertility under high grazing pressure by rabbits, at least when other natural food resources are scarce (Dabney et al., 2001; Gómez et al., 2009a, b).

Implications and concluding remarks

In conclusion, our results support the fact that the establishment of native unpalatable species, such as *A. arvensis* as cover crops, may be implemented in areas with high rabbit grazing pressure, which could help to reduce soil erosion and provide other benefits of enhanced biodiversity. *A. arvensis* is insect-pollinated and dispersed by gravity, unlike *B. rubens* which is an facultative autogamous (Smith, 1981) and is pollinated by direct contact of stigma with anther and by wind, and preferentially dispersed by fauna. However, additional specific experiments are required to verify how far *A. arvensis* could promote plant and insect biodiversity, as well as some ecosystems services, such as pollination or control/mitigation of pests species, favoring the presence of ancillary insects in olive groves.

However, it is necessary to bear in mind that to be actually effective in term of erosion protection it is necessary to achieve an increase of vegetation cover in the medium long-term well above 30%. Its success in the first year of implantation, in which AA reached around 25% ground cover, suggests that subsequent colonisation would be strengthened by using simple management techniques, such as reduced traffic in lanes and avoiding mowing or spraying herbicides until AA completes its cycle; ensuring that early emergence of AA (self-seeding) just after the first autumn rains will stimulate initial plant growth due to high temperatures in early and mid-autumn in this region. This will allow the attainment of a larger ground cover during the winter. If rabbit grazing pressure is not too high, the implantation of other species such as *B. rubens* could ensure a larger ground cover, which could reduce soil erosion and enhance biodiversity in woody crops more effectively. Besides, further research is needed to optimize sowing technique, with proper management of the cover crops mowing dates to insure self-seeding, and/or the re-seeding of a fraction of the olive orchard each year, to reduce the percentage of bare soil during critical periods (Gómez et al., 2017).

Acknowledgements

We would like to thank Simon for helpful comments on the manuscript and the farmers for their cooperation. We are also grateful to the estate keepers and owners for their hospitality and assistance. This work was supported by the projects (AGL 2012-40128-C03-01, and P12-AGR-931) and EU–FEDER funds. AJC holds an FPI pre-doctoral scholarship by MINECO.

Figure S1. Olive orchards (A and B) and location of the study plots (fenced and unfenced).

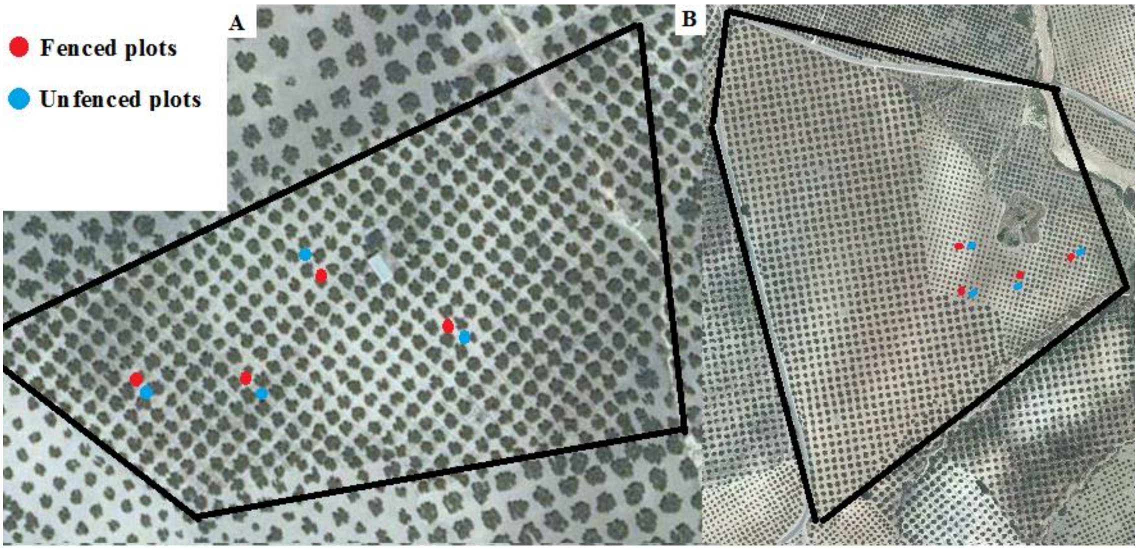

Figure S2. Views of *B. rubens* and *A. arvensis* in fenced and unfenced plots. Each plot was sown with both species separately (3 m x 3m).

Capítulo 3.2

Efectos de la sobreabundancia de ungulados silvestres sobre pastizales naturales en el sur de España

Carpio, A.J., Oteros, J., Lora, Á., Tortosa, F.S. (2015b). **Effects of the overabundance of wild ungulates on natural grassland in Southern Spain.** *Agroforestry Systems*, *89(4)*, 637-644.

Resumen

Los aumentos en la deposición de nitrógeno afectan a la biodiversidad y la composición de la vegetación natural. Una cantidad significativa de este nitrógeno puede provenir no sólo de la agricultura y la ganadería intensivas, sino también de los ungulados silvestres cuya abundancia y área de distribución están aumentando actualmente en la Península Ibérica. En este estudio hemos estimado la abundancia de dos especies de ungulados silvestres (ciervo y jabalí) y la cantidad de nitrógeno contenido en sus excrementos y en la hierba. También hemos registrado la comunidad herbácea. Los resultados muestran que la densidad de estos ungulados está correlacionada positivamente con un aumento en el nitrógeno de la hierba, lo que afecta adversamente al porcentaje de leguminosas en el pasto. Estos resultados sugieren que las altas densidades de ungulados pueden estar afectando a las comunidades vegetales aumentando la cantidad de nitrógeno como resultado de la deposición de excrementos. Por lo tanto, se debe revisar el sistema actual de gestión de la caza mayor para que sea compatible con la conservación de las comunidades de plantas y las especies de pequeños herbívoros que pueden verse afectadas negativamente por los cambios en la calidad y cantidad de los pastos.

Abstract

Increases in the deposition of nitrogen affect biodiversity and the composition of natural vegetation. A significant amount of this nitrogen may originate not only from intensive agricultural and livestock farming, but also from wild ungulates whose abundance and area of distribution are currently increasing in the Iberian Peninsula. In this study we have estimated the abundance of two species of wild ungulates (red deer and wild boar) and the amount of nitrogen contained in their droppings and in the grass. We have also recorded the herbaceous community. The results show that the density of these ungulates is positively correlated to an increase in the grass nitrogen, which adversely affects the percentage of leguminosae in pastures. These results suggest that high densities of ungulates may be affecting plant communities by increasing the amount of nitrogen as a result the deposition of droppings. The current system of big game management should therefore be reviewed to make it compatible with the conservation of plant communities and small herbivore species that may be negatively affected by changes in pasture quality and quantity.

Introduction

The composition of grasslands is related to their structure and species diversity. It has been found that the first few years during which cattle graze at low densities on ploughed soil can generate a stable structural pattern in the grass (Van Den Bos and Bakker 1990; Yates et al. 2000). Similar results have been found in Mediterranean Spain (Peco et al. 2006) where low grazing intensities, along with fine material (clay), content of organic matter, total nitrogen, potassium availability and assimilable water, have led to the maintenance of high levels of grass diversity. However, herbivores may control the function of ecosystems, by mediating the transformation and flux between energy and matter (Lawton 1994; Pastor and Naiman 1992), by limiting the abundance of some important plant species. This affects resource abundance for organisms such as nitrogen fixers (Ritchie and Tilman 1995).

Changes in the composition of pastureland species associated with an increase in soil nitrogen (hereafter N) deposition caused by grazing have been widely reported in Europe in a range of plant communities (Powlson 2000; Fernández et al. 2001; Vaieretti et al. 2013). Excessive N fertilisation has strong impacts on the environment and soil, including soil microorganisms (Bodelier and Laanbroek 2004), and on acidification and eutrophication (Hornung and Sutton 1995; Sutton et al. 2011). This problem is of such magnitude that European legislation has been approved in order to take measures (IPPC and NEC Directives) focused on attempting to reduce ammonia (NH_3) emissions from livestock farming, especially pig and poultry production (Directive 2001/81/EC).

Increased emissions of NH_3 as a result of intensive farming have been identified as the major cause of many of these effects (Hristov et al. 2011). Earlier studies have also shown that foliar N concentrations in sampled vegetation decline with the distance from livestock buildings (Pitcairn et al. 1998). The abundance and distribution of wild ungulate species have increased over the last few decades in both Europe and North America owing to their higher economical benefits when compared with cattle (Côte et al. 2004; Forrester and Wittmer 2013), thus leading to an increase in the total area devoted to hunting species (Bueno et al. 2009). Open areas and traditionally managed wood pastures are consequently disappearing as a result of land abandonment by farmers and marginalisation (Garbarino et al. 2012).

Site productivity (measured as soil fertility) and herbivore body size have been reported as two important factors in regards to the effect of grazing on plant diversity (Knapp et al. 2012). Differences in site productivity can therefore lead to grazing having a positive effect on plant diversity (Belsky 1992; Collins et al. 1998), but also a neutral (Adler et al. 2005; Stohlgren et al. 1999) or negative effect (Milchunas et al. 1998; Howe et al. 2002; Wardle et al. 2001). Herbivore body size has also been found to be of some importance as regards the effect of grazing on plant diversity. Large herbivores increase plant diversity at higher productivity but decrease diversity at low productivity, while small herbivores may not have consistent effects on the productivity gradient (Bakker et al. 2006).

In Iberia, the populations of both wild boar (*Sus scrofa*) and red deer (*Cervus elpahus*) have greatly increased over the past few decades (Acevedo et al. 2008, Bosch et al. 2012), reaching high densities in hunting estates in South Central Spain on which they receive extra feeding during summer and early autumn (Rodriguez-Hidalgo et al. 2010). The high densities of wild ungulates may actually be acting as a livestock system from the point of view of nitrogen input through droppings, particularly in the southern half of the Iberian Peninsula in which some of the highest densities of deer and wild boar ever known have been recorded, reaching densities of more than 50 deer/Km² and 90 wild boar/km² in intensively managed hunting areas (Acevedo et al. 2011; Bosch et al. 2012). These high densities are maintained by surrounding hunting estates with 2 m high fences (Torres-Porras 2009). The growing numbers of these ungulates in Europe have resulted in increased herbivore pressure which affects ecosystems in many ways (Cuevas et al. 2010; Kuijper 2011) and is affecting the natural vegetation (Knight 2003; Monzon et al. 2012). They are also causing an important reduction in plant diversity (Horsley et al. 2003) in addition to alterations in successive steps (Seagle and Liang 2001), affecting other small game species such as rabbits (Barrio et al. 2013; Carpio et al. 2014b) and partridges (Carpio et al. 2014c).

The aim of this study is to evaluate the effect of the increased abundance of wild ungulates on grassland composition in a southern Spain, through the increase in the amount of nitrogen as a result the deposition of droppings. The high abundance of ungulates (Acevedo et al. 2008; Bosch et al. 2012) and the low productivity of the Mediterranean forest (Zaragoza-Castells et al. 2008) lead us to hypothesise a negative relationship between the grassland structure and composition and red deer and wild boar densities.

Material and Methods

Study area

Data were collected on 9 different hunting estates (5 open vs. 4 fenced) in southern Spain (located between 38º 17′ N, 4º 56′ W and 37º 57′ N, 5º 3′ W), which were separated by between 5.6 and 23.7 km (average ± 12.4 ± 4.9km). The altitude ranges from 400 to 800 m.a.s.l. This area has a sub-humid Mediterranean climate with virtually no rainfall in summer (June-August). The dominant vegetation includes tree species such as holm oak (*Quercus ilex* subsp. *ballota*) and cork oak (*Quercus suber*), together with pine plantations (*Pinus pinea* and *Pinus pinaster*), accompanied by shrub species dominated as *Cistus* spp., *Erica* spp., *Pistacia* spp., *Phyllirea* spp. and *Rosmarinus officinalis,* with scattered pastures and small areas of crops. These are the dominant species in both Mediterranean forests and in the "dehesa", a savannah-like semi-natural landscape used for animal breeding (Moreno and Pulido 2009). Both landscapes are found throughout the central and southern areas of Spain (Spanish Ministry of the Environment 2002). The study sites are mainly devoted to the recreational hunting of wild boar and red deer.

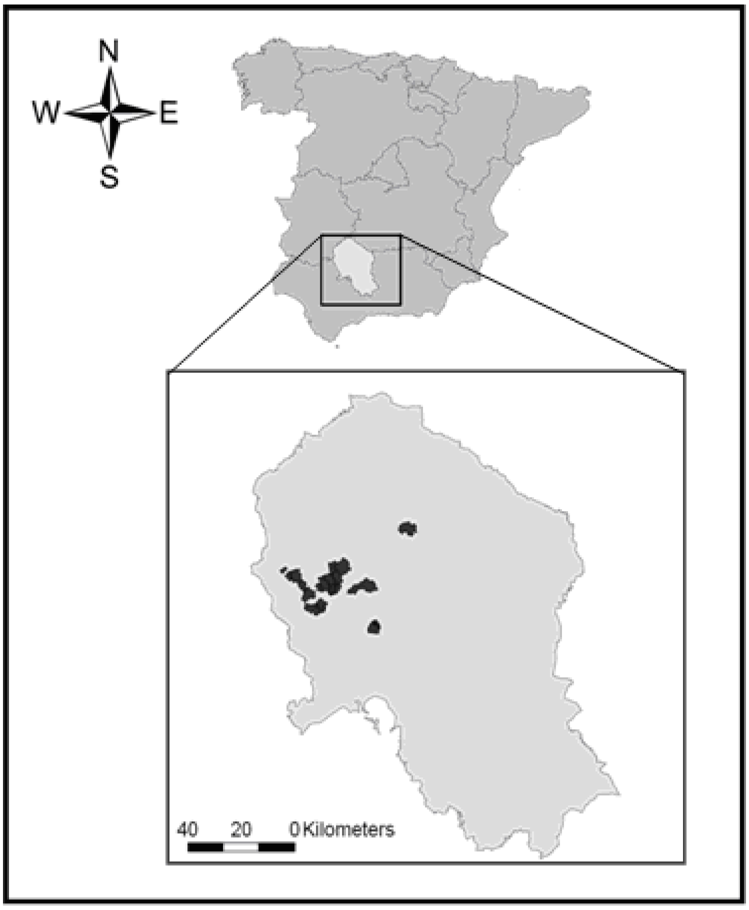

Figure 1. Map of Spain showing the location of the sampling sites (Córdoba province in grey).

Estimating red deer abundance

Deer abundance was estimated on each hunting estate, and these estates were considered as discrete management units. We performed two spotlights census, which were carried out on the same non-linear transect in August and September 2011 by driving at 10-15 km/h. Each transect was an average of 20.3 km ± 2.34 (S.E.) in length (Carpio et al. 2014b). The distance from the observer to the deer or to the centre of a deer group was measured, and compass bearings were taken to determine the angle between deer, or deer groups, and the transect line. The distance between the observer and the deer was measured with a Leica LRF 1200 Scan telemeter (Solms, Germany) (range 15–1100 m; precision ±1m/±0.1%). The abundance of the deer populations was estimated using distance sampling (Buckland et al. 2004, Distance 5.0 software). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using cosine, hermite polynomial and simple polynomial adjustment terms, which were fitted sequentially. The selection of the best model and adjustment term was based on Akaike's Information Criterion (AIC) as used in the studies by Acevedo *et al.* (2008) and Barrio *et al.* (2010a).

Estimating wild boar relative abundance

We estimated the wild boar abundance index by following the protocol of Acevedo *et al.* (2007) based on the frequency of faecal dropping on walked transect. The counts took place in two transects of 4 km in each of the 9 estates in September and October 2011. Each transect count consisted of 40 segments of 100 m in length and 1 m in width, divided into 10 sectors of 10 m in length. Sign frequency was defined as the average number of 10-m sectors containing droppings per 100-m transect (Carpio et al. 2014c), and a single average value of wild boar abundance was calculated per estate. This was done using a frequency based indirect index which was calculated according to Acevedo et al. 2007, using:

$$\mathrm{FBII} = \frac{1}{n}\sum_{i=1}^{n} S_i$$

Faecal nitrogen and nitrogen in diet

In this study, faecal nitrogen was used as an indicator of the quality of the species' diet (Hamel et al. 2009; Massey et al. 1994). Both faecal nitrogen (faecal N) and dietary nitrogen (NDiet) were estimated by creating 2 transects of 4 km each on the estates (n = 18) in spring, at which time deer droppings (5-10 faeces / sample) and vegetation samples were collected at intervals of 1000 m (n = 8) to ensure that the samples were spatially independent (Acevedo et al. 2011). A total of 144 samples were obtained for each of our two units of study (Carpio et al. 2014b). The concentration of nitrogen was estimated using the EUROVECTOR EA 3000 elementary analyser, which determines the quantitative carbon, nitrogen, hydrogen and sulphur content of the samples. This technique is based on the Dumas method (Simmone et al. 1997), which in this case consisted of the complete thermal oxidation of 1 to 2 mg of the sample by combustion in an oxygen enriched atmosphere at a temperature of 1020 ° C. The combustion gases are drawn through an interne gas (He) to a chromatography column where they are then separated and detected using a thermal conductivity detector. We thus obtain the percentage content of each element in the sample with regard to the samples weight, in this case percentage of nitrogen (Acevedo et al. 2011).

Habitat structure and composition

Ten "One-dimensional linear transects" of 50 m length were studied on each hunting estate during the month of May (90 transects employed), on which grass coverage was calculated and vegetation was classified at the family level (Gregoire et al. 2003; Affleck et al. 2005; Barabesi 2007; García et al. 2009). The grass cover per unit area provides information on the state of conservation of grasslands and can also be seen as an indirect estimate of the density of herbaceous vegetation (Lazo et al. 1992). The location of transects within each study area was determined using a stratified sampling experimental design, signifying that all of the landscapes from each plot studied were represented in the sampling exercise with the same proportion. The main landscapes in the study area have been considered: broad-leaved forest, coniferous forest, mixed forest, moors and heartland, sclerophyllous vegetation, transitional woodland-shrub, natural pastures and dehesas (the dominant landscape). The percentage of herbaceous cover occupied by leguminosae was also calculated in these transects (area occupied by leguminosae / area occupied by all herbaceous vegetation *100) (Ritchie et al. 1998).

Statistical analysis

The response variables used were 'nitrogen in plants' and 'percentage of leguminosae', and these were transformed by using the LN function to fulfil the normality criteria. The relationships between ungulate abundance (which were studied separately for red deer and wild boar, respectively) and nitrogen in plants (dependent variable, Model 1), and between ungulate abundance and percentage of leguminosae (dependent variable, Model 2) were tested by using two linear mixed models (LMM). A normal distribution function and an identity link were used in both cases. State (two levels: open vs. fenced) was included in the models as a factor. Red deer and wild boar abundances, the nitrogen in deer droppings and the percentage of grass and leguminosae, were included in Model 1 as explanatory variables, while red deer and wild boar abundances, the nitrogen in deer droppings, nitrogen in plants and percentage of grass were included in Model 2 as explanatory variables. The interaction between red deer and wild boar abundances was also included as co-variable in both models. The sampling site was included (9 levels) as a random factor, as each hunting estate has features that may have random effects in the final result.

The selection of models was based on Akaike's Information Criterion (Nelson et al. 2005) by comparing nested models following a backwards procedure (Zuur et al. 2009). The assumptions of normality, homogeneity and independence in the residuals were met in all the models (Zuur et al. 2009). Statistical analyses were performed using IBM SPSS Statistics 20 and SAS 9.0 statistical software. The significant p-value was set at $p = 0.05$.

Results

The best relative fit of the model and adjustment term for distance-sampling was the hazard-rate cosine based on the lowest AIC score. The average red deer density, expressed as the number of deer per 100 ha, ranged between 25 and 68. The coefficients of variation of distance-sampling estimates ranged between 2.95% and 38.86%. The wild boar frequency index ranged from 0.04 to 0.47 (average ± SE 0.26 ± 0.15). The nitrogen content in the deer droppings ranged between 1.74 and 3.42% (average ± SE 2.47 ± 0.3), while the nitrogen in plants had a range of between 0.84 and 4.59% (average ± SE 1.81 ± 0.53).

41 families of herbaceous vegetation were identified in the transects of 50 m in length, of which only 14 families covered more than 1% of the surface area sampled (Figure 2). In the shrub layer, the most common species were *Cistus ladanifer, Pistacea lentiscus, Genista hirsuta, Cistus monspeliensis, Rosmarinus officinalis, Lavandula stoechas subsp. sampaiana, Lavandula stoechas subsp. luisieri, Cistus albidus, Phlomis purpurea, Retama sphaerocarpa, Quercus coccifera, Daphne gnidium, Cistus crispus, Quercus ilex, Scirpus holoschoenus,* while in the forest stratum they were *Pinus pinea, Pinus pinaster, Quecus ilex, Quecus faginea, Olea europaea, Arbustus unedo, Fraxinus angustifolia and Quercus suber.*

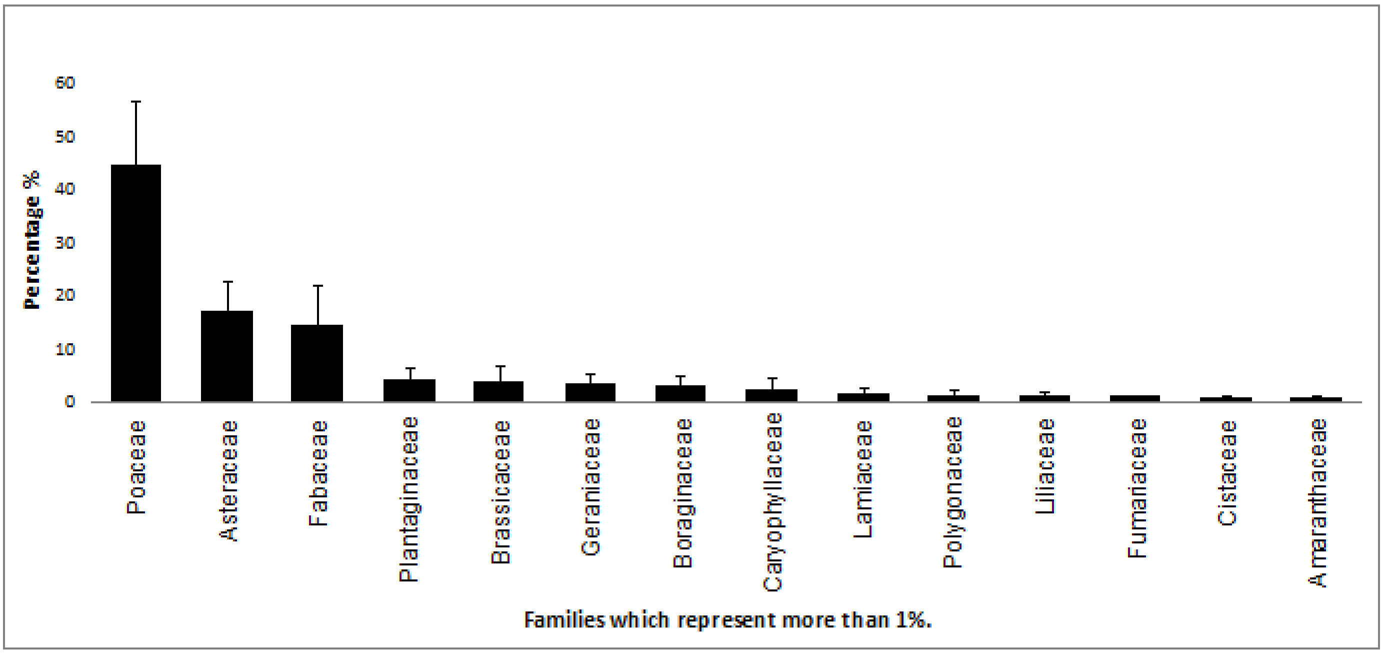

Figure 2. Percentage of herbaceous families sampled, representing more than 1% in terms of area covered.

The nitrogen content in plants (Model 1) was found to be positively affected by deer density ($p < 0.05$), with the best model only including this variable (Table 1). With regard to the variables related to leguminous cover (Model 2), the best model was the full model that included Open/fenced estate, deer density, wild boar density, wild boar * red deer density, nitrogen in plants and nitrogen in deer droppings. The nitrogen in deer droppings, meanwhile, was only associated with leguminous cover (Table 1). This faecal nitrogen showed a negative relationship with leguminosae cover, showing these feces have higher nitrogen concentration in areas with less leguminosae.

Table 1: β coefficients, p and F values of the best LMMs to explain nitrogen content in plants (Model 1) and the percentage of leguminosae (Model 2). Significant p-values are highlighted in bold type.

<table>
<tr><th colspan="4">Nitrogen content in plants (Model 1, ΔAICc = 16.68)</th></tr>
<tr><td></td><td>F</td><td><i>p</i></td><td>β</td></tr>
<tr><td>Deer density</td><td>4.92</td><td><0.05</td><td>0.43</td></tr>
<tr><td colspan="4">Percentage of leguminosae (Model 2, AICc = 177.4)</td></tr>
<tr><td>Open/Fenced</td><td>2.032</td><td>0.17</td><td>0.68</td></tr>
<tr><td>Deer density</td><td>1.03</td><td>0.26</td><td>4</td></tr>
<tr><td>Wild boar density</td><td>0.4</td><td>0.96</td><td>2.3</td></tr>
<tr><td>Wild boar*deer density</td><td>0.73</td><td>0.41</td><td>-8</td></tr>
<tr><td>Nitrogen in deer droppings</td><td>4.29</td><td><0.05</td><td>-0.7</td></tr>
<tr><td>Nitrogen in plants</td><td>1.65</td><td>0.21</td><td>0.23</td></tr>
</table>

Discussion

Grazing is expected to promote positive feedback in productive systems and negative feedback in unproductive systems (Bardgett and Wardle 2003; Ritchie et al. 1998; Vaieretti et al. 2013; Wardle et al. 2004). Mediterranean forest has very poor nutrients (Zaragoza-Castells et al. 2011), despite which wild ungulates are kept at very high densities on fenced hunting estates on which extra feeding is provided during the limiting season (Rodriguez- Hidalgo et al. 2010).

Studies on the relationship between herbivore abundance and plants, along with the factors related to the overabundance of herbivores and its negative effects, are common (Kuijper 2011; Monzón et al. 2012; Perea and Gil 2014). An overabundance of ungulates (Acevedo et al. 2008; Bosch et al. 2012) may provide plants with extra nutrients (e.g. nitrogen), signifying that plants can allocate more resources to these existing sheets, thus increasing their photosynthetic capacity and / or the production of more leaves and the subsequent increase in their biomass (Bowman and Conant 1994).

Our data show that deer density positively correlates with the nitrogen content in plants. This variable was not affected by wild boar abundances, nitrogen in deer droppings or the percentage of grass and coverage of leguminosae, and only deer density was identified as a predictor for nitrogen in plants. However, nitrogen in deer droppings (see discussion below), was negatively associated with leguminosae cover. Overall, our results show a positive and significant relationship between deer density and the nitrogen content in plants. A high content of N in the soil have a negative effect on the plant community (Pitcairn et al. 1998) and also limit abundances of nitrogen-fixers such leguminosae, which are less efficient in situations of high nitrogen availability (Ritchie et al. 1998).

This correlation between nitrogen contents of vegetation and deer density has been previously discussed by several authors. Ungulate grazing is known to greatly affect the availability of nitrogen in the soil, plants and the microbial flora associated with grasslands (Danell et al. 2003). Wu et al. (2011) have shown that this variation is not uniform, and is different depending on the stocking density, as found with sheep when NO_3 increased at higher sheep densities. A higher quantity of faecal nitrogen in these areas of high density may result from the fact that the plant species in these zones with N rich tissue have proteins that are less assimilable by deer, as is the case of the leguminosae (Ritchie et al. 1998), thus leading to an increase in faecal nitrogen. Another reason to explain the higher concentration of faecal nitrogen at high ungulate densities is the high concentrations of tannin in the vegetation (Torres-Porras 2009), as a plant defence mechanisms against herbivores (González-Hernández et al. 2000). Tannins inhibit the digestion of protein and fibre, and may be bound to protein and form insoluble complexes that are retained in the digestive tracts and excreted in faeces, thus diminishing the amount of digestible protein in forage and increasing the amount of nitrogen in faeces (Kariuki and Norton 2008).

With regard to wild boar rooting activity, according to our results, this was also found to affect soil properties and nutrient cycling (Mohr et al. 2005; Palacio et al. 2013), thus increasing compacting and nitrogen availability, which alters the composition of plant species (Bueno et al. 2009; Cuevas et al. 2010), therefore favouring nitrophilous plants and diminishing the leguminosae in the grass (Kuijper et al. 2009), and reducing the quality of the remaining grass which may affect other herbivorous species such as rabbits (Ritchie et al. 1998).

The increased availability of soil nitrogen (through waste products from mammalian herbivores and rooting), as occurs with livestock (Pitcairn et al. 1998), may have a number of adverse effects. For example, this increasing availability of nitrogen may alter the composition of plant species (Ritchie et al. 1998), thus favouring plant species that rapidly take up N and grow relatively faster, because the higher N content of plant tissue may be required to support greater metabolic activity and growth (Tilman 1988). This reduces the amount of leguminosae in the grass (Kuijper et al. 2009) and possibly decreases its biodiversity (Fernandez-Olalla et al. 2006).

Conclusions

This study supports the hypothesis that native wild ungulates at high densities reduce the diversity of Mediterranean plant communities. Results have evidenced a positive relationship between red deer density and nitrogen content in the herbaceous community. High densities of red deer but not wild boar have an important impact on nitrogen concentration in plants, leading to an increase in nitrogen availability. Thus favouring nitrophilous plants and reducing the leguminosae in the grass, which may decrease the quality of the grass that is available for other herbivores such as rabbits. The increases in the total area devoted to big game management species and the high ungulate abundances that have taken place on most hunting estates lead us to predict a decrease in pasture quality. More studies are required to test the subsequent negative effect on other herbivores such us rabbits, owing to the high ecological value of this keystone species in Mediterranean Iberia.

Acknowledgements

We should like to thank E. López and the students Oscar, David and Macarena for their help in collecting field data. We are also grateful to the estate keepers for their hospitality and assistance in the field work, and to the Andalucía Autonomous Government’s Environmental Council for financing this work via a project to improve the habitat of the black vulture in Córdoba province, thanks to which we have been able to carry out this work. Our thanks are also due to the editor and the anonymous reviewers for their thorough suggestions and comments.

Capítulo 3.3

Efecto de la densidad de ungulados silvestres sobre los invertebrados en un ecosistema Mediterráneo

Carpio, A.J., Castro-López, J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., Tortosa, F.S. (2014). **Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem.** *Animal Biodiversity and Conservation, 37(2),* 115-125.

Resumen

En las últimas décadas, la abundancia y distribución de determinadas especies de caza mayor, especialmente el ciervo rojo (*Cervus elaphus*) y el jabalí (*Sus scrofa*), han aumentado en el centro sur de España como resultado de las estrategias de gestión de la caza. La alta densidad de estas especies de ungulados puede afectar a la abundancia de invertebrados epigeos. Pusimos a prueba las relaciones entre las abundancias de especies de caza mayor y la biodiversidad, la riqueza de taxones, la biomasa de invertebrados y su frecuencia en nueve fincas de caza y en comparación con zonas de exclusión de ungulados. En sí la exclusión de ungulados afectó a la riqueza de invertebrados, ya que se encontraron valores más bajos en las parcelas abiertas, mientras que las más altas diferencias en la diversidad de invertebrados entre parcelas cercadas y abiertas se encuentran en zonas con alta densidad de jabalíes. Donde las densidades de jabalíes fueron altas, el número de invertebrados disminuyo, mientras que donde ellos eran bajos, el ciervo rojo tuvo un efecto positivo sobre la abundancia de invertebrados. Así las parcelas cercadas parecían ofrecer refugio a los invertebrados, sobre todo donde los jabalíes eran abundantes. Este estudio apoya la idea de que la estructura de las comunidades de fauna es dañada por las poblaciones de alta densidad de ungulados, probablemente debido a la disminución de la disponibilidad de alimentos debido al sobrepastoreo, las condiciones modificadas de micronichos ecológicos y la depredación directa. Sin embargo, los efectos dependen del grupo de invertebrados, ya que las especies saprofitas podrían beneficiarse de la alta abundancia de ungulados. Nuestros resultados reflejan la necesidad de controlar la densidad de población de ungulados en condiciones mediterráneas, en el suroeste de Europa y la necesidad de implementar parcelas de exclusión de ungulados.

Abstract

In recent decades, the abundance and distribution of certain big game species, particularly red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*), have increased in south central Spain as a result of hunting management strategies. The high density of these ungulate species may affect the abundance of epigeous invertebrates. We tested the relationships between big game abundance and biodiversity, taxon richness, the biomass of invertebrates and their frequency on nine hunting estates and in comparison to ungulate exclusion areas. Ungulate exclusion itself affected invertebrate richness, since lower values were found in the open plots, whereas the highest differences in invertebrate diversity between fenced and open plots was found in areas with high wild boar density. Where wild boar densities were high, the number of invertebrates decreased, while where they were low, red deer had a positive effect on invertebrate abundance. Fenced plots thus seemed to provide refuge for invertebrates, particularly where wild boar were abundant. This study supports the idea that the structure of fauna communities is damaged by high density populations of ungulates, probably due to decreased food availability owing to overgrazing, modified conditions of ecological microniches and direct predation. However, the effects depended on the group of invertebrates, since saprophytic species could benefit from high ungulate abundance. Our findings reflect the need to control ungulate population density under Mediterranean conditions in south-western Europe and to implement ungulate exclusion plots.

Introduction

The soil invertebrate community participates actively in ecological processes that are essential for substrate soil fertility and plant succession (Hedlund and Öhrn 2000; Osler and Sommerkorn 2007). Sources of soil disturbance and their effect on invertebrates, including the use of pesticides, phytosanitary treatment and other measure, have been thoroughly studied in agricultural ecosystems (Vickery et al. 2009; Raebel et al. 2012). However, knowledge of the factors affecting invertebrate communities in forest ecosystems is scarce (McIntyre 2000).

Ungulate density and range has increased throughout Europe and North America over the last century (Clutton-Brock and Albon 1992; Côté et al. 2004; Gordon et al. 2004; Sarasa and Sarasa 2013) as a result of the extirpation of large predators (Breitenmoser 1998), changes in sylviculture and agriculture, and the intensification of game management (Apollonio et al. 2010). This increase in wild ungulate populations may have a strong impact on soil nutrient status and biota due to grazing, rooting, trampling and dunging, and changes in plant community due to herbivory can also affect invertebrate community structure (see Spalinger et al. 2012), but specific studies on these relationships are scarce. High densities of either livestock (Rosa et al. 2009) or wild ungulates (Côté et al. 2004; Mohr et al. 2005) are known to affect epigeous invertebrate communities, which are useful bioindicators (Gerlach et al. 2013) and important food resources for many species of birds, including the red-legged partridge, a key prey for many predators and the most important game bird in Spain (Wilson et al. 1999). Previous studies on the effect of ungulates on invertebrates have been conducted in areas in which ungulates are invasive (Cuevas et al. 2010, 2012) and in temperate climates, focusing on deciduous forests (Côté et al. 2004; Mohr et al. 2005; Mizuki et al. 2010). However, few studies have reported the effect of native ungulates on invertebrate soil diversity in semiarid areas, such as Mediterranean habitats (Gebeyehu and Samways 2006). Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are the principal wild ungulate species in Southern European Mediterranean habitats, reaching very high abundances when intensive hunting management is performed (Vicente et al. 2007), ranging between 0.04 to 66.77 deer km^{-2} (mean= 19.51; n= 22 populations) (Acevedo et al. 2008). In fact, the red deer is considered by some authors to be among the most invasive species in the world (Lowe et al. 2000) and its negative effect on some arthropod taxa such us Orthoptera or other phytophagous insect has been reported in subalpine grasslands (González-Megías et al. 2004; Spalinger et al. 2012).

A high abundance of wild boar has also been reported to have a strong impact on edaphic fauna through disturbance (Herrero et al. 2006; Giménez-Anaya et al. 2008), rooting, and the direct consumption of meso- and macroinvertebrates (Cuevas et al. 2010). However, despite the large increase in the densities of wild boar and deer, little is known about the ecological impact of their overabundance on Mediterranean ecosystems (Barrios-García and Balliari 2012; Carpio et al. 2014b) and particularly on the epigeous invertebrate assemblage, essential elements in the diet of many birds (Holland et al. 2006).

The aim of this study was to determine the impact of wild boar and red deer on diversity, richness and biomass of epigeous invertebrates in a semiarid Mediterranean environment from south central Spain, within the native distribution range of these two ungulate species.

Material and methods

Study area

Data were collected on 9 different hunting estates, which had an average area of 2470 hectares (range 1480-3600 ha), located in southern Spain. The altitude ranged from 400 to 800 m.a.s.l. The dominant vegetation included tree species such as holm oak (*Quercus ilex*) and cork oak (*Quercus suber*), pine plantations (*Pinus pinea* and *Pinus pinaster*), shrub species such as *Cystus* spp., *Erica* spp., *Pistacia* spp., *Phyllirea* spp. and *Rosmarinus officinalis,* and scattered pastures and small areas of crops (Vicente et al. 2007). These savannah-like landscape units are called ‘dehesas’. The study sites are mainly devoted to recreational hunting for wild boar and red deer.

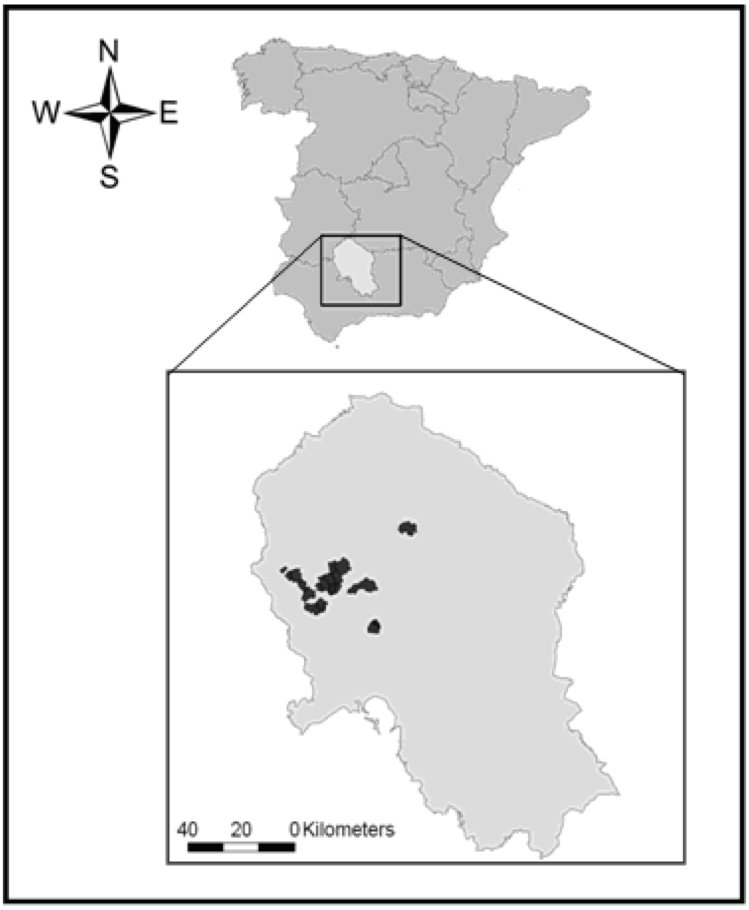

Figure 1. Map of Spain showing the location of the sampling sites (Córdoba province in light grey).

Estimating red deer and wild boar abundance

Deer population size was estimated at hunting estate level, the estates being considered as discrete management units. Two spotlight counting events between September and October 2011 were used to estimate the deer population size at each estate. Transects (mean length = 20.3 km ± 2.34 SE) were driven at 10-15km/h (Carpio et al. 2014b). The distance from the observer to the centre of a deer group was measured, and compass bearings were taken to determine the angle between deer, or deer groups, and the transect line. The distance between the observer and the deer was measured with a Leica LRF 1200 Scan telemeter (Solms, Germany) (range 15–1,100 m; precision ± 1 m/± 0.1%). The abundance of the deer populations was estimated by distance sampling (Buckland et al. 2004, Distance 5.0 software). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using cosine, hermite polynomial and simple polynomial adjustment terms, which were fitted sequentially. The selection of the best model and adjustment term were based on

Akaike's Information Criterion (AIC). The best relative fit of the model and adjustment term for distance-sampling was the hazard-rate cosine based on the lowest AIC score. However, this census method suffers significant variations depending on the type of game mode that is practiced (hunts or stalking).

Two 4 km transects per site were sampled for signs of wild boar activity following the guidelines of Acevedo *et al.* (2007). Each transect consisted of 40 segments of 100 m in length and 1 m in width. Every 100 m segment was divided into 10 sectors of 10 m in length. Sign frequency was defined as the average number of 10-m sectors containing droppings per 100-m transect (Carpio et al. 2014c), and a single average value of wild boar abundance was calculated per estate.

Experimental plots

We used 5 ungulate proof fences in each one of the 9 hunting states. These fenced plots (hereafter FP) were constructed three to five years prior to data collection and they were constructed from steel. Each FP was 0.5 ha, with a mesh size of 150 mm×100 mm in order to prevent the ungulates access, although they were accessible to other animals (Carpio et al. 2014c). Two pitfall traps were randomly placed in each FP, resulting in a total of 90 traps where ungulates were excluded. Another two pitfall traps were placed 100m outside of each FP as controls (Open Plots, OP), resulting in 180 pitfall traps in total.

We conducted two surveys of invertebrates. The pitfall traps consisted of plastic receptacles, with a capacity of 0.75 litres and an opening diameter of 12 cm, buried at ground level (Paschetta et al. 2013). These were half filled with a solution of salts (to preserve the specimens caught) and soap (to break the water surface tension). The trapped invertebrates were collected 14 days after the traps had been set (Allombert et al. 2005). The contents of the receptacles were passed through a sieve. The invertebrates were preserved in 100 ml plastic containers with 70% alcohol and later identified by stereomicroscope in the laboratory. Specimens were identified to order level (Barrientos 2004), as in some previous studies on the diet of farmland birds (Holland et al. 2006).

We studied the diversity and structure of invertebrate orders larger than 0.02 mm (mesofauna and macrofauna) present in our study area, excluding microfauna (less than 0.02 mm) (Swift et al. 1979). We therefore studied the most important groups in the diet of red-legged partridge chicks (Holland et al. 2006; Aebischer and Ewald 2012). We excluded pitfall traps containing necrophagous insects (11% of placed traps) and also those in which more than 50% of individuals belonged to the order Hymenoptera (13% of placed traps) owing to the proximity of ant nests as these could exert a repellent effect on other arthropods (Blum 1978).

For each sampling point, we calculated the invertebrate dry weight (B), taxon richness (S) and the Shannon index (Shannon 1948). To obtain the dry weight, the contents of the pitfall traps were dehydrated in an oven at 80º C for 24 hours. A precision scale (0.001 g) was used. We calculated the values for each variable from the average of the two pitfall traps in each pair of sampling periods (OP and FP).

Vegetation structure

The vegetation structure was described by creating a buffer area of a 25 m radius around each pitfall trap and the percentage of grass, scrub and woodland cover was estimated by eye, following similar protocols for general habitat-species studies (Morrison et al., 1992). All the estimates of vegetation structure were performed by the same observer (A.J.C).

The amount of plant biomass was assessed from cuttings in an area of 25 cm^2 of herbaceous vegetation. Two sampling points were randomly selected in both the fenced and the open plots. The sampled vegetation was dried in a drying oven with hot air circulation at 60 ° C until a constant weight was obtained. An electric balance (precision: 0.01 g) was used.

Statistical analysis

The relationships between ungulate abundance (separately for red deer and wild boar, respectively) on invertebrate richness, dry mass, the Shannon index and absolute frequency (number of invertebrates per sample) were tested using generalized linear mixed models (GLMMs). With regard to the absolute frequency models, the analyses were carried out separately for each of the 4 taxonomic groups into which the samples had been pooled. The taxonomic categories were "Hymenoptera" (n = 1120), "Insecta" other than Hymenoptera (16 orders, n = 1743), class "Arachnida´´ (including orders Araneida, Acari, Opiliones, Scorpionida, Pseudoescorpionida and Solifugae*;* 6 orders, n = 906), and "others" (including the subphylum Myriapoda, order Isopoda, and classes Oligochaeta and Gastropoda; 9 taxa, n = 787).

Treatment (two levels: open vs. fenced plots) was included in the model as the factor, whereas red deer and wild boar abundances, in addition to the vegetal biomass

(g) and percentage of grass, shrub and tree covers, were included as co-variables. We also included the interaction between the treatment and the abundances of ungulates and the interaction between deer and wild boar density. The estate was included (9 levels) as a random factor. Since every plot was sampled twice, the sampling dates were included in the model as repeated measures.

A normal distribution function and an identity link were used for dry mass, and the Shannon index, and a Poisson function and log-link function were used for richness and absolute frequency models. Rather than using criteria based on parsimony to select the "best model" (which favour precision vs. bias) we used the full models: first, because our models had high degrees of freedom (9 explanatory variables) and there was no need to guard against over-fitting; second, to protect from the bias of regression coefficients, and third, to preserve the accuracy of confidence intervals while using other non-collinear factors for control purposes (multiplicity adjustment, while our understanding of the underlying biological processes led us to believe that the important variables to control for had been included). The assumptions of normality, homogeneity and independence in the residuals were assessed in models with normal distribution function (Zuur et al. 2009). Statistical analyses were performed using InfoStats and SAS 9.0 statistical software. The significant *p*-value was set at $p = 0.05$.

Results

The best relative fit of the model and adjustment term for distance-sampling was the hazard-rate cosine based on the lowest AIC score. The average red deer density, expressed as the number of deer per 100 ha, ranged from 25 to 68 (average 39 ± 14 SD). The coefficients of variation of distance-sampling estimates ranged from 2.95% to 38.86%. The abundance indices for wild boar ranged from 0.04 to 0.47 (average 0.26 ± SD 0.15).

We identified 5781 invertebrates, 3201 of which were captured in FP and 2580 in OP (table 1). They were spread over 33 taxa (17 insect orders, 6 Arachnida orders, 6 Myriapoda orders, 1 Crustacean order, 1 Gastropoda class, 1 Oligochaeta class and a group corresponding to indeterminate individuals; figure 2).

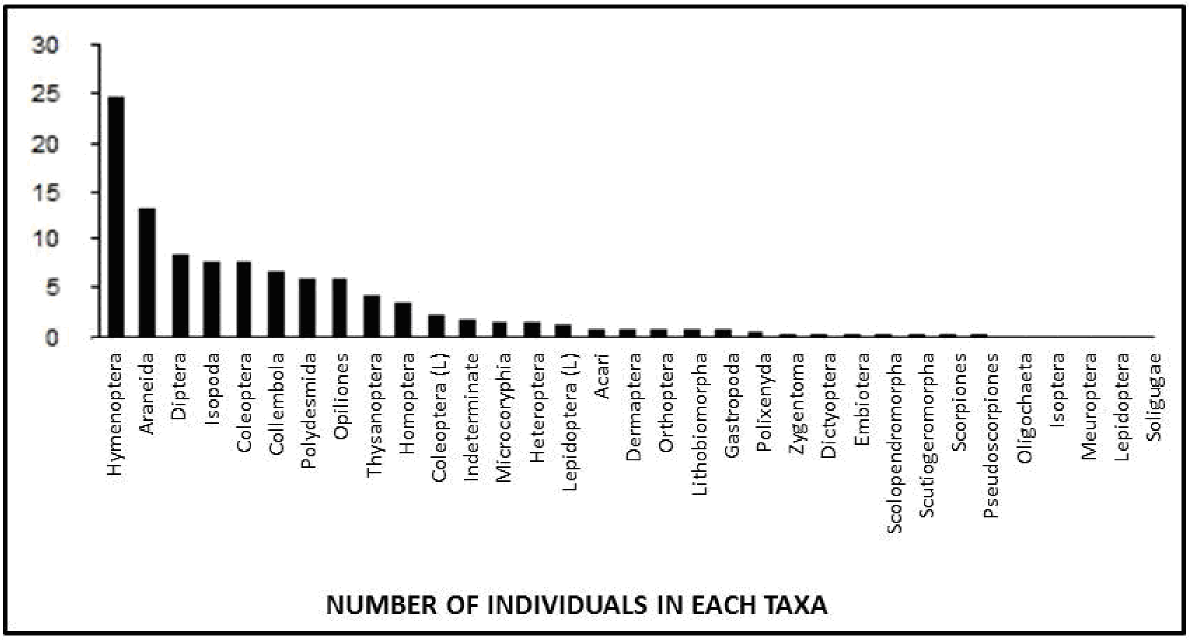

Figure 2. Percentage of trapped invertebrates belonging to each order as regards the total.

Table 1. Mean and standard deviations for the variables quantifying invertebrate abundance.

	MARCH COLLECTION		APRIL COLLECTION		MARCH + APRIL	
	OP	FP	OP	FP	OP	FP
SHANNON INDEX						
TAXON RICHNESS	1.56±0.36	1.75±0.28	1.57±0.37	1.65±0.32	1.56±0.36	1.66±0.31
WEIGHT	7.06±2.31	8.13±1.89	7.3±2.24	8.22±2.41	7.11±.45	8.32±2.15
ARTHROPODS	0.15±0.18	0.13±0.11	0.08±0.08	0.16±0.18	0.12±0.15	0.14±0.15
ABSOLUTE FREQUENCY	36.44±5.1	37.8±3.07	43±4.91	56.09±5.67	39.22±3.5	47.05±3.4

The invertebrate dry mass was marginally significant and positively associated with the percentage of grass cover (table 2, $F_{1,123} = 3.62$, $p = 0.059$), whereas invertebrate richness differed statistically between treatments, with the values for the OP being lower than those for the FP ($F_{1,123} = 7.8$, $p < 0.05$). The Shannon Index was statistically related to the interaction between treatment and wild boar abundance, meaning that the differences in arthropod diversity were only evidenced when high wild boar densities occurred ($F_{1,123} = 4.31$, $p < 0.05$; table 2). This was mainly due to an increase in the diversity index in the FP with high densities of wild boar (fig. 3), with diversity remaining similar in the OP.

Table 2. Full model on the effects of ungulates on invertebrate richness, dry mass and Shannon diversity index. (*p< 0.05).

	Taxon Richness		*Dry mass*		*Shannon index*	
	F	β	F	β	F	β
Treatment	7.8*	1.21	1.62	0.42	0.07	1.01
Deer density	0.01	2.18	0.44	-2.76	0.03	0.63
Wild boar abundance	0.01	-3.36	0.54	-0.95	0.03	-0.82
Shrub	0.1	0.0017	0.05	0.0006	1.10	0.0009
Deer density *Wild boar abundance	0.01	0.59	0.28	3.67	0.01	0.36
Treatment*Deer density	0.61	-3.25	0.63	1.76	1.57	-0.81
Plant biomass	0.17	-0.15	0.01	0.0052	4.31	0.03
Wooded	1.1	0.017	0.05	-0.0017	3.1	0.0045
Grass	0.43	-0.0004	3.62	1.9	1.65	-0.0001
Treatment*Wild boar abundance	1.78	4.92	1.33	-2.23	4.3*	1.17

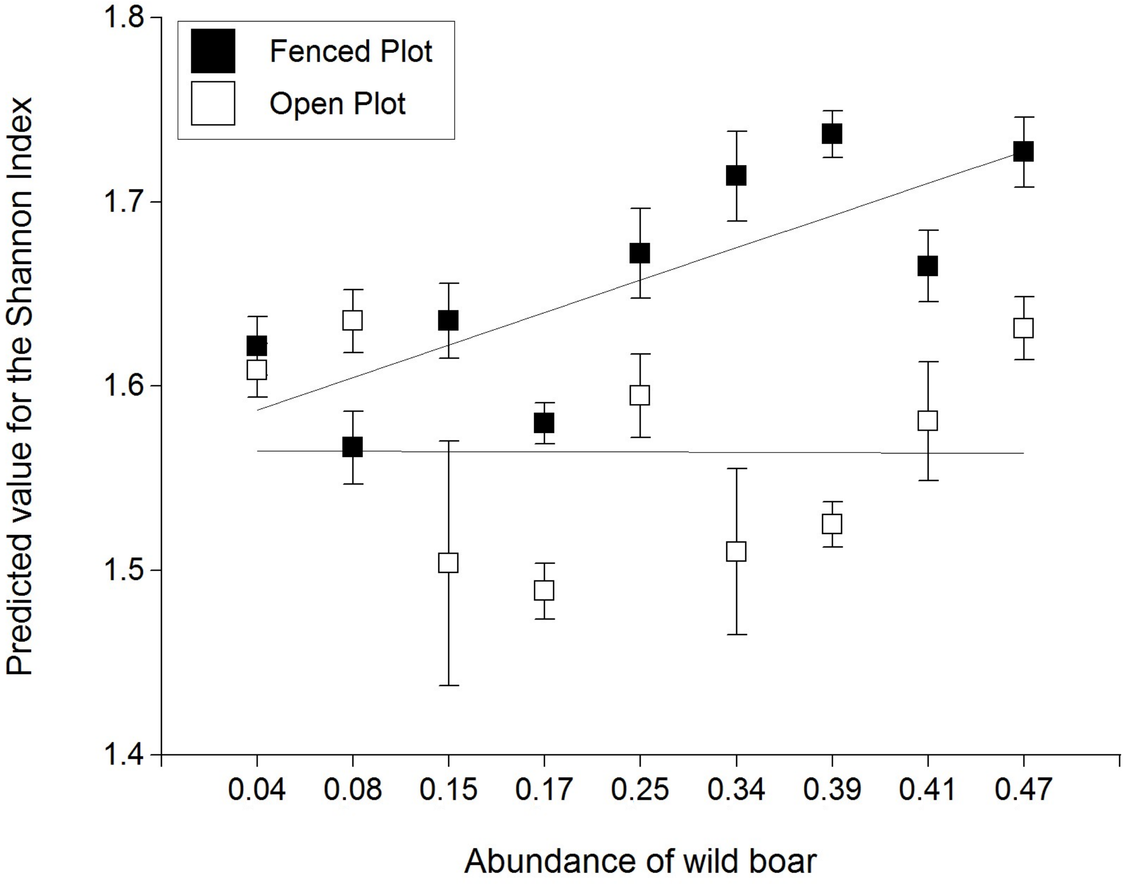

Figure 3. Shannon index as a function of wild boar abundance index per estate (mean ± S.E.).

Table 3 shows the models concerning the relationships between invertebrate numbers on the surface (absolute abundance) and ungulate densities, both overall and separately for each taxonomic group: Insecta (no Hymenoptera), Hymenoptera, Arachnida and “others”. The percentage of shrubs was statistically and negatively related to both Hymenoptera counts and the total amount of arthropods. Interestingly, the interaction between deer and wild boar abundances was statistically related to the total invertebrate counts (fig. 4A) and the number of invertebrates included in the "others" group (fig. 4B). Independently of red deer abundance, when high wild boar densities occurred the number of invertebrates decreased, although at low wild boar abundance a positive association between red deer density and the number of invertebrates was recorded. Those invertebrates included in the "others" group were more frequent in areas with high abundance of both red deer and wild boar. A positive relationship between red deer density and the absolute frequency of trapped invertebrates was also found (fig. 5A, 5B).

Table 3. Full models on the effects of ungulates on the number of invertebrates (*Insecta*, *Hymenoptera*, *Arachnida*, *Others* and *Total*, respectively).

	Insecta		*Hymenoptera*		*Arachnida*		*Others*		*Total*	
	F	*β*	*F*	*β*	*F*	*β*	*F*	*β*	*F*	*β*
Intercept	1.1	0.44	1.57*	1.48	0.14	1.78	1.17	-10.2	2.86**	3.18
Treatment	0.43	0.14	0.22	0.16	0.22	0.27	0.025	-1.26	0.39	0.21
Deer density	2.2	2.10	0.36	-0.75	0.004	0.47	5.99*	80.53	5.19*	3.75
Wild boar abundance	0.26	0.17	0	0.095	0.009	-0.45	3.33	50.54	2.13	1.65
Shrub	0.5	0.025	7.31**	-0.13	0.02	0.012	2.12	-1.96	9.88**	-0.17
Deer density *Wild boar abundance	0.96	-2.82	0.023	0.49	0.005	0.39	5.36*	-177.4	4.29*	7.59
Treatment*Deer density	2.31	-0.63	0.003	-0.061	0.14	-0.67	0.14	-9.1	0.42	-0.79
Plant biomass	0.58	0.049	0.07	-0.026	0.06	-0.04	1.17	2.51	0.37	0.19
Wooded	2.5	-0.084	0.43	-0.049	0.02	0.017	0.004	0.12	0.31	-0.086
Grass	0.54	0.001	0.78	-0.002	0.16	-0.001	0.06	-0.015	0.43	-0.002
Treatment*Wild boar abundance	2.32	0.88	0.07	-0.22	0.09	0.022	0.45	13.98	0.89	0.94

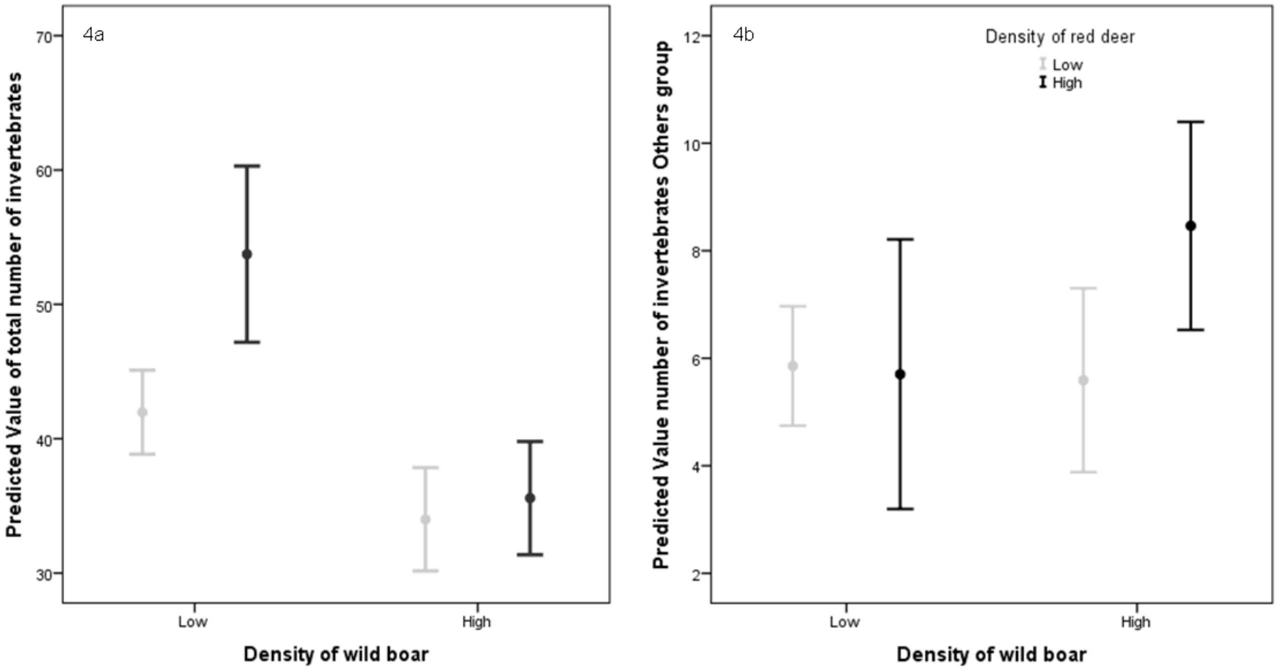

Figure 4. Total number of invertebrates (4a) and number of invertebrates included in Others group (4b) as a function of interaction of wild boar and red deer abundance index groups (categorized according to the median ± 95% CI of the abundance indexes).

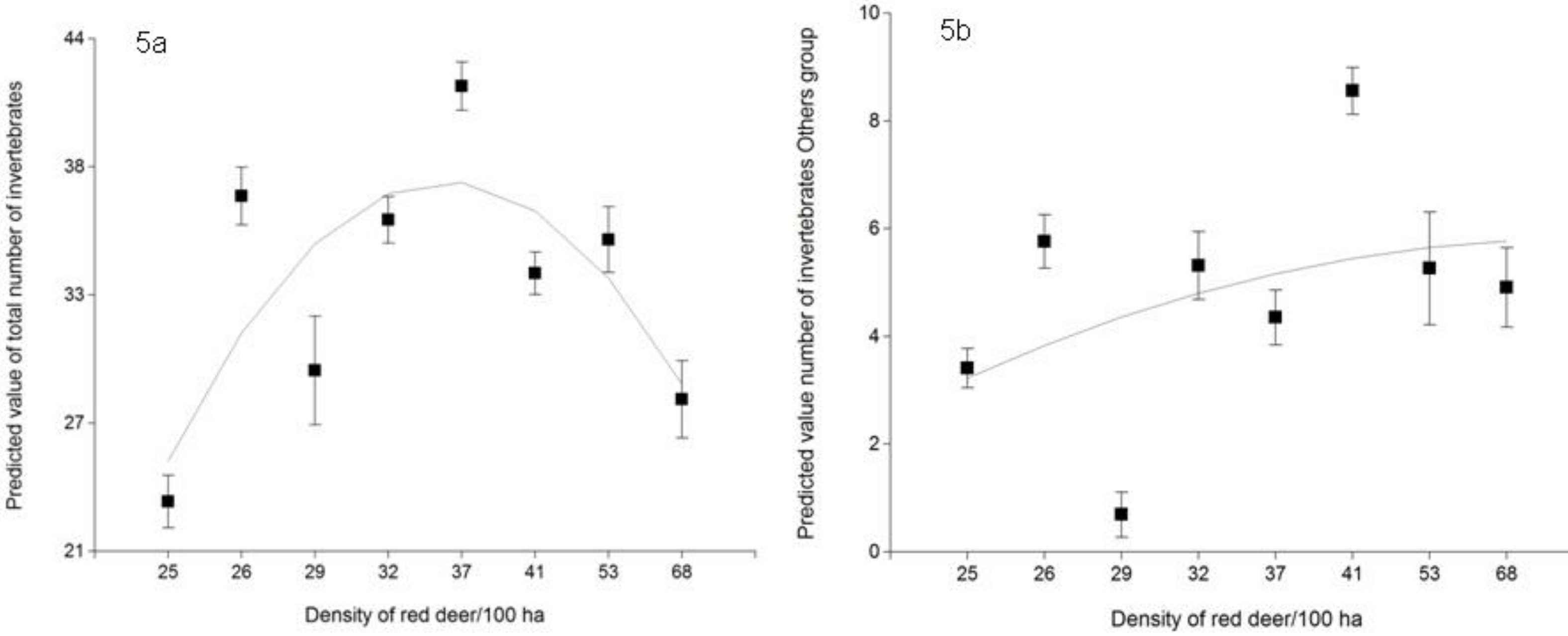

Figure 5. Total number of invertebrates (5a) and number of invertebrates included in Others group (5b) as a function of red deer density per estate (mean ± S.E.).

Discussion

Our main results were that 1) higher values of invertebrates richness were found in ungulate exclusion areas, and 2) the high densities of wild boar had a particularly negative effect on invertebrates diversity. These findings support the negative relationships between high wild boar abundance and invertebrates in Mediterranean ecosystems, which may be considered to be arthropod hotspots (Hernandez-Manrique et al. 2012).

The higher abundance of invertebrates in the FP may be caused by a local attraction effect, since invertebrates might seek refuge in fenced patches in which they actively look for the conditions inside the plots where no wild board predation (Grayson and Hassall 1985) or overgrazing occurs. Overgrazing is known to cause a decrease in the food that is available to the edaphic fauna (Dennis et al. 2001, 2008; Rosa García et al. 2009, 2010) and suitable places for egg production, laying and incubation. Moreover, inside the fenced plots, the invertebrates would avoid disturbance from wild boar and red deer, which strongly affect soil compaction/structure through trampling and rooting activities (Massei and Genov 2004; Bueno 2011). This could alter the establishment of a range of invertebrate species with different ecological requirements (Thiele-Bruhn et al. 2012), thus reducing the diversity of invertebrates. Our study supports previous findings in other environments showing that the overabundance of wild boar damages the structure of fauna communities (Côté et al. 2004; Allombert et al. 2005; Mohr et al. 2005; Albon et al. 2007; Cuevas et al. 2012; Wirthner et al. 2012). However, in our study, the principal predictor of the invertebrate dry mass was the percentage of pasture cover, probably because pasture cover benefits certain abundant species more than others, and the ungulate effect is not appreciated in terms of invertebrate biomass.

Moreover, the differences on invertebrates diversity (Shannon Index) between fenced and open areas was higher in hunting states with higher wild boar density. In others words, the values of Shannon Diversity Index was much higher in ungulate proof areas than in open areas characterized by high wild boar densities. This may be due to the less favourable habitat in the surroundings as a consequence of overgrazing and rooting activity, possibly attracting more invertebrates to undisturbed patches (Gardiner and Hassall 2009). Indeed, the wild boar diet includes not only vegetation but also many meso- and macroinvertebrates (Cuevas et al. 2010). Therefore, high wild boar densities may cause an intense disturbance of edaphic fauna, and invertebrates from the area tend to aggregate more in FP than in areas with lower wild boar abundance.

Interestingly, the interaction between deer and wild boar abundances was statistically related to the total counts of invertebrates and the number of invertebrates included in the "others" group. Independently of red deer abundance, when wild boar densities were high, the number of invertebrates decreased, indicating that the wild boar, at high densities, have an overall negative impact on invertebrates. However, when wild boar abundance was low, a positive association between red deer density and the number of invertebrates was evident. We observed a positive relationship between red deer density and the absolute frequency of trapped invertebrates and the “others” category, which must be explained in terms of the interaction between red deer and wild boar abundances (also significant, see discussion below). In contrast, as figure 5A shows, the high absolute frequency of invertebrates was recorded at intermediate values of red deer density, which is in agreement with previous studies that suggest a positive effect of moderate grazing pressure (González-Megías et al. 2004).

Our results further suggests that Isopoda and Myriapoda groups, the most abundant taxa found in the "other group", could benefit from high red deer abundances (fig. 5B). These groups have phytophagous but also important saprophytic diets and may therefore benefit from the removal of bushes and the presence of the layer of grass, which provides an increased amount of organic plant matter, and therefore an increased source of food (Bugalho and Milne 2003; Côté et al. 2004). Furthermore, ungulate faeces attract invertebrates that consume the dung and gain moisture from it or consume microbes within it (Stewart 2001).

With regard to the Arachnida and Insecta category, we found no differences in abundance either inside or outside the fenced plots, although grass favoured the presence of the Araneida order (Rosa-García et al. 2009). The composition of the habitat and the development of pastures as a result of moderate deer grazing may benefit the presence of animals included in the Arachnida category (Dennis et al. 2001; Paschetta et al. 2013). On the other hand, our results show that the percentage of shrub cover has negative effects on the abundance of Hymenoptera. A study carried out by Azcarate and Peco (2012) in a Mediterranean ecosystem led them to conclude that the generation of a more heterogeneous environment at the smaller scales increased the species diversity of ants. However, the reasons for the negative influence of shrubs on Hymenoptera remain unclear and more research on the type of ecological relationships that exist between them are therefore necessary as few studies have focused on discovering these relationships in a Mediterranean environment.

General conclusions

This research has evidenced the relationships between ungulate abundance (in high density areas) and edaphic invertebrate abundance and richness under Mediterranean constraints. Overall, this study supports the notion that high density populations of wild boar may damage the structure of soil fauna communities as a result of a decrease in food availability owing to overgrazing, soil disturbance by rooting, and direct predation. The conservation applications of this study refer to wild boar population density control under Mediterranean conditions where big game hunting has become an important industry. In particular, high densities of wild boar have a strong impact on invertebrates when compared to red deer, and a positive association was even noted in regard to the number of trapped invertebrates. Furthermore, since fenced plots evidenced a local scale effect, playing a role as refuges, the implementation of ungulate proof exclusion fences is desirable in order to maintain invertebrate communities, which would in turn enhance the food availability for many birds, including the red legged-partridge. However, more studies are needed to develop field protocols (*e. g.* the size and location of such fenced patches) and to assess population control effects on the invertebrate community.

Acknowledgements

We should like to thank E. López and the students Oscar, David and Macarena for their help in collecting field data, and two anonymous reviewers who have contributed to the improvement of the manuscript. We are also grateful to the estate keepers for their hospitality and assistance in the field work, and to the Andalucía Autonomous Government’s Environmental Council for financing this work via a project to improve the habitat of the black vulture in Córdoba province, thanks to which we have been able to carry out this work.

Capítulo 3.4

Depredación de nidos simulados de perdiz roja en fincas de caza mayor del centro-sur de España

Carpio, A.J., Guerrero-Casado, J., Vicente, J., Tortosa, F.S. (2014). **Predation of simulated red-legged partridge nests in big game estates from South Central Spain.** *European Journal of Wildlife Research, 60(2),* 391-394.

Resumen

En las últimas décadas el jabalí ha estado experimentando una expansión en Europa, lo que puede haber afectado negativamente a las poblaciones de caza menor, y particularmente a la perdiz roja. Nuestro objetivo es evaluar la depredación de nidos de perdiz roja por jabalí a alta abundancia de jabalíes mediante la colocación de nidos artificiales en 9 fincas de caza mayor. Las tasas de depredación se compararon entre nidos colocados en parcelas cercadas sin acceso de jabalíes (pero accesibles por otros predadores) y parcelas abiertas en las que el jabalí podia acceder. La proporción de nidos y huevos depredados fue significativamente menor en las áreas de exclusión de jabalíes, registrando una tasa de depredación del 50% para los nidos y del 38% para los huevos en estas áreas, mientras que en presencia de jabalí la tasa de depredación fue del 80% para los nidos y del 58% para los huevos. Por otra parte, el jabalí fue identificado como el principal depredador de nidos en zonas no valladas, representando el 36% y el 48% de los nidos y huevos depredadoss, respectivamente. Este estudio arroja luz sobre la depredación de los jabalíes en los nidos de las perdices rojas.

Abstract

Over the past few decades the wild boar has been undergoing an expansion in Europe, which may have negatively affected small game populations, and particularly red-legged partridges. We aim to evaluate the red-legged partridge nest predation by wild boar at high boar abundances, by placing artificial nests in 9 big game estates. Predation rates were compared between nests placed in fenced controlled plots with no wild boar access (but accessible by others predators) and open plots in which wild boar gaining access. The proportion of nests and eggs predated was significantly lower in wild boar exclusion areas, recording a predation rate of 50 % for the nests and 38 % for the eggs in these areas, whereas in presence of wild boar the predation rate was 80 % for the nests and 58 % for the eggs. Moreover, the wild boar was identified as the main nest-predator in unfenced areas, accounting for 36% and 48 % of the predated nests and eggs respectively. This study sheds light on the wild boar predation on nests of the red-legged partridges.

Introduction

Wild boar *(Sus scrofa)* has increased its distribution and it is reaching abundances previously unrecorded (Acevedo et al. 2007) which may exert a large and varied number of effects on the environment and sympatric fauna (Barrios-García and Ballari 2012). More specifically, the wild boar may act as a predator of ground nesting birds, such as the red-legged partridge (*Alectoris rufa*) (García and Vargas 2000). The red legged-partridge is the bird game with the highest economical value in Spain, and it is also an important key prey species. However, as a consequence of habitat loss, over-harvesting, and genetic problems associated with the release of farm-reared partridges, the species is currently considered as 'vulnerable' on a world-wide level and SPEC 2 by BirdLife International (Tucker and Heath 1994). Here we hypothesize that wild boar could affect nesting success by predation, which can be affected by habitat and management features of the hunting ground.

Work carried out with artificial nests in Spain showed corvids as the main predators in dry and scrubland patches in mixed crop zones (García and Vargas 2000). However, in areas of the Iberian Peninsula where the wild boar reaches high densities due to the big game management, its role as red-legged partridge nests-predator remains almost unexplored (but see García and Vargas 2000). Therefore, the aim of this study was to assess the relative role of wild boar as partridge nest predator in relation to other predators species and habitat features in big game estates from South Central Spain characterized by a range of wild boar densities usually high. To do so, artificial nests were placed in different habitats and predation rates were compared with nests placed in wild boar exclusion plots.

Material and Methods

Study area and experimental design

Data was collected from 9 different big game estates located in Córdoba province, southern Spain. We placed eggs in 10 nests per estate in April and May 2012. The ten nests were placed in pairs at five sampling points on each estate (N=86). In each case, one of the coupled nests was located within a 0.5 ha exclusion fence (mesh size of 150mm x 100mm) to prevent wild boar from coming into contact with them, although they were accessible by other predators. Four natural eggs of red legged partridges collected from a game farm and two plaster eggs were placed in each nest (N=516) (Yanes et al. 1998). Egg predators were assigned according to the tooth marks on the plaster eggs (Duarte and Vargas 2001). Moreover, automatic cameras were placed in 28 nests to identify predators (14 cameras on nests inside and 14 on nest outside the fence).

Estimating wild boar, carnivore and red-legged partridge abundance

Wild boar abundance was estimated following the methodology employed by Acevedo *et al.* (2007) based on the frequency of faecal dropping on walked transect. Two transects of 4 km per estate were performed in September and October 2011 in order to record the frequency of dropping into 10 sectors of 10 m in length. The carnivores' abundance was estimated through the use of spotlight counts during the months of July and August in order to obtain a kilometric abundance index (KAI). Two routes 20 km long were spotlighted per estate, and any carnivores observed were noted down. We also obtained an index of abundance by counting carnivore scats in the two 4 km long transects above mentioned. Red-legged partridge abundance was estimated by driven transect sampling (Borralho et al. 1996), performing two transect of 20 km in each hunting state.

Structure of vegetation

The habitat in which each nest had been placed was classified according to the characteristics of the vegetation as (i) *dehesa* (open habitat), (ii) scrubland and (iii) edge (ecotone between i and ii). The maximum height of the vegetation in a 1 m perimeter around the nest was also measured (Taylor and Ford 1999). These variables were selected because habitat and height of the vegetation affect to nest detectability by wild boar (Rands 1988).

Statistical analysis

Since the number of scats per kilometre^{-1} and the numbers of carnivores detected by spotlight counts were highly correlated, a carnivore's abundance index was created with a Principal Component Analysis, in which both estimators were included into one single component, which explained 80.8% of the variance. *Chi*^{2} tests were used to compare the proportion of nests and eggs that were predated between treatment and among predator species. In order to determine the factors that relate to the survival of partridge nests, two sets of Generalized Linear Mixed Models were constructed, in which the dependent variables were whether the nest was total or partially predated *vs.* not predated (Model 1); and the number of eggs predated per nest, (0 to 6 eggs) (Model 2). In these models, the abundances of wild boar, , the height of the vegetation, the treatment place in which the nests were located (fenced or unfenced plots), carnivores PCA index, habitat type (open, scrubland and edge) and the interaction between these two last variables were included as explanatory variables, and 'estate' was considered as random variable. We used a binomial distribution with a logit-link function for the model 1 and a Poisson function with a log-link function for the model 2.

We performed the full arrange of models (all possible combinations), and model selection was performed through a best-subset approach using the Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson 2002). The generated models were ranked according to AICc values, where the model with the lowest AICc is the best one. We also reported the ΔAICc value in order to compare the difference between each candidate model and the best model. As a rule, a $\Delta i < 2$ suggests substantial evidence for the model (and then for the variables included) (Burnham and Anderson 2002), so we finally selected any model with $\Delta i < 2$ respect to the model with lowest AICc. Model averaging procedure based on sum of Akaike weights was performed in order to calculate the relative importance of predictor variables. Statistical analyses were performed using InfoStat software.

Results

In the study area, red-legged partridge abundances ranged from 0.11-0.64 partridges/km, carnivores abundance ranged from 1.86-13.20 scats/km; ranging the PCA index from -1.59-2.33, while the wild boar frequency index ranged from 0.04-0.47. Thirty out of the 86 nests were not predated, 21 were partially predated and 35 were totally predated (thus is, 65% of nests presented some degree of predation). The average predation per estate was 5.55 ±2.29 (mean ± S.D) for nest and 28.22 ± 10.29 (mean ± S.D) for eggs. Overall, the proportion of predated eggs ($Chi^2 = 6.73$; d.f = 2; $p<0.05$) so as the proportion of predated nests ($Chi^2 = 5.5$; d.f. = 1; $p < 0.05$) were higher in unfenced placements (80 % of nest and 58 % of eggs) that within the fenced plots (50 % of nests and 38 % of eggs).

In unfenced nests, the most frequent nest and egg predator was significantly the wild boar, accounting for 36% of the predated nests (wild boar *vs.* others, $Chi^2 = 324$; d.f. = 1; $p <0.001$) and 47.8% of the predated eggs (wild boar *vs.* others, $Chi^2 = 435$; d.f. = 2; $p <0.001$), followed by rodents (Figure 1). Nests located within the fenced plots were more predated by rodents (40%) (rodents *vs.* others, $Chi^2 = 404$; d.f. = 1; $p < 0.001$), while carnivores were the main consumer in terms of the overall proportion of predated eggs (48%) (carnivores *vs.* others, $Chi^2 =396$; d.f. = 2; $p <0.001$).

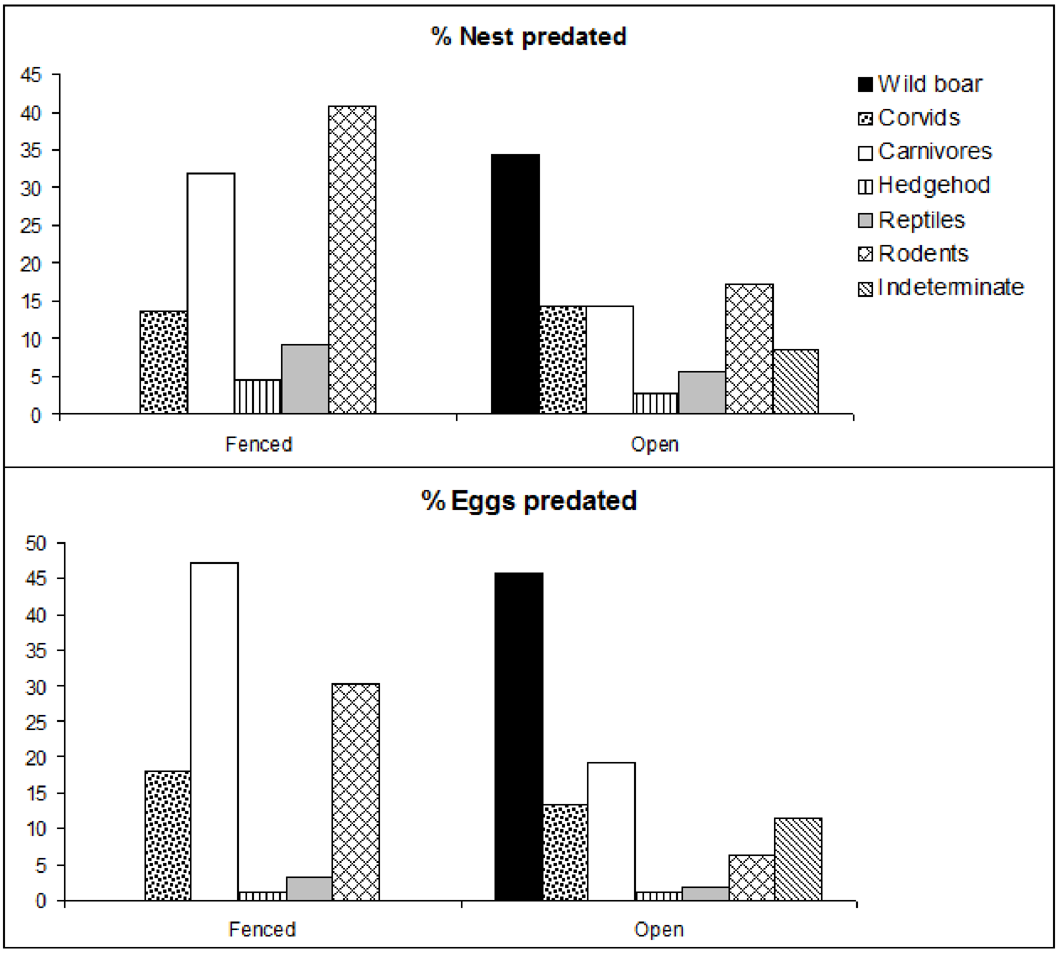

Figure 1. Percentage of nests and eggs preyed by different species according treatment (open vs. fenced).

The treatment was included in all the most parsimonious models (Model 1 and Model 2), being the nests placed in unfenced areas more predated and having a higher number of eggs predated compared with the nest located in fenced plots (mean ± S.D = 3.15 ± 2.62 and 2.29 ± 2.63 for unfenced and fenced, respectively) (Table 1). Wild boar abundance, the height of vegetation and the interaction between carnivore index and habitat type were also retained in some of the best candidate models (Table 1).

Table 1. Best candidate models to explain nest predation (Model 1) and eggs predation (Model 2). The number of estimated parameters (k), the Akaike information criteria for small sample size (AICc) and the difference between each model and the best model (ΔAICc), and the Akaike weight (*wi*) are given.

Candidate models 1	k	AICc	ΔAICc	*wi*
Treatment + Carnivores * Habitat	2	108.37	0	0.50
Treatment	1	109.42	1.05	0.29
Treatment + Carnivores * Habitat + Wild boar	3	110.29	1.92	0.19
Candidate models 2				
Treatment + Vegetation height	2	263.02	0	0.47
Treatment + Vegetation height + Carnivores*Habitat	3	264.13	1.11	0.27
Treatment	1	264.22	1,2	0.25

Discussion

Most previous studies on red-legged partridge nest predation showed that corvids, feral cats and dogs are the main predators (Duarte and Vargas 2001). In contrast, our results suggest that the wild boar is the principal nest predator in areas devoted to big game exploitation with high density of wild ungulates (0.78-2.22 wild boars/km2 in this study area, Bosch et al. 2012). This wild boar overabundance could determine that the overall rate of predation that we found in open plots was very high (80% of nests) compared to other studies such as Rands 1988 (48.3%) and Yanes *et al.* 1998 (44%), and are even much higher than the only precedent reported in a big hunting game estate in the study region (66.7 %, García and Vargas 2000).

Our study design allowed us quantifying the effect of wild boar on nest predation, recording a 45% extra of predation rate in plots with wild boars presence, and an increase of 122% relative to the baseline nest predation rate in fenced plots. This suggests that the survival of ground-nesting birds could be strongly affected by the presence of high density of wild boars, thus the wild boar overabundance can be considered an additional harmful factors for the red-legged partridge conservation. Interestingly, we found a slightly direct effect of wild boar abundance on nest predation, which may be due to the high wild boar density in all states included in this study which currently are in the highest abundances recorded in Spain (Acevedo et al. 2007).

Although the wild boar overabundance can produce significant impacts in different ecosystems components (Barrios-García and Ballari 2012), little is known regarding the ecological impact of the current densities in Iberian ecosystem. Our results evidence that the current wild boar densities in the big game estates in Central Spain could affect to the ground-nesting birds, and it is therefore advisable reduce their numbers in order to make compatible the big game exploitation and biodiversity conservation.

Acknowledgements

We should like to the gamekeepers on the estates for their hospitality and assistance in the field work, and to the Andalucía Autonomous Government's Environmental Council for financing this work via a project to improve the habitat of the black vulture in Córdoba province, thanks to which we have been able to carry out this work.

Capítulo 3.5

Factores que afectan a la abundancia de la perdiz roja *Alectoris rufa* en cotos de caza mayor*:* implicaciones para la gestión *y* conservación

Carpio, A.J., Oteros, J., Vicente, J., Tortosa, F.S., Guerrero-Casado, J. (2015). **Factors affecting red-legged partridge abundance in big game estates: Implications for management and conservation.** *Ardeola*, *62(2)*, 283-298.

Resumen

La perdiz roja *Alectoris rufa* no sólo es el ave de caza más importante, sino que también es una importante presa para muchos depredadores en Iberia. Sin embargo, sus poblaciones han disminuido significativamente en las últimas décadas, principalmente como resultado de la intensificación de la agricultura en zonas agrícolas. Sus abundancias también han sufrido un descenso significativo en zonas forestales durante los últimos decenios donde la gestión de ungulados silvestres y sus abundancias han incrementado. En este escenario, nuestro objetivo ha sido evaluar los factores que afectan a la abundancia de perdiz roja en un contexto de alta abundancia de ungulados silvestres (jabalí y ciervo) en el centro sur de España. Los factores incluidos como predictores fueron las abundancias de carnívoros, jabalí y ciervo, características de la vegetación, la proporción de nidos depredados y la disponibilidad de invertebrados. La abundancia de ciervo mostró una relación negativa con la abundancia de perdiz en primavera (también se evidenciaron tendencias negativas no significativas para carnívoros y jabalí), mientras que las variables relativas a la disponibilidad de alimentos (biomasa herbácea, abundancia de hemípteros y el peso total de los invertebrados) tuvieron un efecto positivo en la misma estación. Por otra parte, en otoño, las abundancias de ciervos y carnívoros y la tasa de depredación de nidos en primavera se asociaron negativamente con la abundancia de perdiz. La biomasa de herbáceas y la abundancia de hemípteros se correlacionaron negativamente con la abundancia de jabalíes, mientras que la altura máxima del pasto estuvo negativamente asociada con la abundancia de ciervo y jabalí. En general, nuestros resultados muestran que las altas densidades de ungulados podrían afectar negativamente a la abundancia de perdiz mediado por (i) una reducción en la disponibilidad de alimento (invertebrados y biomasa de herbáceas) y (ii) la depredación de nidos por el jabalí. Esta investigación ha puesto de manifiesto que los actuales sistemas intensivos de gestión de la caza mayor en el centro sur de España no son compatibles con la conservación de la perdiz roja, y que por lo tanto, estos efectos deben ser considerados a la hora de definir las políticas para la gestión de la caza mayor y la conservación.

Abstract

The red-legged partridge *Alectoris rufa* is not only the most important bird game species but also an important prey species for many predators in Iberia. However, its populations have significantly declined in recent decades, principally as the result of agricultural intensification on arable land. Its abundance has also undergone significant decline in forested areas over the last few decades, where wild ungulate management and abundance have increased. In this scenario, we aimed to test the factors that affect red-legged partridge abundance in relation to high wild ungulate (wild boar and red deer) abundance in South-central Spain. The factors included as predictors were carnivore, wild boar and red deer abundances; vegetation features, nest predation rate and invertebrate availability. Red deer abundance showed a negative relationship with partridge abundance in spring (non-significant negative trends were also evident for carnivore and wild boar), whereas variables related to food availability (grass biomass, Hemipteran abundance and total invertebrate mass) had a positive effect in the same season. Moreover, deer and carnivore abundances and spring nest predation rate were negatively associated with partridge abundance in autumn. Plant biomass and Hemipteran abundance were negatively correlated with wild boar abundance, whereas maximum pasture height was negatively related to red deer and wild boar abundance. Overall, our results show that high ungulate densities may negatively affect partridge abundance, which may be mediated by (i) a reduction in food availability (invertebrate and herbaceous plant biomass) and (ii) nest predation by wild boar. This research has shown that current intensive big-game hunting management schemes in South-central Spain are often incompatible with red-legged partridge conservation, and that these effects should be taken into account when defining big-game management and conservation policies.

Introduction

The abundance and range of wild ungulates have increased throughout Europe and North America over the last century (Clutton-Brock and Albon 1992; Côté et al. 2004; Gordon et al. 2004). This expansion has been facilitated by several factors, including the regulation of exploitation and the control of poaching (Gortázar et al. 2000), the abandoning of agricultural land in mountain and forest areas (Acevedo *et al.*, 2006; Vargas et al. 2007), and the establishment of protected and conservation areas (Côté et al. 2004). However, the key factor is considered to have been anthropogenic expansion, which has primarily been carried out for hunting purposes (Gortázar et al. 2000; Acevedo and Cassinello 2009).

In the Iberian Peninsula, and particularly in central and southern areas, there are high densities of red deer *Cervus elaphus hispanicus* and wild boar *Sus scrofa* on many hunting estates. Indeed, in areas with intensive game management aimed to boost big-game species, red deer can reach densities of over50 individuals/km² (Vicente et al. 2007; Acevedo et al. 2008), and wild boar densities can even attain 90 individuals/km² (Acevedo et al. 2007; Bosch et al. 2012). However, despite the large increase in the densities of wild boar and deer, little is known about the ecological impacts of the overabundance of these species on Mediterranean ecosystems (but see Carpio et al. 2014a, 2014b, 2014c) for its impacts on other species; Gortázar *et al.* (2006) for associated disease-related constraints; Perea *et al.* (2014) for impacts on vegetation.

One species that could be sensitive to the abundance of wild ungulates is the red legged-partridge *Alectoris rufa*, which has high socio-economic and ecological value as a game species and through its role as important prey for several species of predators in Iberia (Calderón 1983). Despite the importance of the red-legged partridge in Spain and Portugal, its natural populations are estimated to have undergone a significant decline of over 50% between 1973–2002 (Blanco-Aguiar 2007). Furthermore, recent results of the SACRE programme (SEO/BirdLife 2014) show that the red-legged partridge as one of the ten species that have declined most severely in recent years (the abundance was 33% lower in 2013 with respect to that in 1998). However, despite the negative population trend, the red-legged partridge is currently listed as “least concern” worldwide (BirdLife International 2012, www.iucnredlist.org).

According to several studies, the most harmful factor for partridge distribution is habitat change resulting from agricultural intensification (Vargas et al. 2006; Blanco-Aguiar et al. 2007), which has had direct effects, such as the deterioration of suitable nesting sites (Newton et al. 2004), a reduction in food availability, an increase of predation risk owing to habitat simplification (Benton et al. 2003) and exposure to toxic biocides, for example through ingestion of dressed seeds (Mineu and Palmer 2013; López-Antia et al. 2015). In addition, other factors such as overhunting and releases of farmed partridges have also been identified as harmful to wild partridges (Caro et al. 2014).

The factors affecting partridge populations in forest and mountain areas have received less attention than those acting in lowland and agricultural areas. In woodland and forest ecosystems from southern Spain (often devoted to big-game), one of the main factors that explains the decrease in partridge populations is the impoverishment of habitat quality as a consequence of land-use changes (Delibes-Mateos et al. 2012). Such changes include increases in large patches of dense homogeneous scrublands, pine reforestation characterised by a high tree density that prevents the growth of scrubland and pastureland, and the spread of oak-savannas (“dehesas”) that offer scarce scrub cover (refuge) as a consequence of intensive grazing pressure (Fernández-Alés et al. 1992). This has led to a loss of habitat heterogeneity, thus making many woodland and mountain areas unsuitable as partridge habitat (see Lucio 1991).

Nonetheless, in these areas, one factor that may also affect partridge populations could be the high densities of wild ungulates: resulting in food competition, trampling or changes in habitat structure, and nest predation by wild boars (Carpio et al. 2014c). High densities of wild ungulates are known to affect the growth, reproduction and survival of plants, since they consume their stems, flowers, leaves and fruits, thus favouring species that are less frequently consumed (Côté et al. 2004; Mohr et al. 2005; Acevedo et al. 2008; Putman et al. 2011a; Cuevas et al. 2012; Perea et al. 2014). Plant species, moreover, closely determine the insects and other invertebrates that are present and that are critical for partridge nestlings during their first weeks after hatching (Holland et al. 2006). Therefore, an intense disturbance in plant communities as a result of high ungulate densities may reduce their diversity and the species richness that is available for partridges (Stein et al. 2010). We consequently hypothesise that high abundances of wild ungulates could reduce partridge abundances as a consequence of a decrease in food availability (plants and insects), and nest predation by wild boar. To assess this, the factors that affect red-legged partridge abundance in relation to high wild ungulate (wild boar and red deer) abundances were tested on big-game estates in South-central Spain.

Material and methods

Study area

Data were collected on nine different hunting estates in southern Spain (fig. 1), averaging 2,470 hectares in extent (range 1,480–3,600 ha; table 1). The dominant vegetation includes tree species such as holm oak *Quercus ilex* and cork oak *Quercus suber*, together with pine plantations (*Pinus pinea* and *Pinus pinaster*) and scrubland dominated by species of *Cistus*, *Erica*, *Pistacia*, *Phyllirea* and *Rosmarinus* with scattered pastures. The study sites are mainly devoted to recreational hunting of wild boar and red deer. The red-legged partridge is not hunted in the study area and no management measures, such as releases or habitat improvement, are applied to enhance their populations.

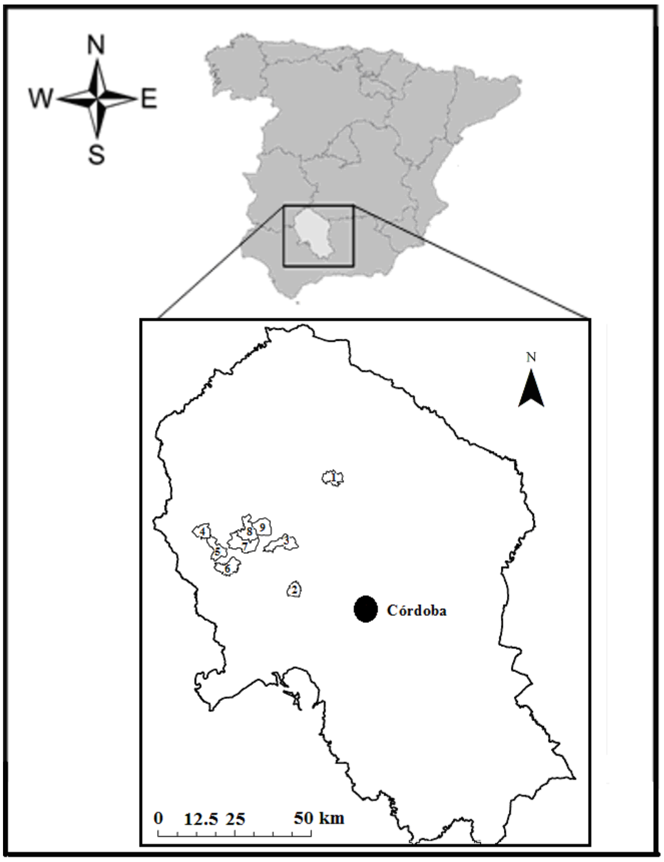

Figure 1. Map of Córdoba Province showing the location of the sampling sites

Table 1. Description of the nine study areas. Red deer density (red deer/ha), wild boar abundance (FBII: frequency based indirect index), carnivore abundance (KAI: droppings/km), carnivore abundance (Spotlight: carnivores/km), spring and autumn partridge abundance (KAI: partridges/km), surface area (ha.), scrubland, woodland and

pasture (% of total surface area) and transect length for red deer census (Total km: census 1 + census 2).

Estate code	Red deer density (ind/ha)	Wild boar abundance (FBII)	Carnivore abundance (KAI)	Carnivore abundance (Spotlight)	Spring partridges abundance (KAI)	Autumn partridges abundance (KAI)
1	0.25	0.15	3	0.1	0.63	1.02
2	0.4	0.25	2.7	0.07	0.45	0.6
3	0.26	0.04	12.6	0.24	0.42	0.43
4	0.29	0.34	0.6	0.02	0.35	0.66
5	0.37	0.38	1.86	0.19	0.29	0.75
6	0.32	0.17	0.4	0.16	0.26	0.47
7	0.53	0.41	0.74	0.02	0.14	0
8	0.68	0.47	5.9	0.16	0.11	0.3
9	0.41	0.08	13.2	0.16	0.44	0.44

Estate code	Surface (ha)	% Shrubland	% Woodland	% Pasture	Total Transect length for red deer census (Km).
1	2200	32	6	63.7	40
2	1590	30.7	23	40	42.2
3	3600	28.5	15.8	70	41.2
4	1480	14.7	24.5	59.8	37.2
5	2540	32.6	12	58.6	42
6	2747	31.1	16	51.2	37
7	3343	31.2	37.5	39	41.2
8	3308	40	26	47.2	36
9	1860	26.2	27.5	75.7	30.5

Estimating ungulate and carnivore abundances

Deer population size was estimated at the hunting estate level, each estate being considered as a discrete management unit. Two spotlight counting events (two replicates on consecutive days) between September and October 2011 were used to estimate the deer population size on each estate. Transects (mean length = 20.3 km ± 2.34 SE) were driven at 10–15 km/h along dirt tracks covering the whole estate but excluding those tracks close to the estate boundary. The distance from the observer to the deer or to the centre of a deer group was measured with a Leica LRF 1200 Scan telemeter (Solms, Germany) (range 15–1100 m; precision ±1m/±0.1%), and compass bearings were taken to determine the angle between these and the transect line. Deer population densities (individuals per hectare) were estimated using Distance 5.0 software (Buckland et al. 2004). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using cosine, hermite polynomial and simple polynomial adjustment terms, which were fitted sequentially. The selection of the best model and adjustment term was based on Akaike's Information Criterion (AIC).

Wild boar abundance was estimated following the methodology employed by Acevedo *et al.* (2007) based on dung frequency along a walked transect. According to this method, two 4-km transects per estate, located at least two kilometres apart, were performed in September and October 2011. Each transect comprised 40 segments 100 m in length and 1 m wide, divided into ten sectors of 10 m in length. Sign frequency was defined as the average number of 10m sectors containing dung per 100-m transect (Carpio et al. 2014c), and a mean value of wild boar abundance was calculated per estate using the following formula:

$$\mathrm{FBII} = \frac{1}{n}\sum_{i=1}^{n} S_i$$

where *Si* is the number of sign-positive sectors and *n* the total number of sampled sectors.

The number of carnivore scats per km in these transects was also recorded (similarly to Carpio et al. 2014c). Carnivore abundances were additionally estimated through the use of spotlight counts during July and August 2011 in order to obtain a kilometric abundance index (KAI). Two 20-km routes (two replicates on consecutive days) were spotlighted per estate, and any carnivores observed were noted. Those detected were the red fox *Vulpes vulpes*, stone marten *Martes foina* and common genet *Genetta genetta*.

Estimating red-legged partridge abundance

Red-legged partridge abundance was estimated during two seasons in 2011 (April and October), coinciding with the population minimum just before breeding and the population peak following juvenile recruitment respectively (Borralho et al. 1996; Gortázar et al. 2002). The transects on each estate, whose average length was 20.6 km ±

3.5 (± S.E.), were measured by driving at a speed of 10-15 km/h, and two replicates of each transect per estate and season were carried out, at no more than 3-day intervals. The transects were conducted by two people (one driver and one observer) during the first three hours after sunrise and in good weather conditions (Gortázar et al. 2002), and they covered optimal habitats for partridges (oak savannahs, pastures and sparse scrublands), avoiding dense pine forest and dense scrubland patches, in which detectability/visibility is poor. Simple counts were made and a kilometric abundance index (KAI) was calculated for each estate by dividing the number of observations by the total length of the transect (the low number of observations preventing using ``Distance software´´ to estimate partridge densities).

Invertebrate sampling

Since invertebrates are important food resources partridge chicks, two invertebrate surveys were conducted at random points 50–100 m from transects for estimating partridge abundance. The first took place in the last two weeks of March 2012 while the second was carried out in late April 2012. Five sampling points were established on each of the nine estates and two pitfall traps were placed at each one (90 pitfalls in total).The pitfall traps were buried at ground level and consisted of plastic receptacles with a capacity of 0.75 litres and an opening diameter of 12 cm (Paschetta et al. 2013). They were half-filled with a solution of salts (to preserve the specimens caught) and soap (to break the water surface tension). The trapped invertebrates were collected 14 days after the traps had been set (Allombert et al. 2005) and were preserved in 100 ml plastic containers with 70% alcohol. The invertebrates were subsequently identified to order level under a stereomicroscope, this degree of identification having figured in earlier studies of partridge diet (Holland et al. 2006). The diversity and structure of invertebrates larger than 0.02 mm (mesofauna and macrofauna) were studied and any microfauna (< 0.02 mm) were excluded. The invertebrate dry mass and taxon richness were calculated for each sampling point. In order to obtain the dry mass, pitfall trap contents were dehydrated in an oven at 80º C for 24 hours before weighing on a precision scale (0.001 g). All index values were calculated from the average of the two pitfall traps in each pair of sampling periods. In addition, for each sampling point, the number of invertebrates belonging to the following groups was determined: a) Hemiptera (including Homoptera and Heteroptera), b) Coleoptera (both larvae and adults), c) Hymenoptera, d) Diptera, e) Collembola and f) class Arachnida (which includes subclass Acari, and the orders Scorpionida, Pseudoscorpionida, Opilionida, Solifugae and Araneae). These groups are considered to be the most important in the partridge diet (Holland et al. 2006).

Vegetation structure and plant sampling

Ten circular walking transects were conducted on each estate during May 2011 around the insect sampling points, using a 50m cord to measure the distance. Shrub and pasture cover, along with maximum grass height, were measured on these transects, since these indexes have been considered as indirect measures of pasture availability for different herbivore species (Lazo et al. 1991). Finally, all individuals of the plant families identified as the most important in the partridge diet (Fabaceae, Poaceae and Asteraceae, according to Holland et al. 2006) within the transect were noted and the percentage cover of each family was calculated.

In addition, plant biomass (g) was assessed from cuttings in an area of 25 cm^2 of herbaceous vegetation randomly selected around every transect. The vegetation sampled was dried to constant mass in a drying oven with hot air circulation at 60° C and weighed using an electric balance (precision: 0.01 g).

Nest predation

The nest predation rate by wild boar was obtained using data recorded by Carpio *et al.* (2014c) on the same hunting estates in 2012, using only nests located in areas accessible to wild boars (N = 45), i.e. five artificial nests per estate. In this experiment, nests were formed using four natural red-legged partridge eggs supplied by a game farm and two plaster eggs (N = 270). Egg predators were identified from tooth marks on the plaster eggs and by automatic cameras placed at 14 nests. All nests were checked for predation after 23 days and to discover the percentage of eggs depredated by different predators (for more details see Carpio et al. 2014c).

Statistical analysis

The variables red deer density, vegetation height, Collembola and Coleoptera, were log-transformed to fit the parameters of normality in accordance with the Kolmogorov-Smirnov test. A Principal Component Analysis was performed for carnivore abundance, which brought together the two carnivore abundance estimates (scats/km and KAI) into a single factor that explained 90.3% of the variance. The absence of spatial autocorrelation was checked by calculating the Moran's indices of each variable. The Partial Least Squares Regression (PLSR) technique was used to construct two initial general models and four specific models (see below). PLSR is a useful regression calibration technique when the number of predictor variables is similar to or higher than the number of observations, and/or the predictors are highly correlated (Carrascal et al. 2009). This modelling procedure was based on a linear transformation of the original descriptors into a small number of orthogonal factors (latent variables), and an attempt was made to maximise the covariance between the descriptors and the dependent variable. In the general models, the dependent variables were partridge abundances in spring and autumn respectively, and the independent variables were: red deer, wild boar and carnivore abundances; plant biomass, maximum pasture height, rate of nest predation, percentage cover of shrub and pasture land, invertebrate species richness and biomass, frequency of the most important invertebrate groups (Collembola, Coleoptera, Diptera, Hemiptera, Hymenoptera and Arachnida), and finally, percentage cover of the plant families that are most important to partridges (Fabaceae, Asteraceae and Poaceae). Final models were constructed using only the variables with the highest standardised regression coefficient obtained in the full models, which allowed the optimal of the regression coefficient (Q^2) to be obtained, and both models were validated by following the full cross-validation technique.

In addition, four specific PLSRs were performed using as response variables those previously indentify as important predictors in the partridge abundance models (PLSR general models) that could be affected by high ungulate density (Hemiptera, invertebrate mass, vegetal biomass and maximum height of grass). In these specific models, red deer and wild boar abundances together with habitat related variables were included as independent ones. Statistical analyses were performed using Unscrambler 9.7 software.

Results

Red deer density ranged from 25 to 67 individuals per km² (mean 39 ± 0.14 S.E.), and the abundance index for wild boar ranged from 0.04 to 0.47 (mean 0.26 ± 0.15 S.E.). The kilometric abundance index (KAI) for partridge ranged from 0.11 to

0.64 individuals/km (mean 0.34 ± 0.15 S.E.) in spring and from 0 to 1.02 (mean 0.51 ± 0.27 S.E.) in autumn. 65% of the eggs were predated, and only 20% of nests were not totally or partially predated. The wild boar was the main predator and consumed 45.8% of predated eggs (for more details on predation rates see Carpio et al. 2014c). With regard to invertebrate sampling, 2,580 animals were identified, 2,047 of which were of the most important taxa in the partridge diet (fig. 2).

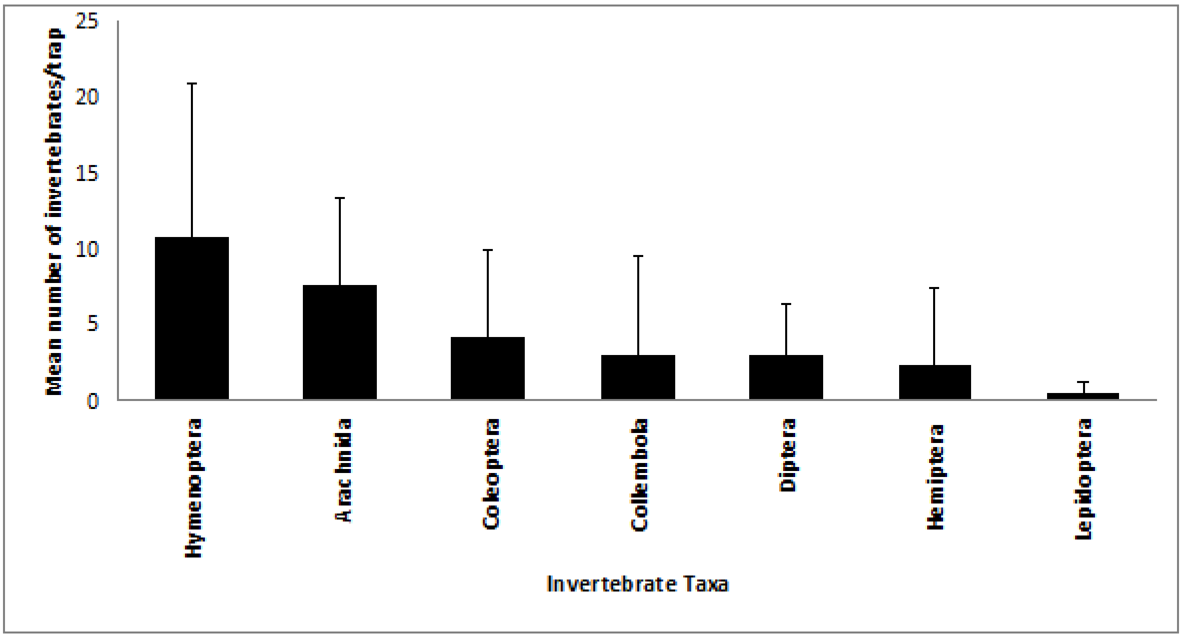

Figure 2.Mean number of individuals (±S.E.) capture per pitfall trap belonging to the most important invertebrate taxa in the partridge diet, according to Holland *et al.* (2006).

The general PLSR analysis for spring abundance resulted in a significant model (with two principal components) that explained 59% ($R^2X = 0.59$) of the variance from the independent variables ($R^2X_{PC1} = 0.45$& $R^2X_{PC2}=0.14$) and 83% ($R^2Y = 0.83$) of the variance of the dependent variable ($R^2Y_{PC1} = 0.71$ & $R^2Y_{PC2} = 0.12$). The PLS autumn abundance analysis resulted in another significant model (with only one principal component) that explained 37% ($R^2X = 0.37$) of the variance from the independent variables and 60% ($R^2Y = 0.60$) of the variance in the dependent variable. Table 2 shows the regression coefficients of the variables retained in the final models, which summarise the effect of each parameter on partridge abundance in the spring and autumn models. In the spring model, three parameters had a significant effect on partridge abundance: red deer abundance had a negative effect, whereas Hemiptera, invertebrate mass and vegetal biomass had a positive correlation. In the autumn model, deer density and carnivore abundance had a negative effect on partridge abundance, and only the percentage of unpredated eggs had a positive effect.

Finally, the specific PLSR models (table 3), using as response variables those which affect red-legged partridge abundance (Hemiptera, vegetal biomass, invertebrate mass and maximum grass height), showed that the wild boar abundance index was negatively correlated with Hemiptera, vegetal biomass and grass height, whereas red deer abundance was only negatively correlated with grass height. The PLSR model using the invertebrate mass as a response variable was not significant ($R^2X = 0.5; R^2Y = 0.11; Q^2 = -0.041$), and therefore those results are not given.

Table 2. Regression coefficients of the variables retained in the final PLSR general models. *p<0.05.

Spring model $R^2X=0.59$ $R^2Y=0.83$ $Q^2=0.73$	
Variable	*Coefficients*
Deer Density	-0.44*
Carnivores Abundance	-0.233
Wild boar density	-0.223
Maximum height	0.188
Hemiptera	0.192*
Invertebrates mass	0.196*
Vegetal Biomass	0.211*
Autumn Model $R^2X=0.37$ $R^2Y=0.60$ $Q^2=0.55$	
Variable	*Coefficients*
Deer Density	-0.505*
Carnivores Abundance	-0.436*
% Non depredated eggs	0.308*

Table 3. Regression coefficients of the important variables retained in the PLSR specific models.*p<0.05.

Hemiptera (PLSR 1)

$R^2X=0.58$ $R^2Y=0.26$ $Q^2=0.21$	*Coefficients*
Wild boar abundance	-0.14*
Vegetal Biomass	0.13*
Fabaceae	0.14*
Maximum height of grass	0.09

Vegetal Biomass (PLSR 2)

$R^2X=0.65$ $R^2Y=0.29$ $Q^2=0.26$	*Coefficients*
Wild boar abundance	-0.24*
Fabaceae	0.17
Maximum height of grass	0.13
Red deer	-0.11

Maximum height of grass (PLSR 3)

$R^2X=0.65$ $R^2Y=0.29$ $Q^2=0.26$	*Coefficients*
Wild boar abundance	-0.23*
Red deer abundance	-0.22*
Fabaceae	0.24*
% of pasture land	0.26*

Discussion

This study has shown that red legged partridge abundance on big-game hunting estates in Southern Spain is (i) negatively associated with high red deer abundance, (ii) positively associated with variables indicative of higher food availability, some of which were affected by both wild boar and red deer, and (iii) negatively affected by nest predation. This highlights the fact that big and small game species are currently spatially segregated in southern Spain (Vargas et al. 2007; Delibes-Mateos et al. 2009a), probably not only as a consequence of land-use changes and big game management leading to high abundances, but also through direct and indirect effects of wild ungulates on small game species. Therefore, the high population densities that ungulates reach in some woodland areas could be considered as an additional threat to partridge populations. Among other aspects, Caughley 1981 (reviewed by Côté et al. 2004 in the case of red deer) proposed that animals are overabundant when they cause ecosystem dysfunction, including a loss of biodiversity. In the light of this consideration, our results suggest that the current ungulate densities attained on many hunting estates can be considered as cases of overabundance, since they can reduce the abundance of other species as a consequence of a reduction in food resources (invertebrate and vegetation) and an increase in nest predation rates (by wild boars), particularly in the case of ground-nesting birds (Barrios-García and Ballari 2012). What is more, this reduction in numbers of partridges and other birds may result in additional trophic cascade effects, thus affecting the prey resources of endangered predators (Lozano et al. 2007).

Our results further show that partridge abundance was negatively correlated with red deer density in both seasons (fig. 3). These negative relationships could result from a decrease in food availability as a consequence of overgrazing and trampling in areas of high red deer densities. In fact, our results show that partridge abundance was positively related with vegetal biomass, which is a good estimator of pasture availability (Lazo et al. 1991).Although the maximum grass height did not show a significant effect, it was included in the best model showing a negative association with partridge abundance in spring, being in turn negatively affected by red deer density. Grass shortening may not only affect partridges as a result of food reduction but may also indirectly affect their vulnerability to predation (Hudson and Rands 1988), since partridges (and their nests) are much more vulnerable in low herbaceous cover (Lucio 1991).

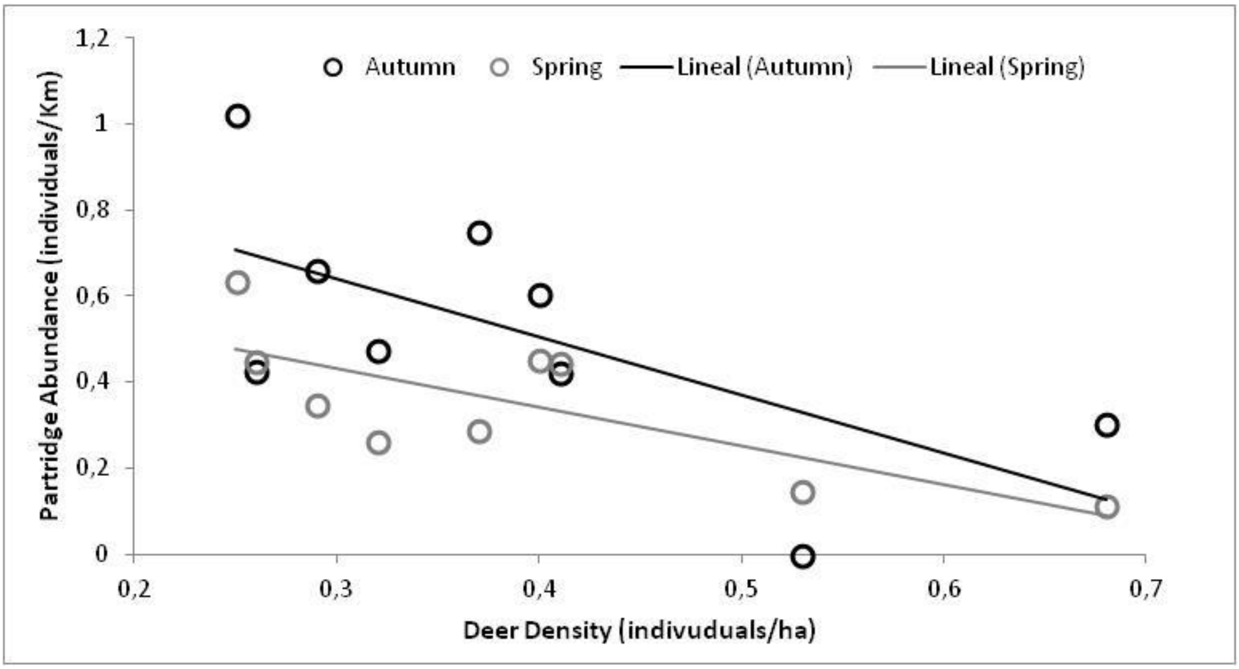

Figure 3. Red-legged partridge abundance in spring (grey) and autumn (dark) as a function of red deer density.

Although wild boar abundance was not significantly correlated with partridge abundance, our results indicate that they may affect partridges by direct predation of nests (Carpio et al. 2014c), by a negative impact on invertebrates (Carpio et al. 2014a), and by reducing grass biomass and height. In the present study, wild boar abundance was negatively correlated with Hemiptera frequency (table 2), which showed a significant positive relationship with partridge abundance in spring, suggesting that wild boar overabundance could also decrease the availability of insects for partridges. Moreover, this negative effect on invertebrates could affect chick development, since invertebrates are the main protein source for young chicks and protein intake is essential for proper growth and the development of thermoregulatory mechanisms (Liukkonen-Anttila et al. 2002; Southwood and Cross 2002). Wild boar abundance was also negatively correlated with grass biomass and height, which were previously identified as important predictors ofred-legged partridge abundance in spring. This highlights the strong impact that boar rooting behaviour can have on grassland communities (Bueno et al. 2010).

Our results also show that partridge abundance in autumn was also negatively affected by egg predation in spring, wild boar being the main nest predators in the study area (Carpio et al. 2014c). This negative association in autumn suggests that juvenile recruitment and population growth (which takes place from late spring to autumn) may be strongly affected by nest predation, and the role of the wild boar as a nest predator can therefore be considered as an important harmful factor on hunting estates with high densities of this ungulate. Boar feeding behaviour may not only affect red-legged partridge populations but also those of other ground-dwelling birds (Barrios-García and Ballari 2012). Indeed, Selva *et al.* (2014) have similarly recently shown that the proportion of depredated nests was higher in areas adjacent to ungulate feeding sites than at control sites, suggesting that game management should always consider potential indirect effects and the complex interactions that occur at ecosystem level.

Finally, it is also noteworthy that partridge abundance was negatively correlated with carnivore abundance in autumn. However, considering only this negative relationship may not be sufficient for understanding the possible effects of predation on partridges, and it is necessary to test the dietary and numerical responses of the carnivores to red-legged partridge abundance in order to elucidate predator-partridge relationships (Fernández de Simón 2013).

Although this was a short study at a limited number of sites we consider that our results may be extrapolated to other hunting estates characterised by high densities of wild ungulates. The relationships between partridge abundance, food availability indicators and ungulate densities shown here may similarly be extrapolated to other areas of Spain in which there is an increase in the abundance of wild ungulates but it is necessary to confirm plausible effects of wild ungulates on partridges and other birds over a wider range of habitats and locations. This matter may be of major conservation concern in woodland areas in Southern Spain, in which several endangered predators persist and rabbits and red-legged partridges remain at low densities (Delibes-Mateos et al. 2009a; Guerrero-Casado et al. 2013c). In conclusion, this paper further shows that current big-game hunting management schemes in South Central Spain are often incompatible with the conservation of the main bird game species. The effects shown must therefore be considered as signs of ungulate overabundance and should be taken into account when deciding the most appropriate big-game management and conservation policies. Wild ungulate density should be therefore managed in order to make big-game hunting compatible with partridge conservation, although more studies are needed to determine the threshold value of ungulate abundance. An additional management option to promote partridge populations in areas of South Central Spain that are devoted to big game could be the establishment of ungulate exclusion areas, since nest predation rates are lower in the absence of wild boar (Carpio et al. 2014c); and pasture cover and height as well as invertebrate richness is higher within ungulate exclusion fences (Carpio et al. 2014a).

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Capítulo 3.6

La alta abundancia de ungulados silvestres en una región mediterránea: ¿es esto compatible con el conejo Europeo?

Carpio, A.J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., Tortosa, F.S. (2014). **The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit?** *Wildlife Biology, 20(3)*, 161-166.

Resumen

El paisaje del sur de la Peninsula Iberica se ha alterado a lo largo de las últimas cuatro décadas como resultado del abandono de la tierra, mientras que la abundancia de jabalíes (*Sus scrofa*) y ciervo (*Cervus elaphus*) ha aumentado simultáneamente, el conejo europeo (*Oryctolagus cuniculus*) ha disminuido. En este trabajo exploramos: (i) las relaciones entre las especies de caza mayor (ciervos y jabalíes) y la abundancia de conejos, y (ii) si estas relaciones podrían tener efectos sobre la calidad del alimento (nitrógeno total disponible en pastos y porcentaje de leguminosas) y la disponibilidad de alimento (cubierta herbácea). Por lo tanto, seleccionamos 9 fincas de caza mayor con un rango de abundancia de ungulados y un hábitat mediterráneo similar. La abundancia de jabalíes estuvo negativamente relacionda con la abundancia de conejo, mientras que no se evidenciaron relaciones estadísticas significativas entre la abundancia de conejos y la estructura del hábitat y la calidad del forraje. Sin embargo, la abundancia de jabalíes, pero no la de ciervo, se asoció negativamente con la cubierta de leguminosas, y el porcentaje de superficie hozado por el jabalí se asoció negativamente con el porcentaje de cobertura herbácea. En general, nuestros resultados sugieren que la abundancia de jabalíes está negativamente relacionada con la de los conejos y podría tener efectos negativos sobre la abundancia de estos por la competencia de los alimentos como resultado de: i) una disminución en la cobertura herbácea y de leguminosas en el pasto y ii) un aumento en el porcentaje total de suelo alterado como resultado del hozamiento.

Abstract

The landscape in Southern Iberia has, over the last four decades, altered as a result of the land abandonment, while the abundance of wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) has simultaneously increased, and some key prey species such as the European rabbit (*Oryctolagus cuniculus*) have declined. In this work we explore: (i) the relationships between big game species (red deer and wild boar) and rabbit abundance, and (ii) whether these relationships could have effects on food quality (total nitrogen available in the pasture and percentage of leguminosae) and food availability of (herbaceous cover). We therefore selected 9 big game estates with a range of abundance as regards ungulates and similar Mediterranean habitat. Wild boar abundance was statistically negative in relation to rabbit abundance, while no significant statistical relationships between rabbit abundance and habitat structure and forage quality were evidenced. However, wild boar abundance, but not that of red deer, was negatively associated with leguminosae cover, and the percentage of surface rooted by wild boar was negatively associated with the percentage of herbaceous cover. Overall, our results suggest that the abundance of wild boar is negatively related to that of rabbits, and could have a negative effects on rabbit abundances by food competition as a result of: i) a decrease in herbaceous coverage and leguminosae in the pasture and ii) an increase in the total percentage of soil disturbed as a result of rooting.

Introduction

In southern Spain, the fact that traditional agriculture and cattle management in forested areas has been abandoned over the last four decades has contributed to an increase in the total area covered by bushes (Fernández-Alés et al. 1992), which may favour some species whilst others are displaced (Sirami et al. 2008). Changes in land uses drove changes in landscape, since marginal agricultural lands and extensive livestock pasture have been replaced by big game hunting estates, particularly those devoted to wild boar (*Sus scrofa*) and red deer (C*ervus elaphus*) hunting (Bugalho et al. 2011). However, prey species such as the European rabbit (*Oryctolagus cuniculus*) and red legged partridges (*Alectoris rufa*) have undergone a considerable decline in these areas (Delibes-Mateos et al. 2009a).

The European wild rabbit is an essential keystone element as regards both maintaining the high biodiversity of Iberian Mediterranean ecosystems and its role in hunting, which is an important economic activity in Iberia (Delibes-Mateos et al. 2008a). However, rabbit populations have undergone a sharp decline in recent decades, principally as a consequence of optimal-habitat loss (Ward 2005) and the outbreak of two viral diseases: mixomatosis in the 1950's and the rabbit haemorrhagic disease (RHD) at the end of 1980s (Villafuerte et al. 1995). After this decline, the recovery of the rabbit populations has been spatially uneven (Delibes-Mateos et al. 2008b). In some areas, local rabbit populations have recovered and reached high densities to the point that they are considered as an emerging pest (Barrio et al. 2012), while in many other areas their populations remain at low densities or are even extinct (Virgós et al. 2006).

Many areas in which rabbit recovery projects take place (e.g. Guerrero-Casado et al. 2013c) overlap with areas in which high densities or even "overabundance" of big game species occurs as a result of intensive management that favors high densities. In southern Spain, the current local abundances of red deer and wild boar are probably the highest recorded in Europe, reaching densities higher than 50 deer/Km² and 90 wild boar/km² in intensively managed hunting areas (Acevedo et al. 2008; Bosch et al. 2012). According to Caughley (1981), a particular wildlife species can be considered as "overabundant" if, among other things, it causes dysfunctions in the ecosystem (the consequences of "overabundance" are dealt by Côté et al. 2004). Previous studies have highlighted the negative effects of over-foraging by ungulates on vertebrate or invertebrate wildlife, vegetation and soil dynamics (Mohr et al. 2005; Häsler et al. 2012; Macci et al. 2012). High densities of ungulates may affect other species as a result of habitat modification and the degradation of certain resources that are critical for other species (Côte et al. 2004). What is more, ungulates can act as ecosystem engineers through the great impact that they have on general features of habitat, and may strongly modify the structure of vegetation (Putman et al. 2011b). The high density of red deer and wild boar may also have a negative effect on other herbivores as a result of direct food competition (Côte et al. 2004), while wild boar may negatively affect rabbits (Abáigar 1993; Briedermann 2009) and other fauna species by direct predation (Focardi et al. 2000), and the alteration of grassland by rooting activity (Bueno et al. 2010). Although previous works have shown a negative effect of wild ungulates on rabbits (Lozano et al. 2007; Cabezas-Díaz et al. 2011), the effect of current wild ungulate abundance on rabbit abundance has received little attention. In this scenario, the high density of ungulates may act as an additional harmful factor that is limiting the recovery of wild rabbit populations (Cabezas-Díaz et al. 2011), and what is more, these high densities may jeopardise the predators' populations by reducing the amount of prey that is available (Lozano et al. 2007). This could be a major concern in bush and forested areas where their endangered predators, such as the Iberian Lynx (*Lynx pardinus*) or the Spanish Imperial Eagle (*Aquila adalberti*), still inhabit (Delibes Mateos et al. 2009b) and in which wild ungulates attain high densities.

Our general goal was therefore (i) to study the statistical relationships between big game species (red deer and wild boar) and rabbit abundances. Since grass quality is known to affect rabbit abundance (Ferreira and Alves 2009), we (ii) also aimed to test whether ungulate effects could be mediated by their impact on forage quality (total nitrogen available in the pasture, Arnold and Dudzinski 1967, and percentage of leguminosae, Ritchie et al. 1998) and availability (herbaceous cover). Finally, (iii) we addressed the relationships between abundances and forage quality faecal nitrogen in herbivores (rabbit and red deer), which is an indicator of pasture quality (Leslie and Starkey 1987).

Material and methods

Study area

Data were collected from 9 different hunting estates with a high range of ungulate abundance (as commonly occurs in the study area), which were located in southern Spain in the province of Cordoba. The altitude ranges from 400 to 800 m.a.s.l., and the dominant Mediterranean vegetation includes tree species such as holm oak (*Quercus ilex*) and cork oak (*Quercus suber*), together with pine plantations (*Pinus pinea* and *Pinus pinaster*), accompanied by Mediterranean scrubland dominated by *Cystus* spp. *Erica* spp. *Pistacia* spp. *Phyllirea* spp. and *Rosmarinus* spp. with scattered pastures and small areas of crops. These savannah-like landscape units are called 'dehesas'. The study sites are mainly devoted to the recreational hunting of wild boar and red deer.

Estimating red deer density

Deer density was estimated on each hunting estate, and these estates were considered as discrete management units. We performed two spotlights census carried out on the same transect in August and September 2011 by driving at 10-15 km/h. Each transect was an average of 20.3 km ± 2.34 (S.E.) in length. The distance from the observer to the deer or to the centre of a deer group was measured, and compass bearings were taken to determine the angle between deer, or deer groups, and the transect line. The distance between the observer and the animal was measured using a Leica LRF 1200 Scan telemeter (Solms, Germany) (range 15–1100 m; precision ±1m/±0.1%). Red deer density was estimated using Distance Sampling (Buckland et al. 2004, Distance 5.0 software). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using cosine, hermite polynomial and simple polynomial adjustment terms, which were fitted sequentially. The selection of the best model and adjustment term were based on Akaike's Information Criterion (AIC).

Estimating wild boar abundance

We estimated the wild boar abundance index following the protocol described by Acevedo *et al.* (2007). The counts took place in two transects of 4 km per estate in September and October 2011. Each transect count consisted of 40 segments of 100 m in length and 1 m in width, divided into 10 sectors of 10 m in length. Sign frequency was defined as the average number of 10-m sectors containing droppings per 100-m transect (Acevedo et al. 2007), and a single average value of wild boar abundance was calculated per estate.

Estimation of rabbit and carnivore abundance index, and wild boar rooting intensity

We designed 2 to 4 transects of 4 km in length per estate between July-September 2011 (N=24), where we recorded the number of carnivore's scats and rabbit latrines per km (Calvete et al. 2006). A latrine was defined as an accumulation of 20 or more pellets on a surface of 200 x 300 mm (Virgós et al. 2003). Latrine abundance and rabbit density estimated by direct observations have been shown to have a high correlation in the study area (Mediterranean scrubland in Sierra Morena; Gil-Sánchez et al. 2011). The percentage of soil rooting by wild boar in these transects was also calculated, in which a fixed bandwidth of 1 metre was established and the length of each rooting was scored within this band (Bueno et al. 2010). This allowed us to obtain a percentage of rooted soil (Cuevas et al. 2010).

Faecal and diet nitrogen

In this study, faecal nitrogen and nitrogen content in the pasture were used as an indicator of diet quality (Hamel et al. 2009). In spring 2011, 16 samples of deer droppings (10 stools / sample), rabbit and pasture samples were collected on each estate, thus a total of 144 samples was obtained for each group (deer, rabbit and pasture). The concentration of nitrogen was estimated using the EUROVECTOR EA 3000 elementary analyzer, which determines the quantitative carbon, nitrogen, hydrogen and sulphur content of the samples. This technique is based on the Dumas method (Simmone et al. 1997), which in this case consisted of the complete thermal oxidation of 1 to 2 mg of the sample by combustion in an oxygen enriched atmosphere at a temperature of 1020 ° C. The combustion gases are drawn through an interne gas (He) to a chromatography column where they are then separated and detected using a thermal conductivity detector. We thus obtain the percentage content of each element in the sample, in this case nitrogen-analyzed with regard to weight (Acevedo et al. 2011).

Habitat structure and composition

Habitat composition per estate was determined using GIS tools and land use maps from Andalusia (Mapa de usos y coberturas del suelo de Andalucía 1/25000, Junta Andalucía 2007). For this purpose, 10 stratified transects per estate were performed in two different habitats: a) open lands, composed of *dehesa* habitat and pastures, and b) woodlands, composed of Mediterranean scrubs and forests. Pine plantations (where almost no pasture grows) were removed from the study design and sampling. The transects were of 50 m in length and were performed in May (spring production), August-September (low production) and November (autumn production) (San Miguel et al. 1996) 2011 to estimate shrub, woodland and pasture cover, and the percentage of bare soil. The maximum height of the grass in each transect was also recorded by using a ruler as an indirect measure of pasture availability (Lazo et al. 1992). In the spring transects the percentage of cover occupied by herbaceous leguminosae was also calculated (area occupied by leguminosae / area occupied by all herbaceous matter * 100) (Ritchie et al. 1998).

Statistical Analyses

In all cases the analysis were performed at rabbit level transect (N = 24) using InfoStat software. In order to evidence the relationships between the explanatory variables (Table 1) and the dependent variable 'abundance of rabbits' (latrines/km) we performed a two step statistical analysis (similar to Acevedo et al. 2005). In the first step, we discarded a number of variables that had no statistical relationship with the dependent variable (the cut off p value was set a $p < 0.05$). In Step 2, the variables selected in Step 1 were included in a linear mixed model (Model 1, Step 2) (LMM) with a normal error distribution and an identity link function. This model included rabbit abundance (latrines/km) as the dependent variable and the estate (9 levels) as a random factor, such that the transect was nested in the estate.

Following the same two-step procedure as in the previous model, a Pearson matrix (Step 1) was used to select those variables that were significantly associated with the percentage of leguminosae, the percent of herbaceous cover in spring, rabbit faecal nitrogen and red deer faecal nitrogen. These variables were included in four LMMs (Models 2, 3, 4 and 5) with the same characteristics as above (Step 2), where percentages of leguminosae and of herbaceous cover, and the rabbit and red deer faecal nitrogen were the response variables respectively. The explanatory variables were not collinear in any model (Pearson correlation $r_p < 0.8$).

A backward procedure based on Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002) was used to perform model selection, and the model with the lowest AICc was considered the best one. We also reported the ΔAICc value in order to compare the difference between each model and the best model. As a rule, differences in AICc (ΔAICc) higher than 2 between a given model and the model with the lowest AICc indicate low or no empirical support for that model (Burnham and Anderson 2002). The assumptions of normality, homogeneity and independence in the residuals were fulfilled in all cases (Zuur et al. 2009).

Results

The best relative fit of the model and adjustment term for distance-sampling was the hazard-rate cosine based on the lowest AIC score. The average red deer density, expressed as the number of deer per 100 ha, ranged from 25 to 68. The coefficients of variation of distance-sampling estimates ranged from 2.95% to 38.86%. The wild boar frequency index ranged from 0.04 to 0.47 (mean ± SE 0.26 ± 0.15), and rabbit abundance ranged from 1.9 to 14.08 latrines/km (mean ± SE 6.19 ± 4.36).

In the first Pearson correlation matrix (Step 1, Table 1), the wild boar abundance index, the carnivore abundance index, the percentage of leguminosae and the maximum height of grass in spring were significantly correlated with the abundance of rabbits. Hence, the model using rabbit abundance as a dependent variable was constructed with these 4 variables (Step 2), and two best models were selected by following the AICc criteria (ΔAICc = 0.48, Table 2). In both models, the variable 'wild boar abundance' was statistically negatively related to rabbit abundance, whereas carnivore abundance was positively associated with it.

With regard to the factors related to leguminosae cover (Model 2), only wild boar and rabbit abundances and the percentage of herbaceous cover in spring were retained after Step 1 (Table 1). In the final model (Step 2) wild boar abundance was negatively associated with leguminosae cover, whereas the percentage of herbaceous cover was positively correlated with it (Table 2).

Table 1. Variables initially included in the study and used in statistical step 1, indicating which were significantly associated with rabbit abundance[a], percent of herbaceous cover in spring[c], leguminosae cover[b], rabbit fecal nitrogen[d] and red deer fecal nitrogen[e]

Species abundances: Wild boar dropping frequency abundance index[a,b,d,e], deer density [d] (deer/ha), carnivore abundance [a] (scats/Km), rabbit abundance [b] (latrines/km).

Fecal and diet nitrogen: Nitrogen in deer droppings (N=144), nitrogen in rabbit pellets (N=144) and nitrogen in pasture (N=144).

Habitat availability: Percentage of scrubland, woodland and pasture, and edge distance (m).

Grass cover and height: Maximum height [a] and herbaceous stratum cover in spring [b], maximum height and herbaceous stratum cover in summer [e], maximum height and herbaceous stratum cover in autumn [c], percentage of leguminosae cover in spring[a,c], and percentage of rooted soil [c].

As regards the factors related to the percentage of herbaceous cover in spring (Model 3), the percentage of leguminosae, percentage of rooting and percentage of herbaceous in autumn were retained after Step 1 (Table 1). In the final model (Step 2) the percentage of surface rooted by wild boar was statistically negatively associated with the percentage of herbaceous cover, while the percentage of legumes had a positive effect (Table 2).

Table 2. *β* coefficients, *P* and *F* values of the most parsimonious LMMs (Step 2, n = 24 transects in 9 locations, which were included as random factors) to explain rabbit abundance per transect (Model 1a and 1b), the percentage of leguminosae (Model 2), the percentage of herbaceous cover in spring (Model 3), rabbit fecal nitrogen (Model 4) and red deer fecal nitrogen (Model 5). Significant *p*-values are highlighted in bold type.

Rabbit abundance per transect (Model 1a, ΔAICc = 5.63)			
	F	*P*	*β*
Wild boar abundance	9.83	<**0.01**	-17.58
Carnivore abundance	5.44	**0.03**	0.49
Leguminosae cover	0.75	0.4	-0.19
Rabbit abundance per transect (Model 1b, ΔAICc = 0.48)			
Wild boar abundance	9.78	<**0.01**	-15.91
Carnivore abundance	6.07	**0.02**	0.36
Percentage of leguminosae (Model 2, ΔAICc = 0)			
Percentage of herbaceous cover in spring	12.98	<**0.01**	0.13
Wild boar abundance	2.55	0.15	-12.98
Rabbit abundance	1,36	0.26	0.26
Percentage of herbaceous cover in spring (Model 3, ΔAICc = 2.41)			
% Leguminosae	7.59	**0.01**	1.86
Percentage of surface rooted by wild boar	13.83	<**0.01**	-2.63
Rabbit fecal nitrogen (Model 4, ΔAICc = 0)			
Wild boar abundance	2.51	0.16	-0.45
Red deer abundance	0.22	0.64	-0.25
Red deer fecal nitrogen (Model 5, ΔAICc = 0)			
Wild boar abundance	4.24	<**0.01**	0.7
Percentage of herbaceous cover in summer	3.92	<**0.01**	0.01

ΔAICc indicates the improvement in model fit of the final model compared with the next best model. ΔAICc equals zero when the final model is the same as the full model.

Finally, with regard to the factors related to rabbit faecal nitrogen (Model 4), wild boar and red deer abundance were retained after step 1 (Table 1), but they were not significant in the final model. Regarding to red deer faecal nitrogen (Model 5), wild boar and the percentage of herbaceous cover in summer were retained after step 1 (Table 1), and both variables were statistically positively correlated with the red deer faecal nitrogen (Step 2, Table 2).

Discussion

Despite the increase in the abundance and distribution of ungulates in many regions of southern Spain, there are no studies on either the relationship between rabbit abundance and big game or the factors related to rabbit abundance and performance (measured as fecal nitrogen), particularly in the context of high ungulate abundance, which are predominant in large forestry areas in Spain. In our study area, rabbit abundance was negatively correlated to wild boar abundance, which is consistent with previous studies carried out in other areas in Iberia (Lozano et al. 2007; Cabezas-Díaz et al. 2011). These works suggest that wild ungulates induce a "competitor pit effect" that may hinder the recovery of wild rabbit populations. However, to our knowledge the causes of the negative relationship between the abundances of wild boar and rabbit remain unexplored. In our experiment, this negative relationship was analyzed by measuring the coverage of leguminosae, since its high nitrogen content (protein) and low values of structural carbohydrates make it an indispensable component in rabbits' diet (Ferreira and Alves 2009) and essential for reproduction (Villafuerte et al. 1997). Indeed, wild boar abundance (but not that of red deer, see discussion below), was negatively associated with leguminosae cover; and the percentage of surface rooted by wild boar was statistically negatively associated with the percentage of herbaceous cover. Overall, our results suggest that wild boar could have a negative effects on rabbit abundances mediated by: i) a decrease in herbaceous coverage and leguminosae proportion in the pasture and ii) an increase in the total percentage of soil disturbed as a result of rooting.

Wild boars have the potential to exert a large and varied number of effects on the environment (Barrios-Garcia and Ballari 2012). For instance, rooting behaviour removes understory vegetation from large areas, thus modifying soil composition, the PH and the decomposition process, which implies changes in vegetation diversity and structure (Mohr et al. 2005; Bueno et al. 2010). The areas with the highest percentage of leguminosae could attract greater amounts of wild boar (Bugalho and Milne 2003), which use them as a source of protein (Ritchie et al. 1998) and can harm the rabbit by direct competition through the consumption of leguminosae (Côte et al. 2004), since habitat alteration by rooting can affect hundreds of hectares (Bueno et al. 2011).

Nonetheless, the direct predation of rabbits by wild boar, particularly in dens, might also explain part of the negative relationship between both species. Although no empirical studies have been conducted to test the effect of wild boar predation on rabbit, it is known that wild boar prey on young and sick rabbits (Abáigar 1993; Briedermann 2009), which could also affect wild rabbit populations. Contrary to what we expected, we did not detect any effect of deer density on rabbits within the rank of deer abundances studied, which may be owing to the fact that all the areas had high densities (>20ind/100 ha, Acevedo et al. 2008), and the effect of deer was therefore always above a given threshold of overgrazing. Further research, including lower deer density areas, is therefore needed. Wild boar, meanwhile, covered a wide range from scarce to a very high abundance index (Acevedo et al. 2007), which could condition the existence of relationships with rabbit abundance, while the case of red deer is less contrasted.

Interestingly, carnivores had a positive relationship, possibly owing to the attraction effect of rabbits on predators, which concentrate their foraging efforts on higher rabbit abundance areas (Viñuela et al. 1994). This highlights the key role of rabbits as prey and their importance as regards supporting richer predators communities in areas now devoted to big game hunting (Virgós and Travaini 2005).

Management implications

The results obtained show that wild boar may have a negative impact on wild rabbit populations in typical big game estates in Southern Central Spain. The fact that traditional agriculture have been abandoned and intense hunting management has favoured the proliferation of ungulates, without considering the possible effects that these species may have on small game species, and therefore on the availability of these prey for predators. Overall, this study supports the possibility that rabbit abundance may have been affected by a decrease in the availability and quality of food as a consequence of high density populations of wild boar. We therefore argue in favour of the scientifically based management and control of ungulate populations in Mediterranean conditions in order to conserve key prey species, specifically in those areas in which endangered predator species still coexist and rabbit populations remain at low densities.

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Capítulo 3.7

Interpretación del nitrógeno fecal como indicador no invasivo de la calidad de la dieta y la condición corporal en un contexto de alta densidad de ungulados

Carpio, A.J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Tortosa, F.S., Vicente, J. (2015). **Interpreting faecal nitrogen as a non-invasive indicator of diet quality and body condition in contexts of high ungulate density.** *European Journal Wildlife Research, 61(4)*, 557-562.

Resumen

Entender cómo los indicadores no invasivos de la calidad de la dieta, como el nitrógeno fecal (NF), se relacionan con el rendimiento de la población es un activo valioso al evaluar el manejo de los ungulados silvestres. Sin embargo, las relaciones entre NF y la ingesta de proteínas pueden depender de la ingestión de plantas menos palatables que contienen altas cantidades de taninos (que se sabe que reducen las proteínas degradables) y de los sistemas de gestión (como la alimentación suplementaria). Con el fin de describir los factores y el uso potencial del NF como indicador de la calidad de la dieta, se seleccionó un rango de densidades de ciervos (*Cervus elaphus*) en hábitats mediterráneos del centro-sur de España, que se clasificaron bajo diferentes regímenes de manejo (con y sin alimentación suplementaria). Nuestros objetivos específicos fueron (i) identificar los principales factores poblacionales (manejo, densidad) y de la calidad de la dieta relacionados con los niveles de NF, (ii) evaluar la relación entre el desarrollo individual (condición corporal medida como índice de grasa renal, IGR) y el NF, y (iii) proporcionar evidencia del papel modulador que la gestión puede desempeñar en esta relación. El NF se asoció positivamente con la concentración de taninos fecales y la densidad de ciervos. Curiosamente, se observó una correlación positiva entre el NF y el nitrógeno en las plantas en las fincas de caza con suministro de comida, mientras que esta relación no fue evidente en ausencia de alimentación suplementaria. Por otra parte, IGR se asoció negativamente con el NF, y esta asociación negativa fue más marcada en zonas con alimentación suplementaria. Este estudio ejemplifica que la precaución es necesaria cuando se utiliza la interpretación de los valores de NF individuales para monitorear la condición corporal de las poblaciones de ciervos, particularmente en contextos de alta densidad con una calidad de forraje reducida y cuando se proporciona alimentación suplementaria. Sin embargo, cuando se interpreta el NF en consonancia con la condición corporal, los parámetros poblacionales y la calidad de la dieta, se ha demostrado ser un indicador potencialmente simple, rentable y fiable del rendimiento biológico y de la calidad de la dieta.

Abstract

Understanding how non-invasive indicators of diet quality, such as faecal nitrogen (FN), relate to population performance is a valuable asset when assessing the management of wild ungulates. However, the relationships between FN and protein intake may depend on the ingestion of less palatable plants containing high quantities of tannin (which is known to reduce degradable proteins) and management schemes (such as supplemental feeding). In order to describe the factors and potential use of FN as an indicator of diet quality, we selected a range of red deer (*Cervus elaphus*) densities in Mediterranean habitats in South Central Spain, which were classified under different management regimens (with and without food supply). We specifically aimed to (i) identify the main population (management, density) and diet quality factors related to FN levels, (ii) assess the relationship between individual performance (body condition measured as kidney fat index, KFI) and FN, and (iii) provide evidence of the modulating role that management may play in this relationship. FN was positively associated with the faecal tannin concentration and the density of deer. Interestingly, a positive correlation was observed between FN and nitrogen in plants on hunting estates with a supplemental food supply, whereas this relationship was not evident in the absence of supplemental feeding. Moreover, KFI was negatively associated with FN, and this negative association was more marked in the presence of supplemental feeding. This study exemplifies that caution is necessary when the interpretation of individual FN values is used to monitor the performance of red deer populations, particularly in high density contexts with a reduced quality of forage, and when supplemental food is provided. However, when FN is interpreted in concomitance with body condition, population parameters and diet quality, it has been proved to be a potentially simple, cost-effective and reliable indicator of biological performance and diet quality.

Introduction

When measuring physical performance in wild ungulates it is necessary to consider the individuals' body condition and health, along with estimates of population density and environmental conditions (Côté et al. 2004; Acevedo et al. 2008; Putman et al. 2011b), since body condition and health interact with population density via the habitat-related factors of diet and nutrient intake (Santos et al. 2013).

Protein is a limiting nutrient for wild herbivores and its availability in plants signifies that nitrogen intake is a potential indicator of diet quality (Putman 1984). Since protein content and digestibility are positively correlated in plants (Robbins 1983), Faecal nitrogen (FN) is therefore a common index that is correlated with the intake of proteins and dietary digestibility (Leslie and Starkey 1985; Hodgman et al. 1996). FN has been widely used as an index of dietary quality in the nutritional ecology of free-ranging and captive ruminants (Hamel et al. 2009; Leslie et al. 2008). The relationship between proteins in diet and FN is, however, controversial. Tannins can bind to proteins during chewing and digestive processes (Mokoboki et al. 2011; Verheyden et al. 2011), and are then excreted in the faeces as tanning-protein complexes, thus leading to a decrease in protein digestibility and an increase in FN values (Mould and Robbins 1981; Robbins et al. 1987). What is more, some cervids have tannin-binding salivary proteins (Shimada 2006). It is therefore difficult to interpret the relationships between FN levels and diet quality.

Wild ungulates' body conditions depend on the quality of their food (Santos et al. 2013). Whether and how diet quality indicators relate to individual performance (in terms of body condition), and which factors determine this relationship are key elements as regards understanding the practical use of FN. Body condition is affected by habitat quality (Taillon et al. 2011), population dynamics (Morellet et al. 2007) and extra food provided by wildlife managers (Santos et al. 2013). In the Iberian red deer (*Cervus elaphus hispanicus*) populations in Spain, high densities are favoured for hunting purposes, and this may impact on the conservation status of vegetation cover (Acevedo et al. 2008). Indeed, the use of supplementary feeding on some estates improves individual (trophy size and body condition) and population characteristics (density) (Vicente et al. 2007; Rodriguez-Hidalgo et al. 2010). Since supplemental feeding provides high quality food in terms of nutritional content and palatability, it may have the potential to modulate the relationship between FN, pasture quality and body condition. The kidney fat index (KFI) has often been used to measure the physical condition of red deer and is widely used with ungulates (Dauphiné 1975; Santos et al. 2013). This method is based on the assumption that the amount of perirenal fat is a reliable indicator of the total body fat, and thus of the body's physical condition (Finger et al. 1981).

Nevertheless, there is little information that can be used to interpret individual and population nutritional indicators (such as FN and nitrogen in the diet) in wild ungulates, particularly in high density conditions and/or when supplemental feeding is provided. In order to describe the factors and potential use of FN as an indicator of diet quality, we selected a range of red deer (*Cervus elaphus*) densities in Mediterranean habitats in South Central Spain, which were classified under different management regimens (with and without food supply). We specifically aimed to (i) identify the main population (management, density) and diet quality factors related to FN levels, (ii) assess the relationship between individual performance (body condition measured as kidney fat index, KFI) and FN, and (iii) provide evidence of the modulating role that management may play in this relationship.

Material and Methods

Study area

Data were collected from nine different hunting estates located in southern Spain in the province of Cordoba, in which the altitude ranges from 400 to 800 m.a.s.l. The dominant vegetation includes tree species such as holm oak (*Quercus ilex*) and cork oak (*Quercus suber*), together with pine (*Pinus pinea* and *Pinus pinaster*), accompanied by scrub species dominated by *Cystus* spp., *Erica* spp., *Pistacia* spp., *Phyllirea* spp. and *Rosmarinus officinalis* with scattered pastures and small areas of crops. The study sites are principally used for the recreational hunting of wild boar and red deer.

Red deer density estimation

Deer abundance was estimated per hunting estate, and the estates were considered to be discrete management units. We performed two spotlight-counts in August and September 2011, driving at 10-15 km/h. Each transect studied was, on average, 20.3 km ± 2.34 (S.E.) in length. The abundance of the deer populations was estimated by means of distance sampling (Buckland et al. 2004, Distance 5.0 software). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using cosine, hermite polynomial and simple polynomial adjustment terms, which were fitted sequentially. The selection of the best model and adjustment term was based on Akaike's Information Criterion (AIC). The best relative fit of the model and adjustment term for distance-sampling was the hazard-rate cosine based on the lowest AIC score.

Sampling and analytical techniques

We used FN from fresh (soft, shiny and not dried) deer faeces collected from the ground. We performed two transects of 4 km in length per estate (n = 18) during the spring, from which deer droppings (10 stools / sample) were collected every 500m (n = 8 per estate) in order to ensure that the samples were spatially independent. In the same transects, pasture samples (the main food resource during this season for Iberian red deer) (Verheyden-Tixier et al. 2008) were collected every 500m within a randomly located ring of 0.5m², where the plants were cut for subsequent analysis (see below). A total of 144 samples of faeces and plants were obtained.

The concentrations of FN and Nitrogen in plants were analysed using the EUROVECTOR EA 3000 elementary analyser, which determines the quantitative carbon, nitrogen, hydrogen and sulphur content of the samples. We thus obtained the percentage content of each element of the sample, which was in this case nitrogen-analysed with regard to weight (Acevedo et al. 2011).

Fifty-four red deer faecal samples (6 per estate) were randomly selected and analysed to obtain their concentration of tannin. Total extractable phenols (TEPH) were determined using Julkunen-Tiitto (1985).

Habitat structure and composition

Habitat composition per estate was determined by using GIS and land use 1/25000 maps of Andalusia (Junta Andalucía 2007). We stratified 10 transects per estate, and the main habitats present were grouped into open land, (composed of *dehesa* (savannah oak) and pastures) and woodland, composed of Mediterranean scrubland and forests. The transects were 50m in length and were studied in May (maximum spring production, San Miguel et al. 1996) 2012 to estimate scrubland, woodland and pasture cover, and the percentage of bare soil. A ruler was used to record the maximum height of the grass in each transect as an indirect measure of the availability of pasture (Lazo et al. 1992). We also calculated the percentage of cover occupied by herbaceous legumes [area occupied by legumes / area occupied by all herbaceous matter * 100] (Ritchie et al. 1998) in each transect.

Morphometric measurement

We collected the data regarding 103 hunted male deer in December 2011 and January 2012. The animals were assigned to three age classes: yearlings, sub-adults (< 3 years old), and adults (≥ 4 years old) (Rodriguez-Hidalgo et al. 2010).

Nutritional status was determined using the "Kidney fat index" (KFI). This was obtained by weighing the perirenal fat which was then expressed as a percentage of the weight of that kidney [KFI = fresh weight of the perirenal fat / fresh weight of the kidney *100] (Riney 1955; Dauphine 1975).

Statistical Analyses

In order to provide evidence of the relationships between FN (N=144) and forage quality, we designed a linear mixed model (LMM, normal error distribution and an identity link function, Model 1) in which management (two levels: feeding supplement vs. no feeding supplement) was included as a fixed factor. Plant nitrogen, red deer density, tannin content and the percentage of leguminosae, scrubland and woodland, were included as co-variables. Since increased protein intake resulting from supplemental feeding could interfere in the relationships between FN and diet quality, the interactions between supplemental feeding and nitrogen in plants, and tannins were also included in the model.

A second linear mixed model (normal distribution with an identity link function, Model 2) was created to study the relationship between KFI (N=103) (dependent variable) and FN. FN was included as a co-variable, whereas supplementary feeding and age class were treated as categorical variables with 2 and 3 levels, respectively. The interactions with supplemental feeding were also added. The population sampled was included as a random factor in both models. The assumptions of normality, homogeneity of variance, and independence of residuals were confirmed in both models (Zuur et al. 2009), and the KFI was therefore log-transformed in order to fulfil normality.

Results

Red deer densities ranged from 25 to 68 deer/100ha (average ± SD 39 ± 14), while the coefficients of variation of distance-sampling estimates ranged between 4.55% and 30.54%. The FN values ranged from 1.7 to 3.4% (average ± SD 2.47 ± 0.30), the nitrogen in plants ranged from 0.8 to 4.5% (average ± SD 1.81 ± 0.53), and the concentration of faecal tannins ranged from 6.7 to 26.8mg tannic acid/g sample (average ± SD 15.8 ± 4.1) (Table 1).

With regard to the factors affecting FN, Model 1 showed a significant positive relationship between red deer density and tannin content in faeces (Model 1, Table 2). There was also a significant interaction between supplemental feeding and nitrogen in plants, signifying that the FN increased in proportion with the amount of nitrogen in plants in the presence of supplemental feeding. No evidence of this relationship was found when the deer were not provided with supplementary food (Figure 1). There was a negative relationship between FN and the percentage of scrubland and woodland.

Table 1. Mean ± SE for FN (%), N in plants (%), faecal tannins (mg tannic acid/g sample), density and type of management for each estate (n = 9).

Estate	Management	Density	FN ± SE	N in plants ± SE	Faecal Tannins ± SE
1	With feeding	0.25	2.188 ± 0.25	1.763 ± 0.53	20.225 ± 3.76
2	With feeding	0.26	2.449 ± 0.32	1.558 ± 0.31	16.131 ± 3.56
3	No feeding	0.29	2.520 ± 0.19	1.652 ± 0.55	15.863 ± 3.14
4	No feeding	0.31	2.389 ± 0.37	1.820 ± 0.56	16.197 ± 4.77
5	No feeding	0.36	2.699 ± 0.21	1.990 ± 0.57	16.075 ± 5.60
6	With feeding	0.40	2.555 ± 0.24	1.722 ± 0.4	15.368 ± 4.91
7	With feeding	0.41	2.482 ± 0.23	1.883 ± 0.46	17.396 ± 7.46
8	No feeding	0.53	2.383 ± 0.28	1.832 ± 0.43	12.549 ± 2.27
9	No feeding	0.67	2.589 ± 0.34	2.121 ± 0.77	17.602 ± 11.4

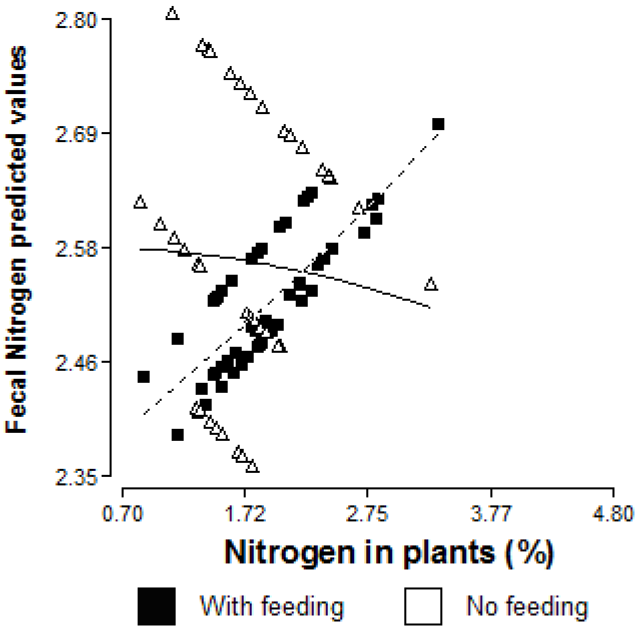

Figure 1. Predicted values of faecal nitrogen (% nitrogen with regard to faecal weight) as a function of nitrogen in plants (% nitrogen with regard to plant weight) (categorised according to supplementary feeding: with feeding vs. no feeding).

With regard to Model 2, which concerns individual KFI, (Table 2), the interaction between supplementary feeding and FN was statistically significant (*P* = 0.02), showing that the negative association between FN and KFI was more marked when food was supplied (Figure 2).

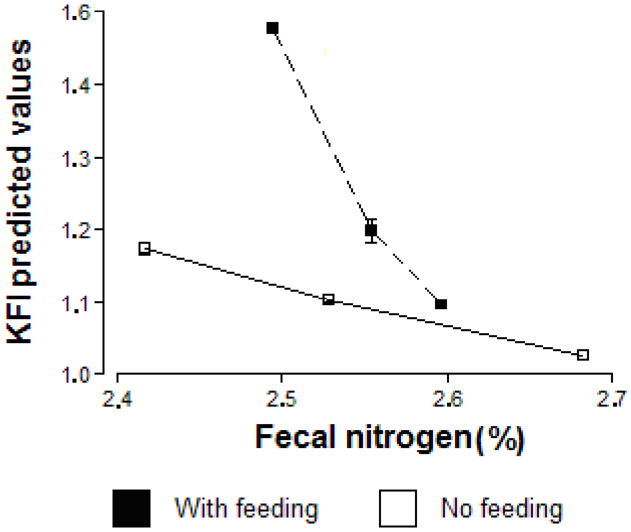

Figure 2. Predicted mean values (± S.E.) of kidney fat index (fresh weight of the perirenal fat / fresh weight of the kidney *100) as a function of faecal nitrogen (% nitrogen with regard to faecal weight) (categorised according to supplementary feeding: with feeding vs. no feeding).

Table 2 – *F*, *p*-values and coefficients of the variables included in the mixed models to explain faecal nitrogen (Model 1) and the Kidney fat index (Model 2). Df: degree of freedom of the numerator. Coefficients for the level of fixed factors were calculated using the reference values of 'feeding' in the 'Supplementary feeding' variable, and 'age 1' in the 'Age class' variable.

Faecal nitrogen (Model 1)				
Variables	*F*	*df*	*P*	Coefficient ± E.S
Intercept	38.5	1	**<0.001**	2.90 ± 0.67
Supplementary feeding	4.53	1	0.06	No feeding = 1.86 ± 0.87
Red deer density	22.17	1	**<0.01**	2.71 ± 0.58
Nitrogen in plants	2.08	1	0.15	-0.02 ± 0.06
Percentage of leguminosae	0.13	1	0.7	-0.01 ± 0.01
Percentage of scrublands	20.48	1	**<0.01**	-0.05 ± 0.01
Percentage of woodland	23.03	1	**<0.01**	-0.07 ± 0.02
Faecal tannins	6.23	1	**<0.05**	0.17 ± 0.08

Supplementary feeding* N. in plants	5.27	1	**<0.05**	-0.26 ± 0.09
Supplementary feeding* F. tannins	3.69	1	0.08	-0.10 ± 0.05
Kidney fat index (Model 2)				
Intercept	85.9	1	**<0.01**	10.3 ± 1.2
Supplementary feeding	33.3	1	**0.02**	No feeding = -7.90 ± 1.39
Age class	1.01	2	0.36	Age 2 = 0.13 ± 0.06 Age 3= 0.15 ± 0.04
Faecal nitrogen	58.6	1	**0.01**	-3.6 ± 0.47
Supplementary feeding*Age class	1.15	2	0.32	No feeding*age2 = -0.19 ± 0.12; No feeding*age3 = -0.10 ± 0.11
Supplementary feeding*Faecal nitrogen	32.7	1	**0.02**	3.08 ± 0.54

Discussion

This study has assessed FN as potential non-invasive indicator of diet quality and its association with individual performance traits (body condition) in contexts of high ungulate density. Interestingly, the relationships between FN and the availability of food and individual body condition were modulated by prevalent management (supplemental feeding).

The highest FN values were found in those areas with the highest red deer densities and tannin concentrations in faeces. At high densities there may be fewer palatable scrub species as a consequence of over-browsing, thus favouring the growth of species that are unpalatable for herbivores (Acevedo et al. 2008; Suzuki et al. 2008). These plants have higher concentrations of tannins (Mould and Robbins 1981; Robbins et al. 1987) which, in plants, act as a defence mechanism (Perea and Gil 2014) against herbivores. Tannins may inhibit the digestion of protein and fibre which are excreted as a non-metabolic nitrogen (Frutos et al. 2004), thus reducing the amount of digestible protein in forage and increasing FN (Kariuki and Norton 2008). Although the digestibility of the N in diet was not assessed, we used the N content in forage as a practical proxy to diet quality. This could explain the higher FN values found in areas with higher deer densities and in which vegetation has high concentrations of tannin. Indeed, the positive association between FN and tannin content in faeces is consistent with the potential role played by tannins as binders of protein in the diet. The tannins in plants are tolerated by ungulates to some extent, but the animals avoid them once certain amounts have been ingested. Other studies on ungulates in different ecosystems have shown a negative relationship between density and faecal nitrogen (e.g. Asada and Ochiai 1999) and have argued that the consumption of plant species with a lower nutritive value as a result of the limited availability of high quality forage leads to a decrease in faecal nitrogen. However, in Asada and Ochiai (1999), the densities ranged from 4.7 to 26.5 deer/100ha, which were much lower than those found in our study area (25 to 68 deer/100ha), and our results must therefore be interpreted in the context of a very high density in Mediterranean environments. An evaluation of a wider range of densities would probably evidence non-linear relationships between FN and diet quality.

The relationship between FN and N in diet was modulated by food supplementation. On the one hand, the results showed that FN was positively associated with N in plants, in populations in which supplemental food was provided. This positive association has been found in several other studies, and is the basis of the belief that FN is a useful indicator of diet quality (e.g. Leslie and Starkey 1985; Ueno et al. 2007). Conversely, in non-supplemented populations, we speculate that most tannin originates from scrubs, which would be more frequently consumed when supplementary feeding is not practised and herbaceous plants are depleted. This may result in plant N being neutralised by tannins and thus in no association being found (Robbins et al. 1987) (Figure 1). According to Mould and Robbins (1981), the relationship between FN and nitrogen in the diet of red deer is no longer linear when the diet contains large amounts of tannins. But when the diet is made up of lower tannin concentrations this relationship remains linear and positive. This suggests that FN is not a straightforward positive indicator of diet quality in terms of protein intake, but probably results from the interaction between diet quality (protein content) and any anti-nutritive factor (such as tannins) that is able to reduce N digestibility.

Finally, our results suggest that individual body condition decreases with increased FN. This is also consistent with the fact that, in the context of high deer density, an increase in plant tannin contents may bind protein and form insoluble complexes that are excreted in faeces as non-metabolic nitrogen, and FN may therefore increase while protein assimilation decreases. This result suggests that animals that excrete both large amounts of N and large amounts of tannins in their faeces have a worse body condition. In supplemented populations we found higher KFI scores at low FN content than in non-supplemented populations, but the KFI values become similar at high FN values (Figure 2). Previous studies agree that supplementary feeding interferes with fitness indexes, thus improving the physical condition of individuals even at high densities (Rodriguez-Hidalgo et al. 2010).

The objective of this paper is to highlight the importance of simultaneously evaluating nutritional indicators, environmental factors and management parameters when monitoring ungulate populations. Caution is therefore needed when the interpretation of FN values is used to monitor the performance of red deer populations. However, FN proved to be a potentially simple, cost-effective and reliable indicator of diet quality once supplemental feeding practices, population density and tannin concentrations had been taken into account. Our study also suggests that, in the context of high ungulate density, the higher values of FN are associated with poor body condition, suggesting that the use of FN as an indicator of body condition should also be interpreted together with others factors such as tannin content and the game management regime.

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CAPÍTULO 4

Interacciones ecológicas entres especies nativas y exóticas

Capítulo 4.1

Papel de la caza en la introducción de especies en Europa

Carpio A.J., Guerrero-Casado, J., Barasona, J.A., Tortosa, F.S. Vicente, J. Hillström, L., Delibes-Mateos, M. (2016). **Hunting as a source of alien species - a European review.** Biological Invasions. 19(4), 1191-1211.

Resumen

Las actividades de caza son responsables de la translocación y repoblación de millones de animales en toda Europa, incluida la introducción de especies exóticas. En un contexto de creciente uso de las translocaciones cinegéticas y de creciente preocupación por el impacto de las invasiones biológicas, nuestro objetivo es revisar el papel de las especies exóticas introducidas principalmente para fines de caza a escala Europea. En particular, exploramos: 1) la importancia relativa de las especies de caza en el contexto de las introducciones de especies exóticas; 2) la evolución temporal del número de especies introducidas para fines de caza; 3) la contribución de los diferentes taxones; 4) el patrón de la composición de las especies de caza introducidas entre países (en términos de similitud) y 5) los factores demográficos humanos subyacentes que impulsan la diversidad de especies de caza introducidas por país. Según nuestros resultados, el 24.3% de los mamíferos y el 30.2% de las aves introducidas en Europa durante el siglo pasado fueron liberados principalmente para fines cinegéticos, en total 93 especies (63 aves y 36 mamíferos), siendo los más importantes los Artiodáctilos, Anseriformes y Galliformes. La composición de las especies difiere entre los países, con una mayor diversidad de especies de caza introducidas en los países más grandes y en aquellos con una mayor densidad de población humana y proporción de cazadores. Esta revisión hace hincapié en que la caza fue una via de entrada significativa para la introducción de especies invasoras en Europa en el siglo pasado. Debido a que algunas de las especies de caza introducidas han tenido graves impactos ambientales en muchas regiones Europeas, y la introducción de especies de caza no nativas sigue ocurriendo, es esencial mejorar las regulaciones y aumentar la conciencia pública con respecto a los animales de caza invasivos. Esto ayudará a preservar la biodiversidad, y a mejorar la sostenibilidad de los actuales esquemas de caza en ecosistemas Europeos cada vez más gestionados.

Abstract

Hunting activities are responsible for the translocation and restocking of millions of animals throughout Europe, including the introduction of alien species. In a context of the growing use of game translocations and of increasing concern about the impact of biological invasions, our goal is to review the role of alien species introduced primarily for hunting purposes on the European scale. In particular, we explore: 1) the relative importance of game species in the context of alien species introductions; 2) the temporal evolution of the number of species introduced for hunting purposes; 3) the contribution of different taxa; 4) the pattern of introduced game species composition across countries (in terms of similarity), and 5) the underlying human demographic factors driving the diversity of introduced game species per country. According to our results, 24.3% of the mammals and 30.2% of the birds introduced into Europe during the last century were released primarily for hunting purposes, in total, 93 species (63 birds and 36 mammals), the most important taxa being Artiodactyls, Anseriformes and Galliformes. The species composition differed among countries, with a higher diversity of introduced game species in larger countries and in those with a higher human population density and proportion of hunters. This review stresses that hunting was a significant pathway for the introduction of invasive species into Europe in the last century. Since some of the game species introduced have had severe environmental impacts on many European regions, and introductions of non-native game species are still occurring, it is essential to improve regulations and increase public awareness regarding invasive game animals. This will help to preserve biodiversity and improve the sustainability of current hunting schemes in increasingly managed European ecosystems.

Introduction

Invasive alien species (IAS) have been identified as one of the most important direct drivers of biodiversity loss, ecosystem degradation and ecosystem service changes (Pejchar and Mooney 2009; Pyšek and Richardson 2010). The threats posed by IAS have consequently been addressed through the development of many international policy instruments, guidelines and technical tools (Monaco et al. 2013). In this context, understanding the pathways of species introductions constitutes a key issue as regards managing and preventing further invasive events. The most common motivation for the introduction of plant and animal species into new areas has by far been the establishment of new food sources (Lambdon et al. 2008; Shimono and Konuma 2008). Other common introduction pathways related to human activities include the wild-bird trade (Carrete and Tella 2008), aquarium fish commerce and inland fisheries (Gertzen et al. 2008), maritime activity (López-Legentil et al. 2015), the commerce of species for aesthetic purposes (Mack and Lonsdale 2001) and horticulture, in addition to unintentional introductions (Hulme et al. 2008).

In Europe, hunting is a social and cultural activity in which millions of people are involved as both participants and beneficiaries, and it is undertaken on millions of hectares of land and wetland. In general, hunting is currently practiced for recreation and involves the harvest of game species and the management activities that are undertaken to enhance these harvests. In this context, wildlife is frequently introduced in order to create or improve hunting opportunities, especially when native game species have become scarce (Blackburn and Duncan 2001; Long 2003). Some of the most commonly used techniques in game management are the relocation of wildlife species for the purpose of introduction (attempts to establish a species outside its recorded distribution), re-introduction (attempts to establish a species in an area that was formerly part of its range, but from which it was extirpated or became extinct) or supplementation (when individuals are added to an existing population of conspecifics) (Griffith et al. 1989; Wolf et al. 1996; Fischer and Lindenmayer 2000). Animals are also commonly released from farms for intensive hunting without the aim of creating or reinforcing populations (e.g. pheasants, partridges or mallards; Champagnon et al. 2009; Caro et al. 2014). From this perspective, hunting is usually considered to be among the most common motivations for the introduction of alien species (Yiming et al. 2006; Genovesi et al. 2012). Although recreational fishing is also a frequent pathway of species introductions (Savini et al. 2010), we have focused on hunting because the ecological, economic and social settings associated with both activities are clearly different.

It is often difficult to distinguish species introduced merely for hunting purposes from those initially introduced for other purposes (e.g. for their fur or for aesthetic purposes) and that were later hunted. Nevertheless, this review focuses only on those species introduced primarily for hunting purposes, and species released for other reasons and that were later harvested as hunting resources have, therefore, been excluded. The transportation and introduction of species are only two of the stages in the invasion process, which also includes the stages of establishment and spread (Kolar and Lodge 2001, 2002; Blackburn et al. 2011). The aim of this review was not to carry out an in-depth assessment of the role of hunting in all of these stages. However, we did consider all the species released primarily for hunting purposes, regardless of the stage at which each species was in the invasion process.

There are numerous studies on biological invasions, including their ecological and economic impacts (Olson 2006; Pejchar and Mooney 2009; Keller et al. 2011a; Barnes et al. 2014), along with the way in which non-native species have been introduced (Hulme 2009; Sanchirico et al. 2010; Hulme 2015). However, the role of hunting as a source of alien species has received relatively little attention in comparison with other aspects like those previously mentioned (Blackburn and Duncan 2001; Jeschke and Strayer 2006). It is, therefore, important to quantify the number of species that have been introduced primarily for hunting purposes, in addition to assessing their origin, distribution and consequences. This review is relevant because most wildlife and habitat management throughout Europe currently occurs in hunting areas. This sector must, therefore, actively participate in conservation policies whose intention is to protect biodiversity based on the premise of the sustainable use of resources, and particularly to reduce the impact of alien species. Our general objective was to identify cases of alien species that were introduced into Europe primarily for hunting purposes during the 20th century. We restricted our review to the last century because historical sources of information do not always exist for a wide range of species (like those covered in this review), and if they do exist, are often not easily available (e.g. Delibes and Delibes-Mateos 2015). In addition, differences between Europe and other continents as regards biogeography, history, culture, traditions, ecology and hunting styles, among other things, prevented us from expanding our review to other continents. We defined five specific goals, which were: 1) to review the relative role of game species in the general context of alien species introductions; 2) to assess the temporal evolution of the number of species introduced for hunting purposes; 3) to assess the relative importance of different taxa; 4) to identify similarity patterns in the composition of introduced game species across countries, and 5) to assess the underlying human demographic factors that drive their diversity in Europe. The final goal was to provide conservation managers with further useful insights and to guide future research on the topic.

Methods

Data collection

We reviewed several lists of species that had been introduced into Europe, which we obtained from either scientific papers, books and technical reports (Jeschke and Strayer 2005; Wolfe et al. 2007; Genovesi et al. 2009, 2012; Nentwig et al. 2010; Kumschick et al. 2011; Baker et al. 2014), or official databases such as the Global Invasive Species Database (``GISD´´), and Delivering Alien Invasive Species Inventories for Europe (``DAISIE´´). Scientific papers that particularly addressed the introduction of species for hunting purposes were searched using three main web engines: Google Scholar^{TM}, ISI Web of Knowledge® and Scopus®. We used the following search terms: 'alien species' OR 'exotic species' OR ‘introduced species’ AND 'hunting' OR 'game species' AND 'Europe'. The Canary Islands, Madeira and Cyprus were excluded from this study because they lie in different biogeographical zones to the rest of Europe (Beierkuhnlein 2006). The list of sources of information used for this review is shown in Table S1. As mentioned above, we identified those species that were, according to the bibliography consulted, primarily introduced for hunting purposes. We defined “introduced game species” as those introduced species that are deliberately sought and legally harvested from the wild, whether for sport, individual consumption, or commercial harvest (Jeschke and Strayer 2006). Game species that were introduced for other purposes (e.g. fur farms), but were later hunted, were not therefore considered in this review. We then combined all this information to obtain one unified database. The full list of species introduced primarily for hunting purposes is depicted in Table S2. This table also shows the stage of the invasion process at which each species is at the European level. According to ``DAISIE´´ and ``GISD´´, the stages of the invasion process are: ``Extinct´´ (completely vanished), ``Not Established´´ (have disappeared from natural environments, but are maintained on farms, parks…), ``Established´´ (occur successfully in the natural environment) and ``Invasive´´ (officially declared as invasive at a European level). We calculated the proportion of mammal and bird species found in each invasive stage.

The biogeographic region from which each species was derived was also identified (Palaearctic, Nearctic, Indo-Malaysia, Afrotropics, Neotropics, Australasia and Oceania), and those widespread species that occupy several regions were classified as either Holarctic, New World or multiregional (Abellán et al. 2015; see Fig. S1). Finally, we evaluated in which country or countries each species occurs (Fig. S2a).

Analyses

Similarities in the composition of alien game species throughout the countries studied were explored using cluster analyses. Hierarchical clustering analyses were performed using Ward's method, in which information is quantified as the sum of squared distances of each element with regard to the cluster centroid (Mirkin 2012). This was done by first calculating the mean vector for all variables and the multivariate centroid for each cluster and then calculating the squared Euclidean distances between each element and the centroid (mean vector) of all the clusters. Finally, the distances for all elements were combined. This clustering method was deemed the most appropriate, since it provides a flexible approach and does not assume any specific distributions of variables (Oteros et al. 2013). The clustering variable was the presence of different introduced game species in each country (Fig. S2a). After clustering the countries, we analysed each group in order to describe the distribution of species composition. The proportion of each species in each cluster as a function of the number of countries in which each species is present was then depicted as a matrix plot using R statistical software (R Core Team). This ranges between 1 (i.e. species present in all countries of one sub-cluster) and 0 (i.e. species absent in all countries of one sub-cluster; Fig. S2b).

In order to determine the underlying human demographic factors driving the diversity of introduced game species per country, two Generalised Linear Models (GzLM) were performed using the total number of introduced game species in each country (model 1) and the proportion of game species in relation to the total number of introduced species in each country (model 2) as response variables. Model 1 fitted a gamma distribution with a log link and model 2 fitted a binomial distribution with a log link, respectively. The variables country size, human population density, percentage of rural population, percentage of hunters and the gross domestic product (GPD) per capita were included as explanatory variables in both models (the data source is shown in Table S1). The selection of the most plausible models was carried out by comparing Akaike's information criterion (AIC) in the models (Burnham and Anderson 2002) following a backward procedure (Zuur et al. 2009). In particular, we compared the Akaike information criteria for small sample sizes (AICc value) in each candidate model and the best model (that with the lowest AICc). As a rule, a $\Delta i < 2$ suggests that the candidate model has a similar explanatory power to the a priori best model (Burnham and Anderson 2002). We therefore selected all the models in which $\Delta i < 2$ with regard to the best model. Statistical analyses were performed using IBM SPSS Statistics 20 software.

Results

1) Game species in the context of alien species introductions in Europe

According to our results, 24.3% of the mammals (34 out of 140 species) and 30.2% of the birds (59 out of 195 species) introduced into Europe during the last century were released primarily for hunting purposes. Of these 93 introduced species, 68 are currently exploited as small game species, and 25 as big game species. We specifically noticed that 34 mammal species (29%) and 59 bird species (34%) of the 117 mammals and 175 birds introduced into Europe according to the DAISE list were introduced primarily for hunting purposes. In the case of GISD, at least 17 (25%) out of the 68 alien mammal species and 8 (25.8%) out of the 31 alien birds species are hunted in their non-native range. In addition, we found that 33% of the mammals (n=3) and 50% of the birds (n=14) introduced into Europe according to Jeschke and Strayer (2005) were released for hunting purposes. Genovesi et al. (2009, 2012) showed that hunting was the origin of 24% (n=7) of introductions of mammals into Europe. Another European review pointed out that food and game were the primary introduction pathways for birds (61 species, which represented 25.8% of total bird introductions) and mammals (31 species, which represented 20% of total mammal introductions) (Hulme et al. 2008). Overall, our results further show that 56.1% of the birds and 60.6 % of the mammals introduced for hunting purposes are currently successfully established in the wild (Table S2).

Within Europe, the introduction of these species has not been spatially uniform, and countries such as France, Italy, Germany or UK stand out in this respect (20 or more introduced game species). On the contrary, other areas such as the Balkans or Baltic states have a much lower incidence of game species introductions (Fig. 1).

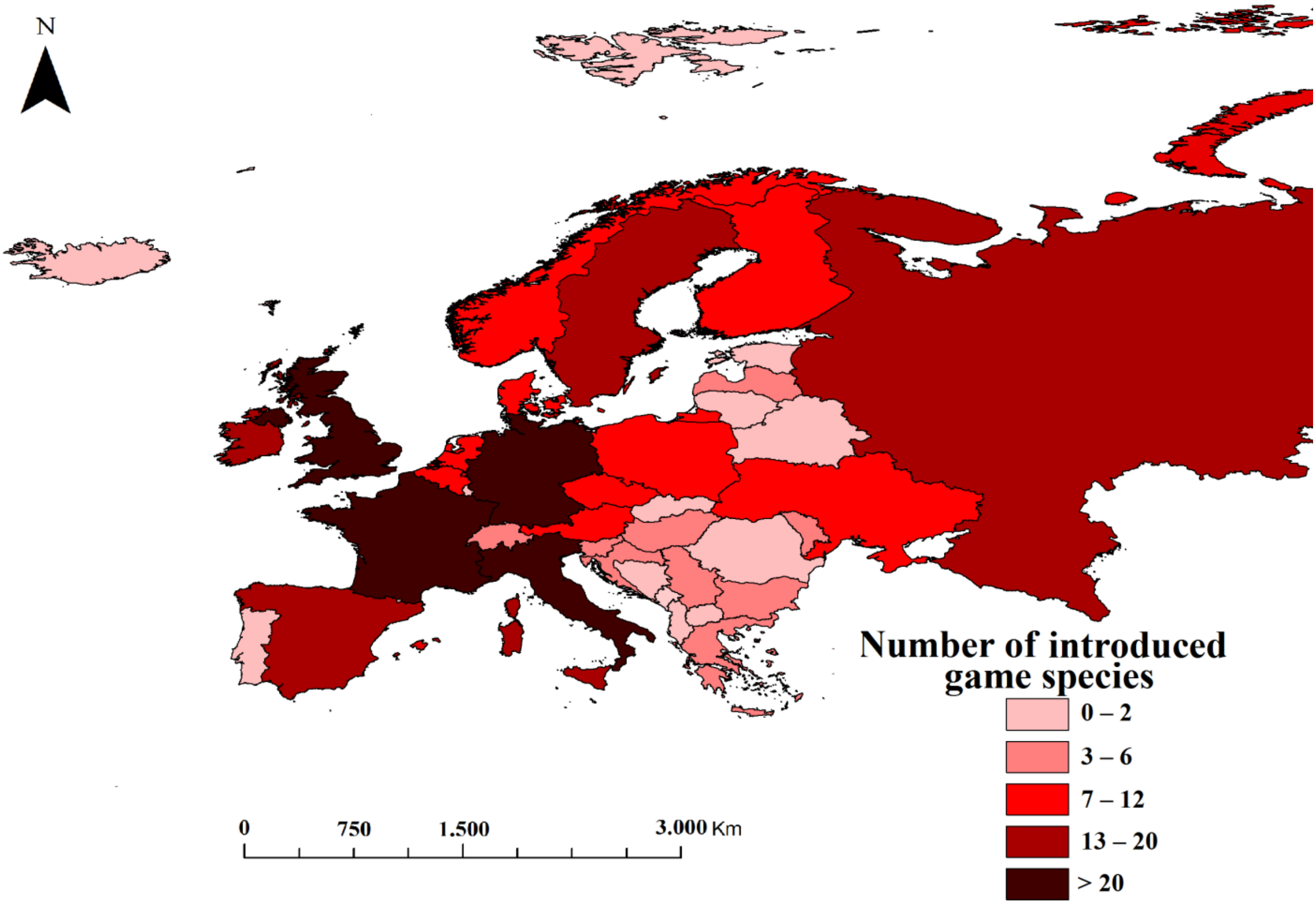

Figure 1. Map depicting the number of species (mammals & birds) introduced into European countries for hunting purposes.

In addition, the origin of these species is also highly heterogeneous. The Palaearctic biogeographic region stands out as the source of the majority of introduced species (46%). It is followed by the Nearctic (16%), the Neotropics (9.6%), Indo-Malaysia (7.5%) and the Afrotropics (6.45%), with similar proportions in both taxa; the Neotropics were the exception as they were the origin of 11.8% for birds but no introduced game mammal came from this region (see Fig. S1).

2) Temporal evolution of the number of species released for hunting purposes in Europe

The introduction of new species as a game management tool has historically been a frequent practice in Europe (Long 1981). However, it has become much less common over the last few decades (Monaco et al. 2013). The aforementioned authors showed that the number of intentional introductions of new alien species for hunting purposes (specifically birds and mammals) has decreased by approximately 50% since the 1980s, reaching its lowest value after 2000. In addition, the rate of introduction events for hunting purposes in comparison with other motives has also decreased during the last few decades (Mónaco et al. 2013; Fig. 2b).

3) Importance of each taxonomic group

Of the introduced game species (n=93), 63.45 % were birds and 36.55% were mammals. Species within other taxonomic groups have not been introduced for hunting in Europe. Most of the 34 introduced mammal species were ungulates (Fig. 2a). In this respect, at least 25 species out of 257 existing species of ungulates have been introduced into Europe to be exploited as game species. Another well-represented group among mammals was lagomorphs, with at least 8 species introduced for game purposes, representing 23.5% of the introduced mammals (Fig. 2a).

Our results further show that the majority of introduced game bird species belong to three orders: Galliformes, Anseriformes, and Columbiformes, accounting for 44%, 42 % and 6.7 % of the total number of introduced bird game species, respectively (Fig. 2a). The family that encompasses the most frequently introduced species within the order of Galliformes is *Phasianidae*: 26 alien species out of the 177 species of this family (14.7%) have been introduced into Europe for hunting purposes (Blackburn and Duncan 2001). Anseriformes is also a very important taxa with a total of 25 introduced species out of the 162 species within this group (15.4%) (Blackburn and Duncan 2001).

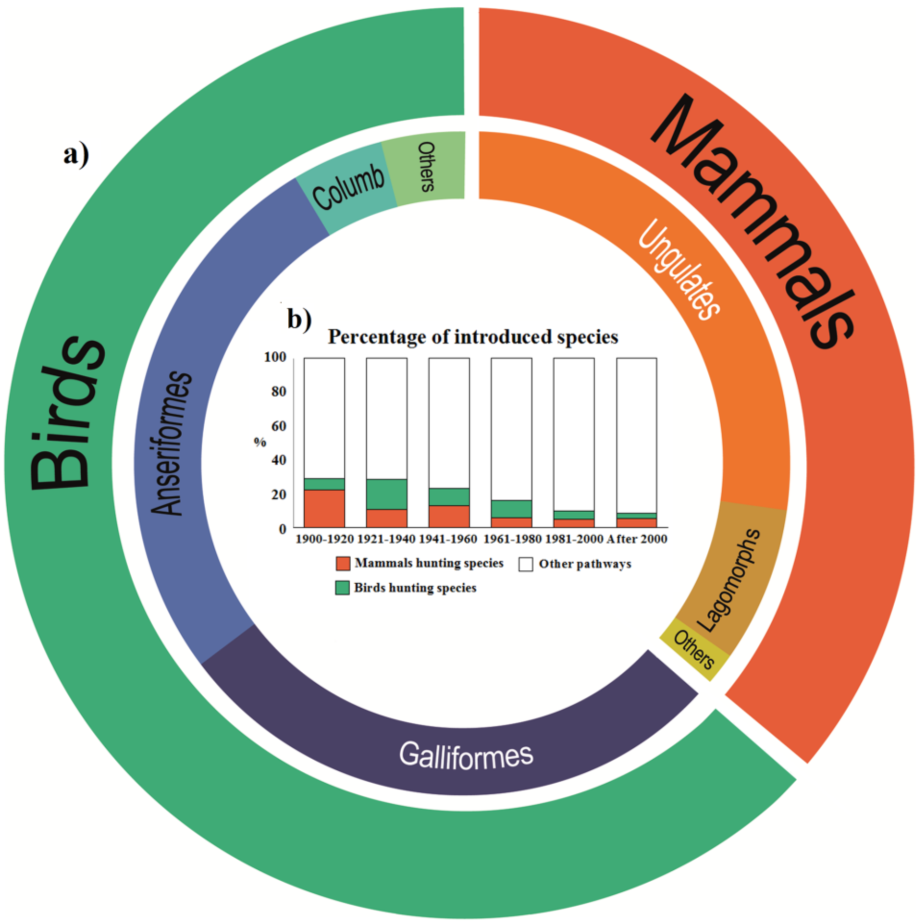

Figure 2. a) Proportion of species of different taxonomic groups within birds and mammals that were, according to our review, introduced into Europe during the 20th century for hunting purposes. Columb. refers to Columbiformes; b) Trend of the percentage of introductions of mammals and birds for hunting purposes and other pathways of introduction. Change over time is shown in 20 year-periods. Information adapted from Monaco et al. 2013 (original data from DAISIE European Invasive Alien Species Gateway; http://www.europe-aliens.org).

4) Introduced species composition by country and underlying factors of their diversity

The clustering analyses carried out grouped different countries according to the similarity of the game species introduced into their territories (Fig. 3). Overall, three main clusters of countries and eight sub-clusters were found. Cluster 1 (C1) included a group of countries in Eastern Europe (e.g. Balkan countries) with a low number of introductions (mean = 3.4 species). A second cluster (C2) was composed of most of the Northern countries (Sweden, Norway, Finland) and several Central European countries (Austria, Poland, Czech Republic), together with Russia and other Eastern European countries (Poland and Ukraine), and was characterized by a medium number of species introduced for hunting (mean =11.7 species). Cluster 3 (C3) was mainly composed of those countries with a larger number of introduced game species (mean = 29.2 species), and it included countries like the UK, Germany, France, Spain or Italy.

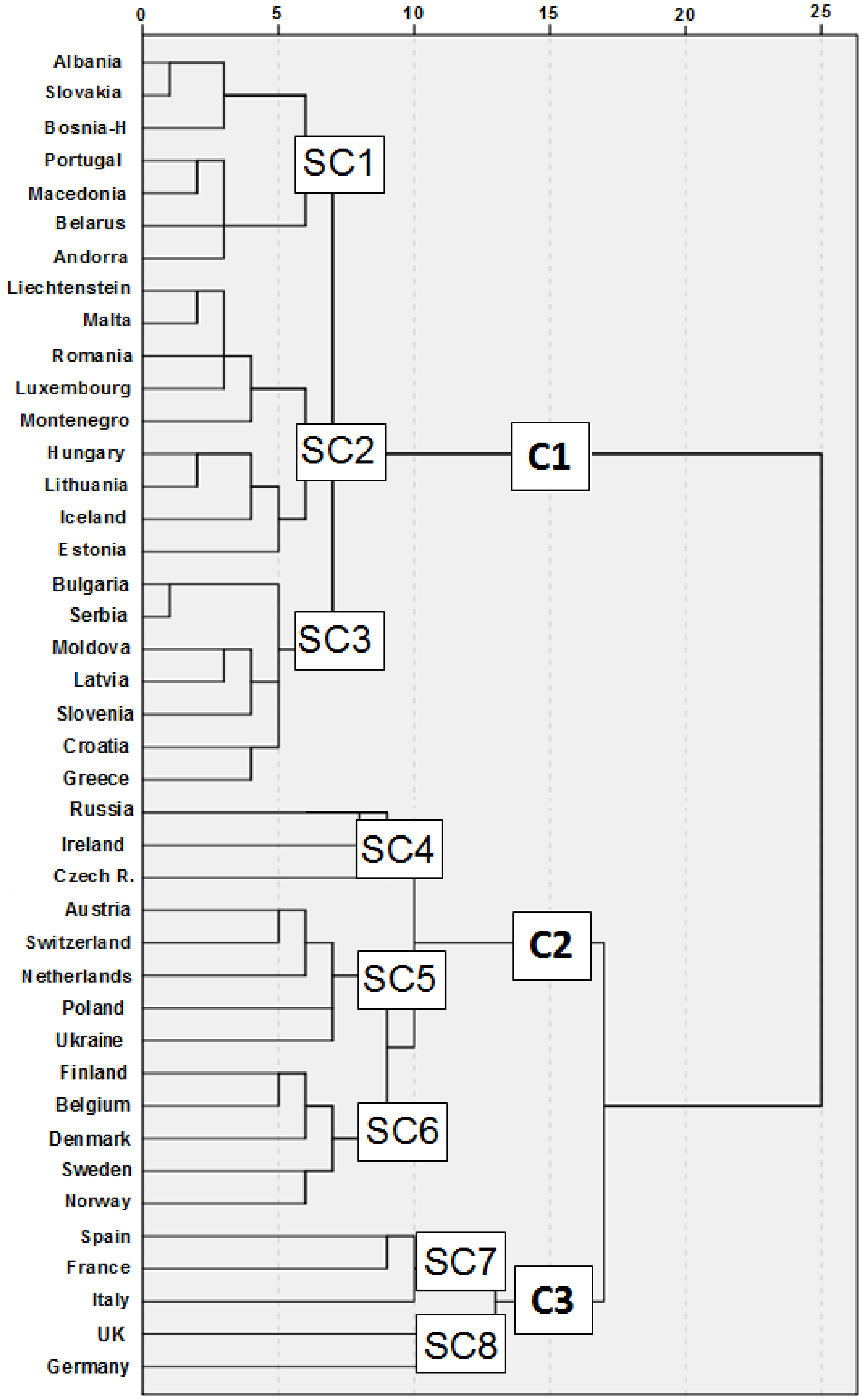

Figure 3. Dendrogram showing three hierarchical clusters and eight sub-clusters of countries grouped according to the similarity of the composition of game species introduced into their territories.

Fig. 4 represents the distribution pattern of different taxonomic groups within each sub-cluster. Ungulates, Lagomorphs, Galliformes and Anseriformes were present in all the sub-clusters, whereas Columbiformes were present in all the sub-clusters with the exception of SC1. However, the proportion of each taxonomic group varied between sub-clusters. For instance, the most important taxon in sub-cluster SC1 was Galliformes, while ungulates stood out in sub-clusters SC2, SC3 and SC4, and Anseriformes in sub-clusters SC6 and SC8. In sub-cluster SC5, SC7 and SC8 Ungulates, Anseriformes and Galliformes were represented in similar proportions.

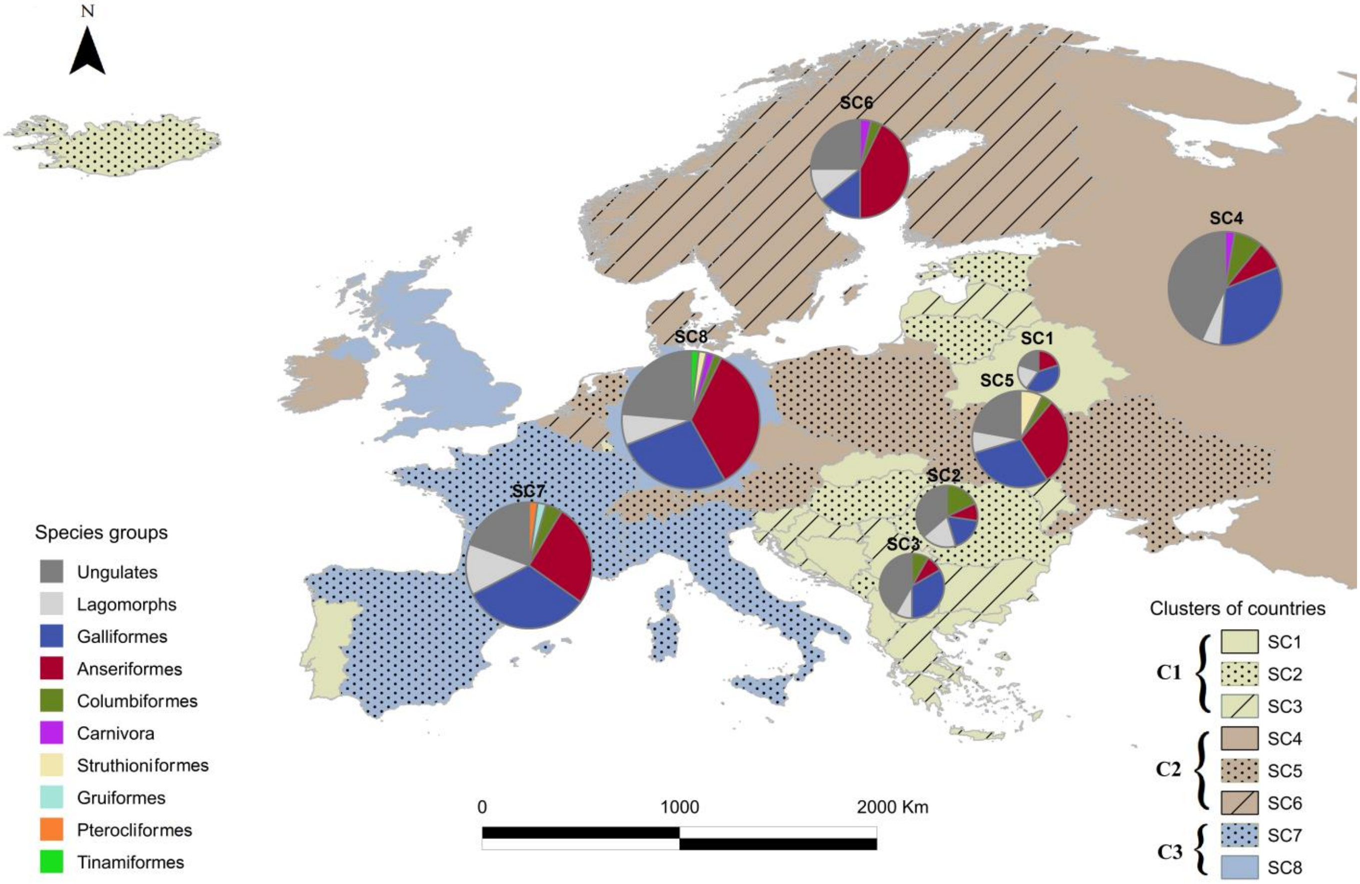

Figure 4. Map representing the clusters and sub-clusters of grouped countries, showing the frequency distribution of each taxonomic group within each sub-cluster. The size of the diagram is proportional to the number of species within each sub-cluster.

Finally, candidate models assessing the effect of countries' characteristics on the total number of alien game species in each country and the proportion of game species with regard to the total number of introduced species in each country are shown in

Table 1. The factors retained in the best models (model 1 and 2) are displayed in Table 2. The results show that the country's size, human population density and percentage of hunters were statistically and positively associated with the total number of introduced game species per country (model 1). Furthermore, the proportion of game species relative to the total number of introduced species was positively associated only with the percentage of hunters (model 2).

Table 1. Candidate models assessing the effect of countries' characteristics on the total number of alien game species in each country (model 1) and the proportion of hunted species relative to the total number of introduced species in each country (model 2). The number of model parameters (k), the Akaike information criteria for small sample sizes (AICc), the difference between each model and the best model (ΔAICc), and the Akaike weight (*wi*) are shown.

	k	AICc	ΔAICc	*wi*
Candidate models (model 1)				
Size + Density + % of hunters + GDP	4	217.172	0	0.43
Size + Density + % of hunters	3	217.329	0.157	0.40
Size + Density + % of hunters + % of rural population	4	219.128	1.956	0.16
Candidate models (model 2)				
% of hunters **+** % of rural population	2	175.476	0	0.38
% of hunters	1	176.299	0.823	0.25
Size + % of hunters **+** % of rural population	3	176.797	1.321	0.2
Size + % of hunters	2	177.112	1.636	0.17

Table 2. Best models explaining the number of alien game species in each country (model 1) and the proportion of introduced hunted species relative to the total number of introduced species in each country (model 2), respectively. Variables that were statistically significant in the models are highlighted in bold type.

Variable	Estimate ± S.E.	Wald	p-value

Number of alien game species (model 1)			
Intercept	0.421 ± 0.23	3.241	0.07
Country size (Km^2)	**0.003 ± 0.0006**	**30.61**	**<0.001**
Population density (people per km^2)	**0.004 ± 0.001**	**13.96**	**<0.001**
% of hunters	**0.102 ± 0.053**	**3.69**	**0.05**
GDP per capita (€)	0.001 ± 0.007	2..93	0.085
Proportion of hunted species (model 2)			
Intercept	-0.82 ± 0.16	24.65	<0.001
% of hunters	0.093 ± 0.03	**7.66**	**<0.01**
% of rural population	-0.01 ± 0.005	2.8	0.09

Discussion

Game species in the context of alien species introductions

Europe has historically been a hotspot of alien species, since several thousands of non-native species have been introduced and have subsequently become established (Vilá et al. 2009; Keller et al. 2011a), including several game species, as our results demonstrate. According to our review, 24.3% of alien mammal and 30.2% of alien bird species were released primarily for hunting purposes, revealing that hunting has been a major motivation for the intentional introduction of species into Europe. Indeed, hunting was one of the main pathways by which non-native species were introduced into Europe during the 20th century (Fig. 5). Although not all species that moved beyond their native range become established in invaded areas (Sala et al. 2000), the introduction of a high proportion of game species has been successful (56 % in birds and 60 % in mammals), possibly owing to the intensive effort made by humans to establish stable populations (Champagnon et al. 2012) in addition to their high reproductive rate (Thompson and King 1994).

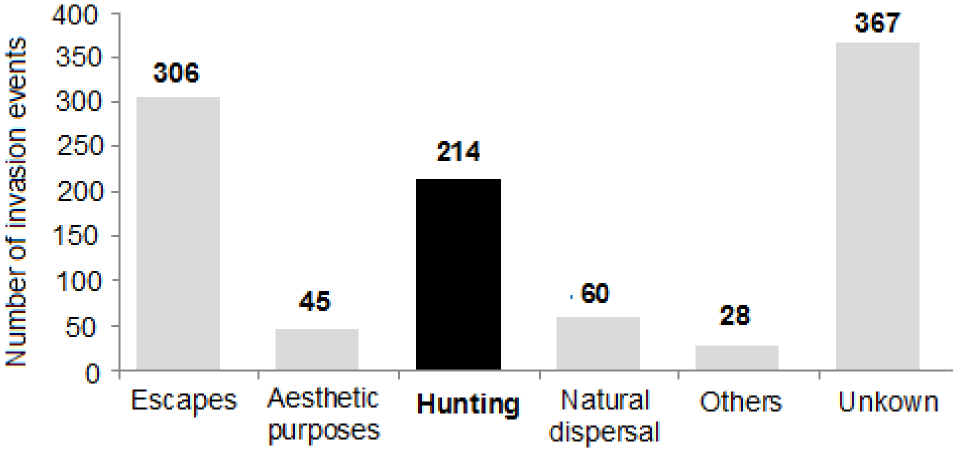

Figure 5. Number of invasive terrestrial vertebrate events in Europe during the last century, associated with particular pathways of introduction (adapted from DAISIE European Invasive Alien Species Gateway; http://www.europe-aliens.org).

Another point to consider is not only the number of species, but also the total number of individuals released. Although, unfortunately, this information is not available in most cases, it is known that massive releases of non-native small game species occur frequently in Europe (Champagnon et al. 2012). For example, it is estimated that 35 million pheasants (*Phasianus colchicus*) and 6.5 million red legged partridge (*Alectoris rufa*) are released annually in the UK (PACEC 2006), while 100-200,000 Japanese quails (*Coturnix japonica*) are released in northwest Spain and other Mediterranean countries such as Italy, Greece, France or Portugal (Puigcerver et al. 2007).

Underlying reasons for game species introductions

Although the eventual goal of hunting introductions is the exploitation of a game species to obtain economic or social benefits, our review stresses the existence of two main motivations behind the introduction of game species: diversifying the number of hunting species and superseding declining native species. Game species have been introduced in order to diversify the spectrum of huntable species, particularly in the case of new species that are valued for their game trophy, which usually has an associated profit. For example, since ungulates are highly valued in trophy hunting (Coltman et al. 2004), several non-native species of deer (such as, *Cervus nippon or Cervus* *canadensis*), ibex (*Capra pyrenaica* and *Capra ibex*), bighorn sheep (*Ovis canadensis*), aoudad (*Ammotragus lervia*), mouflon (*Ovis orientalis*) and Himalayan thar (*Hemitragus jemlahicus*), among others, were introduced throughout Europe during the 20th century. These introductions have generated a considerable income, directly through license fees and indirectly through the purchase of equipment and associated hunting services in general (Long 2003; Arnett and Southwick 2015).

Species substitution may also occur when the species that has been traditionally exploited has undergone a marked decline, and managers introduce a new alien species to supplement the harvest (Clavero 2016). For example, the chukar partridge (*Alectoris chukar*) has been introduced into Spain, France and Italy owing to the fact that the native red-legged partridge has declined, thus reducing opportunities for hunters (Barilani et al. 2007; Blanco-Aguiar et al. 2008). The brown hare (*Lepus europaeus*) has also been introduced to increase hunting opportunities in areas of Sweden and Russia in which mountain hares (*Lepus timidus*) have declined (Thulin 2003).

In addition, it is known that some species (or their hybrids) are more easily farm-reared than others, which may explain why the former have often been used for releasing purposes even when they may be alien species. For example, chukar partridges, along with their hybrids resulting from breeding with red-legged partridges, produce a higher number of chicks in captivity than do red-legged partridges, and are therefore usually released for shooting in Spain (Blanco-Aguiar et al. 2007), although they are not native.

Temporal patterns in game species releases

Although some species are still released in Europe for hunting purposes, the proportion of new species introductions attributed to this activity has declined over the past decades (Fig. 2b). There are several potential reasons for this pattern. First, it is obvious that many alien game species were introduced several decades ago (Grinnell 1925), which reduces the likelihood of introducing new species. Furthermore, the development of more restrictive international regulations in terms of invasive species may also have favoured the reduction in game species introductions. Finally, the increase in regulations for the transportation of wildlife, owing to the risk of disease transmission (e.g. African swine fever, foot and mouth disease, avian influenza or Newcastle disease), with the emergence of organisations such as the World Health Organisation, the World Organisation for Animal Health or the World Trade

Organisation (Fèvre et al. 2006), may also have contributed to reducing animals' movements. Interestingly, the proportion of mammals *versus* birds introduced for game has also changed during the 20th century, with a decline in the importance of the former (Fig. 2b).

Over the past decades, several wild ungulates, such as the red deer (*Cervus elaphus*), the roe deer (*Capreolus capreolus*) or the wild boar (*Sus scrofa*), have expanded their range and increased in abundance throughout Europe, leading to a huge increase in the number of big game animals harvested (Côté et al. 2004; Apollonio et al. 2010; Massei et al. 2015). However, an opposite pattern has occurred in the case of several small game species, many of which have declined dramatically; e.g. the European wild rabbit (*Oryctolagus cuniculus*) and the red-legged partridge in Spain (Blanco-Aguiar et al. 2004; Delibes-Mateos et al. 2009a). This may have caused an increase in the release of these species (Champagnon et al. 2012) in addition to a shift from small game to big game species.

There are some other potential explanations for the recent decline in the number of game species introduced into Europe besides those discussed above. For example, previous bad experiences owing to the low efficiency of releases may have prevented some game managers from carrying out new introductions, as has been reported in the case of the chukar partridge (van Wieren 2012). The foundation of different agencies, such as the International Union for Nature Conservation (IUCN) or the International Union of Game Biologists (IUGB), may have played an important role as regards transferring information concerning the risks associated with the introduction of non-native species to hunters. This may have increased their awareness of this issue, probably preventing some of them from using the release of non-native species as a game management tool (Nentwig 2007; Monaco et al. 2013). Although hunting is currently no longer a 'popular' pathway for the introduction of new alien game species (Fig. 2b), it continues to be an "open gateway" for alien species, and new introductions of alien game species are being reported in different countries. Examples of this are the recent introduction of the cotton-tail rabbit (*Sylvilagus floridanus*) into Italy, or that of the wild boar into Ireland and Sweden (Welander et al. 2000; McDevitt et al. 2013).

Importance of each taxonomic group

Our review shows that the introduction of game species has been biased towards several wildlife orders, mainly Artiodactyls, Anseriformes and Galliformes. Ungulates stand out from the others (with 73.5% of introduced mammals species), probably because of their importance in trophy hunting (Spear and Chown 2009). Ungulate species have been introduced on the whole continent, and this is one of the most important groups everywhere (Fig. 4).

The Lagomorpha constituted the mammal order with the second most introduced game species. For instance, the cotton-tail rabbit was introduced into some European countries for hunting purposes, although wild populations apparently survived only in Italy (Rosin et al. 2008). Other examples are the New England cotton-tail (*Silvilagus transitionalis*) in Germany or the Cape hare (*Lepus capensis*) in Italy (Nentwig et al. 2010).

In the case of birds, Galliformes and Anseriformes were introduced primarily for hunting and ornamental purposes (Long 1981). Examples of Galliformes game species introduced outside their native range include the common pheasant, the red legged partridge and the chukar partridge, the barbary partridge (*Alectoris barbara*) and the rock partridge (*Alectoris graeca*) (Abellán et al. 2015; Barbanera et al. 2015).

The Anseriformes order is an important taxon in countries such as France, the UK, Germany, Sweden or Finland, where examples of species that were introduced for hunting purposes include the Canada goose *(Branta canadensis)* or the ruddy duck *(Oxyura jamaicensis)* (Long 1981; Baker et al. 2014). Another very important order is the Columbiformes, which consists of one single family: *Columbidae*. This family includes 313 species, of which 31 (10%) have been introduced throughout the world (Blackburn and Duncan 2001), and at least 4 of them were introduced into Europe for hunting purposes during the 20th century.

Uneven distribution of introduced game species in Europe and associated factors

Overall, different countries with similar customs and bioclimatic and geographic ranges were grouped into clusters or sub-clusters on the basis of their similar compositions of introduced game species. Interestingly, those countries characterised by a long-standing hunting tradition, such as the UK, Germany, France, Spain and Italy, were grouped in the same cluster, with the highest number of introduced game species. In addition, our results show that the highest number of introduced game species appears in larger countries with a higher population density, which offer better opportunities for game releases (Cardador et al. 2016). Finally, countries with a higher proportion of hunters within the total population were associated with an increasing number of introduced game species and with the proportion of hunted species introduced relative to the total number of introduced species.

Concluding remarks and future directions

The deliberate introduction of non-native game species should be strongly discouraged by precautionary national and international biosecurity policies and practices. ‘Prevention is better than cure’, and proposed new introductions need to be thoroughly assessed (Mack et al. 2000; Jeschke and Strayer 2005; Keller et al. 2007). If new management programmes are not brought into force in Europe, it is inevitable that more alien game species will arrive, and that the impacts of these species on the economy, environment, and human and wildlife and livestock health will continue to grow (Keller et al. 2011b; Blackburn et al. 2014; Schindler et al. 2015). Scientific studies have demonstrated that introduced game species have several negative impacts on those areas into which they have been introduced. These include predation (Barrios-Garcia and Ballari 2012), competition with native wildlife (Bartos et al. 2002; Kumschick et al. 2011; Bertolino et al. 2013), diseases and their related consequences (Kralova-Hromadova et al. 2010), hybridisation (Barbanera et al. 2009, 2010; Baker et al. 2014), and habitat alteration (Kumschick et al. 2011). These ecological impacts may also have important economic effects, including damage to human infrastructures, human health risk, negative effects on human social life, the spread of disease to livestock, and agricultural damage (Nentwig et al. 2010; Keller et al. 2011a; Simberloff et al. 2013; Schindler et al. 2015).

The objective of additional measures should be to boost declining native hunting species populations rather than releasing alien species. Hunting management strategies based on scientific evidence should therefore be carried out in order to ensure sufficient native harvest bags. Another key issue is how to manage certain established alien game species that are already an important hunting resource (e.g. White tailed-deer in Finland; Kekkonen et al. 2016), but cause negative impacts. From a strictly ecological point of view, they should be removed from their non-native range. However, hunters sometimes disagree with this option and it is, therefore, essential for all the stakeholders involved to reach agreements on these measures. Another interesting measure would be that of performing environmental education campaigns targeted towards hunters with the aim of providing information about the negative consequences of alien species. It would also be advisable for these campaigns to provide information regarding the low success of some game species restocking/introduction programmes and how to boost native game species.

The increasing pressure on global biodiversity as the result of invasive alien species, including those introduced for hunting purposes, as stressed in this review, requires considerable additional effort if this target is to be achieved, and strong emphasis should be placed on improving and harmonising legislation targeting biological invasions.

Acknowledgements

We are grateful to those databases that provided data for this review (i.e. DAISIE and GISD). We would also like to thank S. Newton and J. Oteros and two anonymous reviewers for their comments on earlier drafts of the manuscript. This study received financial support from the research project AGL2012-40128-C03-01 and EU–FEDER funds. AJC holds an FPI pre-doctoral scholarship. M. Delibes-Mateos is supported by V Plan Propio de Investigación of the University of Sevilla.

Figure S1 Percentage of species introduced into Europe for hunting purposes grouped by their biogeographic region of origin.

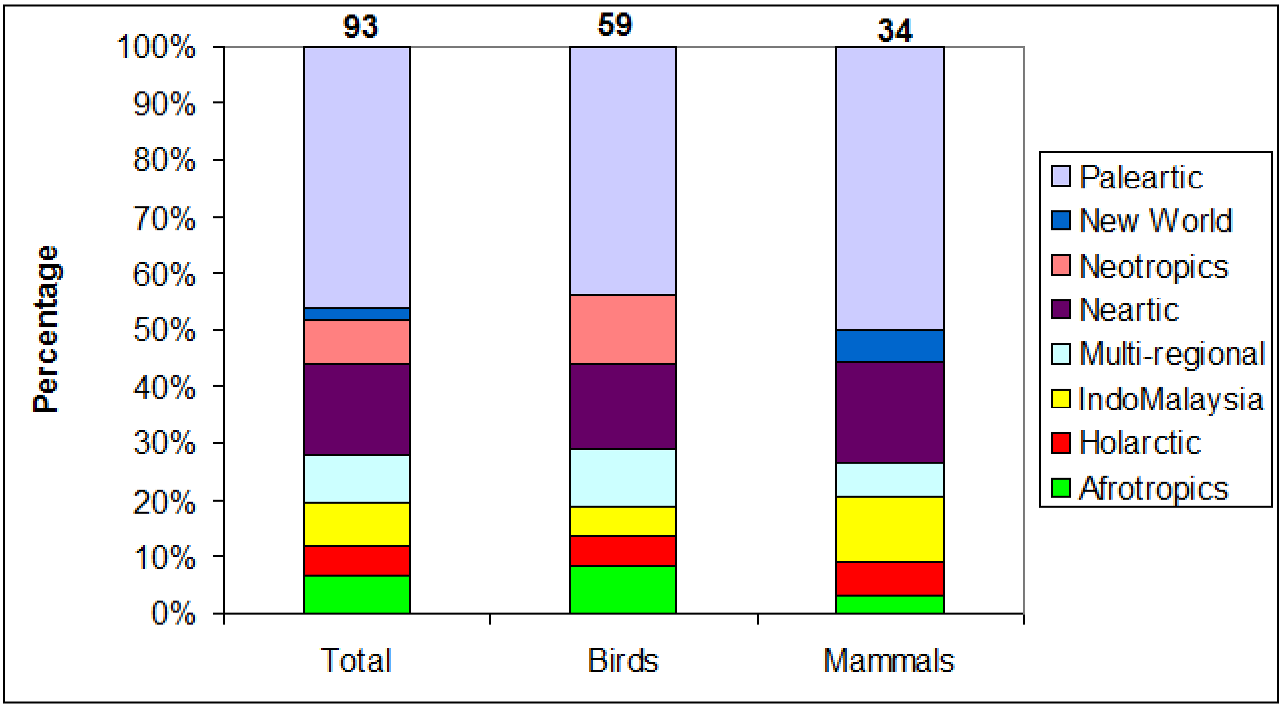

Figure 2Sa Presence (green) or absence (red) of each hunting species in each country.

Figure 2Sb The proportion of each species in each sub-cluster according to the number of countries in which it is present (between 1, present in all countries of one sub-cluster and 0 absent in all countries of one sub-cluster).

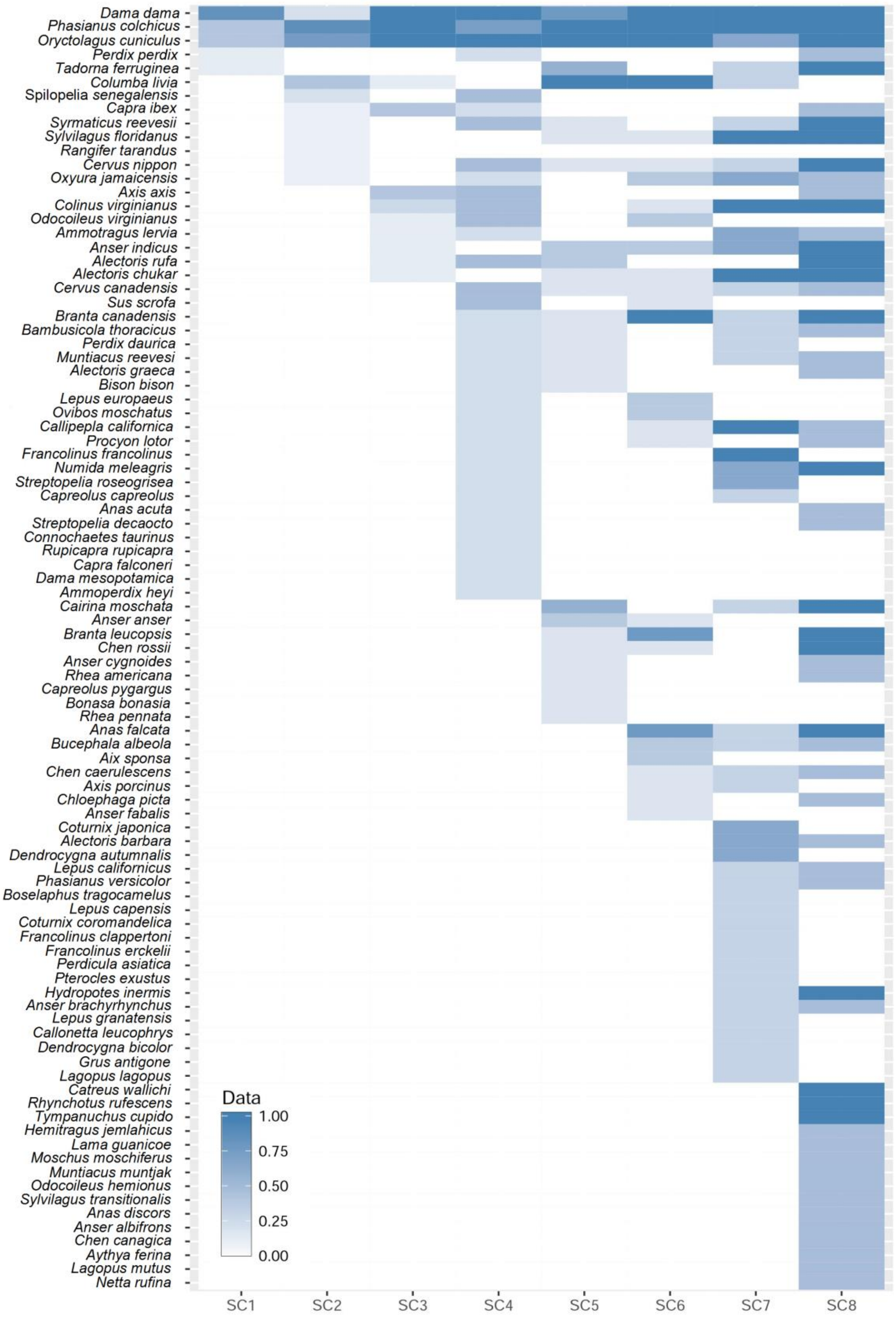

Table S1. Sources systematically reviewed to obtain information on introduction pathways and records of introduced species for hunting purposes in Europe. Sources of introductions also often provide information on case-by-case introduction pathways.

Source

Scientific manuscripts

Abellán, P., Carrete, M., Anadón, J. D., Cardador, L., & Tella, J. L. (2015). Non - random patterns and temporal trends (1912–2012) in the transport, introduction and establishment of exotic birds in Spain and Portugal. *Diversity and Distributions*.

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Long, J.L. (2003). *Introduced Mammals of the World: their History, Distribution and Influence*. CABI Publishing, Oxford, UK.

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Wilson, D. E., & Reeder, D. M. (Eds.). (2005). *Mammal species of the world: a taxonomic and geographic reference* (Vol. 12). JHU Press.

Database

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Data source of the variables

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% rural population (2015). http://datos.bancomundial.org/indicador/SP.RUR.TOTL.ZS

% Hunters (2014). Federación de Asociaciones de Caza de la Unión Europea. http://enrd.ec.europa.eu/enrd-static/networks-and-networking/eu-organisations/eu-organisations/es/face_es.html.

Population density (2015). http://www.census.gov/popclock/world/sp

Country size. https://www.cia.gov/library/publications/resources/the-world-factbook/wfbExt/region_eur.html.

Table S2. Exotic species introduced into Europe for hunting purposes. Information on the biogeographical region from which it was derived and stage of invasion process are provided for each species.

Taxa	Species	Group	Region	Stage
Birds	*Aix sponsa*	Anseriformes	Neartic	Established
Birds	*Anas acuta*	Anseriformes	Multi-regional	Established
Birds	*Anas discors*	Anseriformes	Neartic	Extinct
Birds	*Anas falcata*	Anseriformes	Multi-regional	Unknown
Birds	*Anser albifrons*	Anseriformes	Holarctic	Not established
Birds	*Anser anser*	Anseriformes	Paleartic	Established
Birds	*Anser brachyrhynchus*	Anseriformes	Paleartic	Established
Birds	*Anser cygnoides*	Anseriformes	Paleartic	Established
Birds	*Anser fabalis*	Anseriformes	Paleartic	Established
Birds	*Anser indicus*	Anseriformes	Multi-regional	Established
Birds	*Aythya ferina*	Anseriformes	Paleartic	Established
Birds	*Branta canadensis*	Anseriformes	Neartic	Invasive
Birds	*Branta leucopsis*	Anseriformes	Paleartic	Established
Birds	*Bucephala albeola*	Anseriformes	Holarctic	Unknown
Birds	*Cairina moschata*	Anseriformes	Neotropics	Established
Birds	*Callonetta leucophrys*	Anseriformes	Neotropics	Established
Birds	*Chen caerulescens*	Anseriformes	Neartic	Established
Birds	*Chen canagica*	Anseriformes	Paleartic	Not established
Birds	*Chen rossii*	Anseriformes	Neartic	Unknown
Birds	*Chloephaga picta*	Anseriformes	Neotropics	Not established
Birds	*Dendrocygna autumnalis*	Anseriformes	Neotropics	Not established
Birds	*Dendrocygna bicolor*	Anseriformes	Multi-regional	Established
Birds	*Netta rufina*	Anseriformes	Paleartic	Established
Birds	*Oxyura jamaicensis*	Anseriformes	Neartic	Invasive
Birds	*Tadorna ferruginea*	Anseriformes	Multi-regional	Established
Birds	*Columba livia*	Columbiformes	Paleartic	Established
Birds	*Spilopelia senegalensis*	Columbiformes	Afrotropics	Established
Birds	*Streptopelia decaocto*	Columbiformes	Paleartic	Established
Birds	*Streptopelia roseogrisea*	Columbiformes	Afrotropics	Established
Birds	*Alectoris barbara*	Galliformes	Paleartic	Established
Birds	*Alectoris chukar*	Galliformes	Paleartic	Established
Birds	*Alectoris graeca*	Galliformes	Paleartic	Not established
Birds	*Alectoris rufa*	Galliformes	Paleartic	Established
Birds	*Ammoperdix heyi*	Galliformes	Paleartic	Extinct

Birds	*Bambusicola thoracica*	Galliformes	Paleartic	Extinct
Birds	*Bonasa bonasia*	Galliformes	Paleartic	Established
Birds	*Callipepla californica*	Galliformes	Neartic	Established
Birds	*Catreus wallichii*	Galliformes	IndoMalaysia	Extinct
Birds	*Colinus virginianus*	Galliformes	Neartic	Established
Birds	*Coturnix coromandelica*	Galliformes	IndoMalaysia	Extinct
Birds	*Coturnix japonica*	Galliformes	Paleartic	Established
Birds	*Francolinus clappertoni*	Galliformes	Afrotropics	Established
Birds	*Francolinus erckelii*	Galliformes	Afrotropics	Established
Birds	*Francolinus francolinus*	Galliformes	Paleartic	Established
Birds	*Lagopus lagopus*	Galliformes	Paleartic	Extinct
Birds	*Lagopus mutus*	Galliformes	Holarctic	Extinct
Birds	*Numida meleagris*	Galliformes	Afrotropics	Not established
Birds	*Perdicula asiatica*	Galliformes	IndoMalaysia	Extinct
Birds	*Perdix daurica*	Galliformes	Paleartic	Established
Birds	*Perdix perdix*	Galliformes	Paleartic	Established
Birds	*Phasianus colchicus*	Galliformes	Paleartic	Established
Birds	*Phasianus versicolor*	Galliformes	Paleartic	Not established
Birds	*Pterocles exustus*	Galliformes	Paleartic	Extinct
Birds	*Syrmaticus reevesii*	Galliformes	Paleartic	Established
Birds	*Tympanuchus cupido*	Galliformes	Neartic	Extinct
Birds	*Grus antigone*	Gruiformes	Multi-regional	Extinct
Birds	*Rhea americana*	Rheiformes	Neotropics	Not established
Birds	*Rhea pennata*	Rheiformes	Neotropics	Not established
Birds	*Rhynchotus rufescens*	Tinamiformes	Neotropics	Extinct
Mammals	*Procyon lotor*	Carnivores	Neartic	Invasive
Mammals	*Lepus americanus*	Lagomorphs	Neartic	Established
Mammals	*Lepus californicus*	Lagomorphs	Neartic	Extinct
Mammals	*Lepus capensis*	Lagomorphs	Multi-regional	Established
Mammals	*Lepus europaeus*	Lagomorphs	Paleartic	Established
Mammals	*Lepus granatensis*	Lagomorphs	Paleartic	Established
Mammals	*Oryctolagus cuniculus*	Lagomorphs	Paleartic	Established
Mammals	*Sylvilagus floridanus*	Lagomorphs	New World	Established
Mammals	*Sylvilagus transitionalis*	Lagomorphs	Neartic	Established
Mammals	*Ammotragus lervia*	Ungulates	Paleartic	Established
Mammals	*Axis axis*	Ungulates	IndoMalaysia	Established
Mammals	*Axis porcinus*	Ungulates	IndoMalaysia	Extinct
Mammals	*Bison bison*	Ungulates	Neartic	Established
Mammals	*Boselaphus tragocamelus*	Ungulates	IndoMalaysia	Extinct
Mammals	*Capra falconeri*	Ungulates	Paleartic	Established

Mammals	*Capra ibex*	Ungulates	Paleartic	Established
Mammals	*Capreolus capreolus*	Ungulates	Paleartic	Extinct
Mammals	*Capreolus pygargus*	Ungulates	Paleartic	Extinct
Mammals	*Cervus canadensis*	Ungulates	Holarctic	Established
Mammals	*Cervus nippon*	Ungulates	Paleartic	Invasive
Mammals	*Connochaetes taurinus*	Ungulates	Afrotropics	Unknown
Mammals	*Dama dama*	Ungulates	Paleartic	Established
Mammals	*Dama mesopotamica*	Ungulates	Paleartic	Extinct
Mammals	*Hemitragus jemlahicus*	Ungulates	Paleartic	Extinct
Mammals	*Hydropotes inermis*	Ungulates	Paleartic	Established
Mammals	*Moschus moschiferus*	Ungulates	Paleartic	Extinct
Mammals	*Muntiacus muntjak*	Ungulates	IndoMalaysia	Extinct
Mammals	*Muntiacus reevesi*	Ungulates	Paleartic	Established
Mammals	*Odocoileus hemionus*	Ungulates	Neartic	Extinct
Mammals	*Odocoileus virginianus*	Ungulates	New World	Established
Mammals	*Ovis orientalis musimon*	Ungulates	Paleartic	Established
Mammals	*Rangifer tarandus*	Ungulates	Holarctic	Established
Mammals	*Rupicapra rupicapra*	Ungulates	Paleartic	Established
Mammals	*Sus scrofa*	Ungulates	Multi-regional	Established

Capítulo 4.2

Evaluación del conflicto entre la riqueza de especies de vertebrados exóticas y nativas

Carpio, A.J., Barasona, J.A., Guerrero-Casado, J., Oteros, J., Tortosa, F.S., Acevedo, P. (2017). **An assessment of conflict areas between alien and native species richness of terrestrial vertebrates on a macroecological scale in a Mediterranean hotspot.** *Animal Conservation.* DOI: 10.1111/acv.12330

Resumen

Entender cómo se distribuye la diversidad de especies invasoras en un territorio e identificar los factores que explican dicho patrón son algunos de los retos actuales de la biología de las invasiones. El objetivo de este trabajo fue, por tanto, identificar y caracterizar las áreas colonizadas por un elevado número de especies invasoras con el fin de generar conocimiento con el que minimizar el potencial efecto negativo que las invasoras pueden tener en los ecosistemas hospedadores. Para ello se aplicaron modelos espacialmente explícitos para explicar la riqueza de vertebrados invasores en España. La importancia relativa de los diferentes factores fue evaluada con procedimientos de partición de la variación. Los resultados mostraron que los principales factores explicando el patrón de exóticas son las variables relacionadas con la actividad humana, seguido de las abióticas. El otro predictor significativo fue la riqueza de especies nativas, que mostró una relación positiva con la riqueza de exóticas. Este resultado es compatible con la hipótesis conocida como “the rich get richer”, que predice un mayor número de especies invasoras en las zonas de mayor biodiversidad. En este estudio, además, detectamos zonas de conflicto (ACAs), que son aquellas que tienen un valor medio-alto de riqueza de especies nativas e invasoras. Muchas ACAs se solapan con zonas protegidas, lo que agrava el problema ya que estas áreas generalmente albergan especies vulnerables que se pueden ver afectadas por las invasoras. Esto muestra la necesidad de implementar programas de erradicación, control o mitigación de especies invasoras para reducir su impacto en los espacios protegidos. Además, se han identificado otras áreas de conflicto en lugares próximos a las grandes ciudades, en donde la monitorización y la adopción de medidas preventivas son necesarias para evitar la suelta y posterior expansión de especies invasoras.

Abstract

Understanding how the diversity of invasive species is geographically distributed and identifying the major drivers of that pattern is a relevant challenge as regards invasion biology. The aim of this paper is, therefore, to identify and characterise those areas colonised by a high number of alien species as a means to provide directional indications that can be used to minimise the potential negative effects that the alien species may have on host ecosystems. This is done by applying spatially explicit predictive modelling in order to explain the diversity of vertebrate alien species in Spain. The relative importance of the different factors was assessed using variation partitioning. Our results showed that the main factor as regards predicting the distribution of alien species was the anthropogenic variable, and that this was followed by abiotic variables. The other significant predictor of alien species was the number of native species, which had a positive relationship with the number of alien species. This accord with the "the rich get richer" acceptance hypothesis, which predicts a higher number of alien species in areas with high native species diversity. In this study, we detected Actual Conflict Areas (ACAs), which have high-medium values for the number of both native and alien species. Many of the ACAs identified some overlap with protected areas, which further aggravate the problem as these areas are often the home to endangered species which may be adversely affected by the emergence of alien species. This signifies that eradication, control or mitigation programs should be carried out to reduce the undesirable impact of alien species in these areas. However, other areas of conflict also appeared in unprotected areas near to big cities, where monitoring and preventive measures are necessary to avoid the release of new species and their subsequent spread.

Introduction

The maintenance of global biodiversity is seriously threatened by invasive alien species (Clavero and García-Berthou 2005), which are coloniser species that establish populations outside their native distributional range and have the potential to spread and affect native ecosystems (Lockwood et al. 2007). Biological invasions have emerged as a major component of human-induced global change and are one of the five major pressures driving biodiversity loss, and ultimately the extinction of native species (Lövei 1997; Brook et al. 2008; Roy et al. 2012). Alien species may affect the invaded ecosystems to varying degrees (Hobbs et al. 2006), some resulting in substantial economic and health costs to human societies (Pejchar and Mooney 2009), along with causing the progressive substitution and elimination of native species through predation, hybridisation, the introduction of disease, habitat alteration and competition for resources or space (Gurevitch and Padilla 2004; Kumschick et al. 2014; Macpherson et al. 2016). Known examples of these negative impacts are, among others, the zebra mussel (*Dreissena polymorpha*), which have invaded fresh waters in North America (Ricciardi 2003), and amphibian chytrid fungus (*Batrachochytrium dendrobatidis*), which are responsible for the recent worldwide outbreaks of amphibian chytridiomycosis (Fisher et al. 2009).

Understanding how the diversity of alien species is geographically distributed and identifying the major drivers of that pattern is a relevant challenge in invasion biology. From a theoretical perspective, Elton's (1958) ‘biotic resistance’ hypothesis states that species-rich communities resist biotic invasion better than species-poor communities, as the higher number of biotic interactions in species-rich communities exclude or restrict the recruitment and/or persistence of new arrivals, i.e. invasive alien species. However, the studies testing this hypothesis have yielded seemingly contradictory results, and this discordance could be scale-dependent. Experimental studies carried out on a small spatial scale often conform to Elton's (1958) theoretical prediction, showing a low number of aliens species in highly diverse areas (Hector et al. 2001; Kennedy et al. 2002; Van Ruijven et al. 2003). In contrast, large-scale studies consistently show that biodiversity in host areas promotes alien species’ abilities to invade communities by means of either the influence of traits of native species or certain cumulative effects of species richness (Chapin III et al. 2000; Sax 2002; Deutschewitz et al. 2003; Stohlgren et la. 2003; Espinosa-García et al. 2004; Tilman et al. 2014). Ecological factors that promote native diversity may also facilitate species invasions, and this has been proposed as the ‘acceptance hypothesis’ (Stohlgren et al. 1999; 2003; Fridley et al. 2007): a higher number of both native and alien species is predicted in those areas in which more micro niches are available. On a large spatial scale, the acceptance hypothesis therefore forces the existence of conflict areas - identified as territories with a high-medium diversity of native species and a high risk of invasion by a high-medium number of alien species (Thuiller et al. 2005; Vicente et al. 2011). Conflict areas identify the most probable territories in which alien species can potentially affect the biodiversity of native species (e.g. Acevedo et al. 2007).

In this context, a macroecological large-scale perspective whose objective would be to identify the spatial distribution of alien species in relation to that of native species could be valuable as regards understanding the invasion process and its potential effects on host ecosystems (Kerr et al. 2007; Jeschke and Strayer 2008). What is more, this perspective is appropriate for the management of alien species, since it is critically dependent on adequate large-scale information (Cadotte et al. 2006; McGeoth et al. 2010; Gallien et al. 2012). In this respect, despite the fact that alien species are the second most common threat associated with native species extinction (Bellard et al. 2016), large-scale studies with which to explicitly guide decisions relating to the management of alien species risk assessments are not frequent (but see Rodríguez et al. 2007; Guisan et al. 2013; Thalmann et al. 2015). This is, however, not exclusive to invasion biology, since < 1% of the currently published papers that employ a macroecological perspective are specifically targeted towards conservation decisions (Guisan et al. 2013; Acevedo et al. 2016; Macpherson et al. 2016). In this scenario, it is necessary to disentangle the aspects which drive alien species distribution patterns that can be attributed to different factors (namely, native species richness, human activity and abiotic characteristics) in order to establish solid and efficient alien species management plans. The aim of this paper is, therefore, to identify and characterise those areas colonised by a high number of alien species in Spain, as a means to provide directional indications with which to minimise the potential negative effects that the alien species may have on host ecosystems, mainly in the conflict areas between alien and native species.

Material and Methods

Study area

Spain is a large territory in South-Western Europe consisting of 467.667 km^2. This region is mainly characterised by a Mediterranean climate, with oceanic features in the western and northern areas, and subdesertic features in the south-eastern area. Its geographical isolation and the great diversity of habitats and biotopes have allowed the development of its characteristic flora and fauna, which include a large number of endemic taxa, to the point that it is considered to be a biodiversity hotspot within the Mediterranean Basin that contains more than 30% of the endemic vertebrates species (Myers et al. 2000; Pascual et al. 2011). All of the above features signify that tackling the problem of invasive vertebrate species is becoming very urgent in Spain, since some of these species have become established and have expanded to a significant extent (Muñoz and Real 2006; Real et al. 2008). The legislation in Spain has been reviewed in Royal Decree 630/2013, which promotes severe actions (control, eradication, etc.) in an attempt to control the spread of the catalogued alien species. One of these pieces of legislation is judgment 637/2016, which annuls the exceptions that some years ago allowed the hunting or fishing of some of these alien species, and the marketing or breeding of others. Information on how the ACAs (actual areas of conflict) are distributed and on the main drivers of their distribution patterns is therefore needed in order to prioritise areas and/or species to be controlled and to advance towards a global management plan for biological invasions (see Genovesi et al. 2015).

Alien and native species

The Spanish alien fauna includes 59 vertebrate species (5 amphibians, 15 reptiles, 6 mammals and 33 birds; Appendix 1), 23 of which have an extremely localised distribution, since they do not have ranges greater than 0.03% of the total UTM squares (Appendix 1). The region supports 746 native terrestrial vertebrate species (29 amphibians, 62 reptiles, 111 mammals and 544 birds).

The data regarding vertebrate distribution was obtained from the Spanish Inventory Terrestrial Species website (IEET 2014). The dataset yielded 578,131 records, 2400 of which corresponded to alien species. We compiled the records of fauna distribution on the 10 x 10 km UTM grid squares (5424 in mainland Spain and the Balearic Islands; our territorial unit of analyses). The Observed Alien Species Richness (hereafter, OASR) was obtained as the sum of all the species present in each territorial unit (Figure 1a) (Ribeiro et al. 2009). A map of native species richness (ONSR) was similarly developed, which included all species of terrestrial vertebrates (Figure 1b).

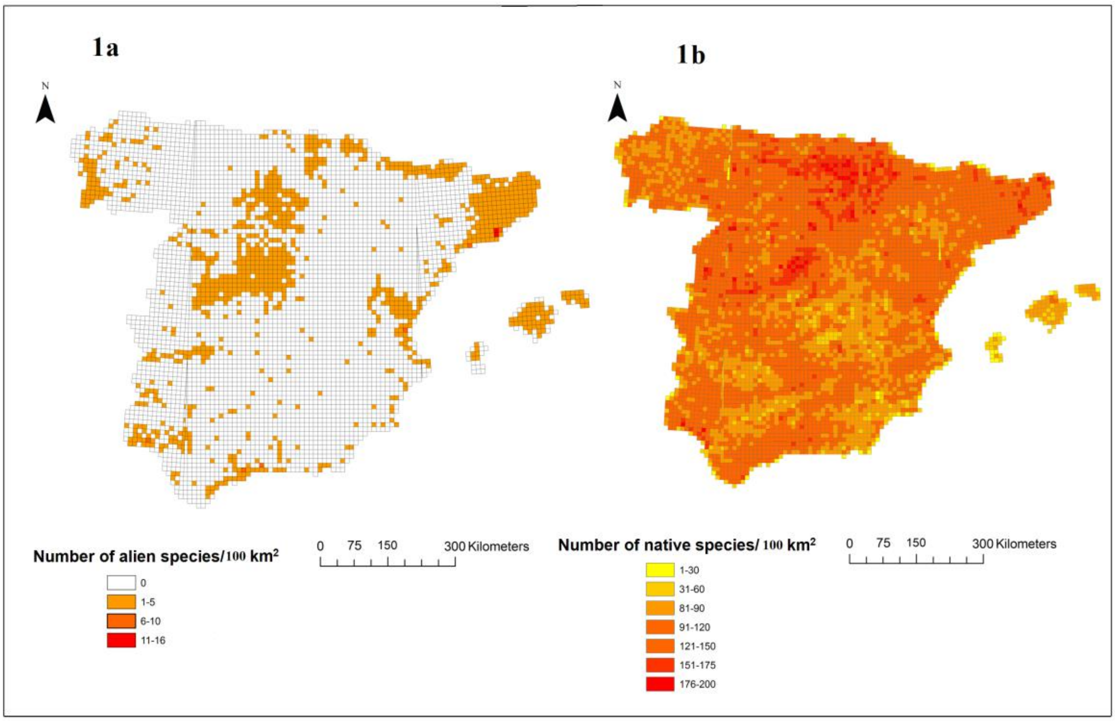

Figure 1. Observed Species Richness maps: a) Vertebrate alien species b) Vertebrate native species.

Richness of alien species

In order to characterize the drivers for alien species richness throughout Spain, a spatially explicit model was calibrated based on climatic, topographic, ecological and land use variables (Rahbek et al. 2007). The ecogeographical variables (EGVs) used for modelling (19 climatic, 8 land use, 3 topographic and 2 ecological variables; see Table 1) were selected on the basis of their significance as regards explaining the distribution of different taxa fauna (Rodríguez et al. 2005; Real et al. 2008; Ribeiro et al. 2009; Sillero et al. 2009). Land use data was compiled from the CORINE database (CLC, 2006) (Table 1), which was provided by the European CORINE Land Cover project (Heymann *et al.*, 1994). The climate and altitude data were compiled from the WorldClim website (Hijmans et al. 2005) (http://www.worldclim.org/). Two procedures were applied to transfer the EGVs to our territorial units (10 x 10 km UTM grid squares): 1) the medium value of every climatic and topographic variable was calculated for each territorial unit; and 2) the percentage of the total area occupied by each type of land use within each territorial unit, thus enabling us to obtain an independent variable for each type of land use.

Prior to the modelling, the dataset was randomly split in order to attain a subset with which to train the models (accounting for 70% of the original dataset), whereas the remainder (30%) was reserved for model validation (Araújo et al. 2005). Multicollinearity among EGVs may result in adverse effects in the modelling process, and the collinear variables in the training dataset were therefore excluded using the variance inflation factor (VIF), with the threshold cut-off value being set at 3 (Zuur et al. 2010). The VIF was analysed using the Heiberger method (Heiberger 2012). The response variable (OASR) was modelled using a generalised linear model, with a negative binomial distribution and a logarithmic link function (Cameron and Trivedi 2013), since the high levels of overdispersion in the data meant that the model could not be fitted with Poisson distributions. The most parsimonious model was obtained using a forward–backward stepwise procedure based on the lowest Akaike Information Criteria (AIC). The model residuals were examined and tested for spatial autocorrelation using Moran's I in order to detect spatial structures (Diniz-Filho et al. 2003).

The predicted richness of alien species (PASR) obtained in the model was quantitatively compared with OASR data in the validation dataset by using Pearsons' correlations. After checking for the predictive performance of the model, it was used to generate PASR values for the whole study area. Statistical analyses were carried out in R 3.0.1 (R Core Team 2013).

Table 1. List of variables and factors used in the model for alien species richness. Land use variables includes Corine land cover code.

Factor	Variable	Resolution
Abiotic	Bio 1*: Annual Mean Temperature[1]	1x1 Km (raster)
	Bio 2: Mean Diurnal Range [1]	
	Bio 3: Isothermality [1]	
	Bio 4*: Temperature Seasonality [1]	
	Bio 5*: Max Temperature during Warmest Month[1]	
	Bio 6*: Min Temperature during Coldest Month[1]	
	Bio 7*: Annual Temperature Range[1]	

	Bio 8: Mean Temperature during Wettest Quarter[1]	
	Bio 9: Mean Temperature during Driest Quarter[1]	
	Bio 10*: Mean Temperature during Warmest Quarter[1]	
	Bio 11*: Mean Temperature during Coldest Quarter[1]	
	Bio 12*: Annual Precipitation[1]	
	Bio 13*: Precipitation during Wettest Month[1]	
	Bio 14*: Precipitation during Driest Month[1]	
	Bio 15: Precipitation Seasonality[1]	
	Bio 16*: Precipitation during Wettest Quarter[1]	
	Bio 17*: Precipitation during Driest Quarter[1]	
	Bio 18*: Precipitation during Warmest Quarter[1]	
	Bio 19*: Precipitation during Coldest Quarter[1]	
	Altitude[1]	20 x20 m (raster)
	Slope[1]	
	Hillshade[1]	
	Wetland (4.1; 4.2)[2]	25 ha, 100m
	Heterogeneous agricultural areas (2.4)[2]	
	Permanent crops (2.2) [2]	
	Forest (3.1) [2]	
	Scrub and/or herbaceous vegetation associations (3.2; 3.3)[2]	
	Arable crop (2.1)[2]	
	Pastures (2.3) [2]	
Antrophogenic	Distance to urban centers with more than 500.000 inhabitants[3]	25 ha, 100m
	Urbanised Land (1.1;1.2;1.3;1.4)[2]	
Biotic	Number of native species per grid (ONSR)[4]	10x10 Km

[1] Wordclim [2] Corine (CLC) [3] Developed by the authors [4] Spanish Inventory Terrestrial Species 2014.

* Collinear variables excluded of the models, using the variance inflation factor (VIF), with the threshold cut-off value being set at 3.

Actual Conflict Areas

We delimited actual conflict areas (ACAs) by using the richness of both groups of species, previously categorised, according to Table 2.

Table 2. Levels of conflict categorised according to ONSR (Observed Native Species Richness) and OASR (Observed Alien Species Richness) values.

ONSR	OASR	Level of conflict
Low	Low	Null
Medium	Low	
High	Low	
Low	Medium	Low
Low	High	
Medium	Medium	Medium
Medium	High	
High	Medium	
High	High	High

Categories for species richness were obtained by means of terciles (33.3 and 66.6%). The use of terciles helps to describe the position of each specific value in relation to the data set and is a means to maximise the representativeness of the data. The territorial units were evaluated according to this criterion, and were assigned to one of the following sequentially exclusive categories: null (low richness of alien species), low (low richness of native species), medium (at least medium richness for one group of species) and high (high levels of species richness for both groups). Medium and high values of ACA are expected to provide information about actual areas of conflict between native species richness and biological invasion. Finally, we compared the value of this ACA for protected areas (Natural and National parks) versus areas without this protection. This was done by comparing the 165 squares of the protected areas (square with more than 50% of the area within a protected area) with 165 squares randomly distributed outside these areas but with similar value of native species richness (categories 1 to 4, according to Table 2). We have explored for differences in the frequency distribution of each of these categories between protected and unprotected squares. For this purpose, a 2 x 2 chi-square table was performed and the distribution of each category was compared.

Results

Predicted potential alien species model

The variables retained in the most parsimonious model for alien species richness are shown in Table 3 (see also Fig. 2); the following abiotic variables were retained: Bio 2, Bio 3, Bio 9, Bio 15, Slope, permanent crop, natural pasture, heterogeneous agriculture areas and scrub, while the anthropogenic variables retained were: distance to urban centre and urban land use. ONSR was used to represent the effect of native species. The Pearson correlation value was $r=0.676$, $p\text{-value}<0.001$ when PASR were related to OASR in the validation dataset. The residuals of the model were not spatially structured according to Moran's I index.

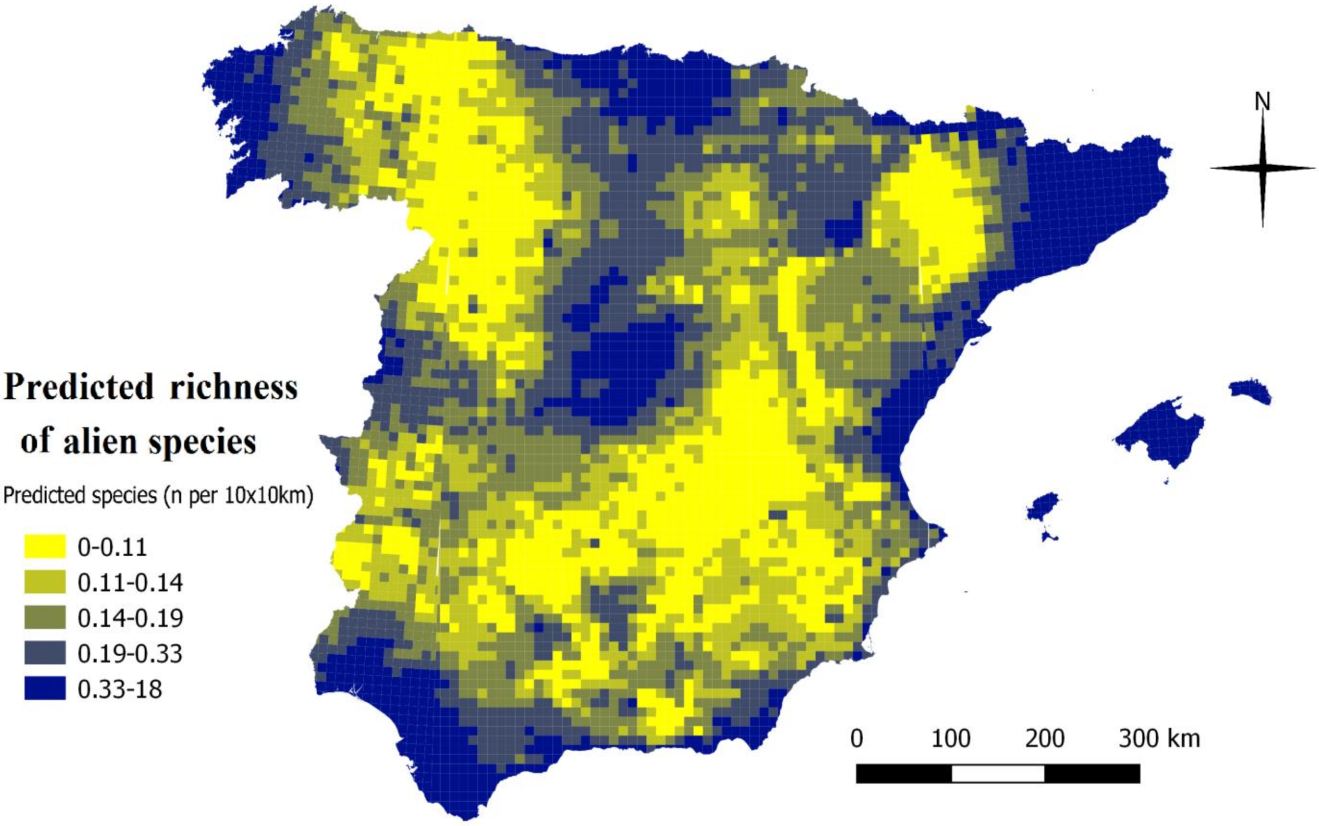

Figure 2. Predicted richness of alien species (PASR).

Table 3. Best-fitting model as regards 70% tracking data. Coefficients (β), Standard error (S.E), p- and z-values of the most parsimonious GzLM (generalised linear model) to explain alien species richness. (AIC = 874).

Variable	β	S.E.	*z*	*p*
Intercept	8.890	1.111	8.002	<0.001
Bio 2	-0.036	2.368e-03	-15.425	<0.001
Urban land use	2.579e-08	1.960e-09	13.160	<0.001
Bio 3	-0.153	0.017	-8.858	<0.001
Bio 9	5.144e-03	7.894e-04	6.516	<0.001
Distance to urban centres	-2.090e-03	6.227e-04	-3.357	<0.001
Permanent crop	-2.301e-09	7.202e-10	-3.196	<0.01
ONSR	4.077e-03	1.155e-03	3.529	<0.001
Natural pasture	-8.001e-09	3.542e-09	-2.259	<0.05
Heterogeneous agricultural areas	-1.959e-09	6.942e-10	-2.821	<0.01
Scrub	-1.702e-10	7.408e-11	-2.297	<0.05
Slope	-0.024	0.010	-2.283	<0.05
Bio 15	5.718e-03	3.181e-03	1.797	>0.05

Bio 2 = Mean Diurnal Range, Bio 3 = Isothermality, Bio 9 = Mean Temperature during Driest Quarter and Bio 15 = Precipitation Seasonality.

The variation partitioning analysis highlighted the relevance of the pure effect of anthropic and abiotic variables, explaining 79.5% and 58.0% of the variation, respectively. However, ONSR explained less than 2% of the variation (Appendix 2). The combination of anthropic and abiotic factors explained a negative proportion of the variation (-38%), which indicates that a factor obscures the effect of the other, because their respective effects oppose each other (Real et al. 2013).

Actual Conflict Areas

Protected landscapes achieve higher values of ACA than unprotected ones (even when considering only areas with similar native species richness than observed in protected areas; Figs. 3 and 4). Chi-square tests showed significantly differences in the frequency distribution of the category 1 (*chi-square* =13.98; p<0.001) and 2 (*chi-square* =11.41; p<0.001) between protected and unprotected areas, achieving equivalent values for the highest classes of conflict (Fig. 4). Interestingly, many areas with high ACA values are located close to big cities.

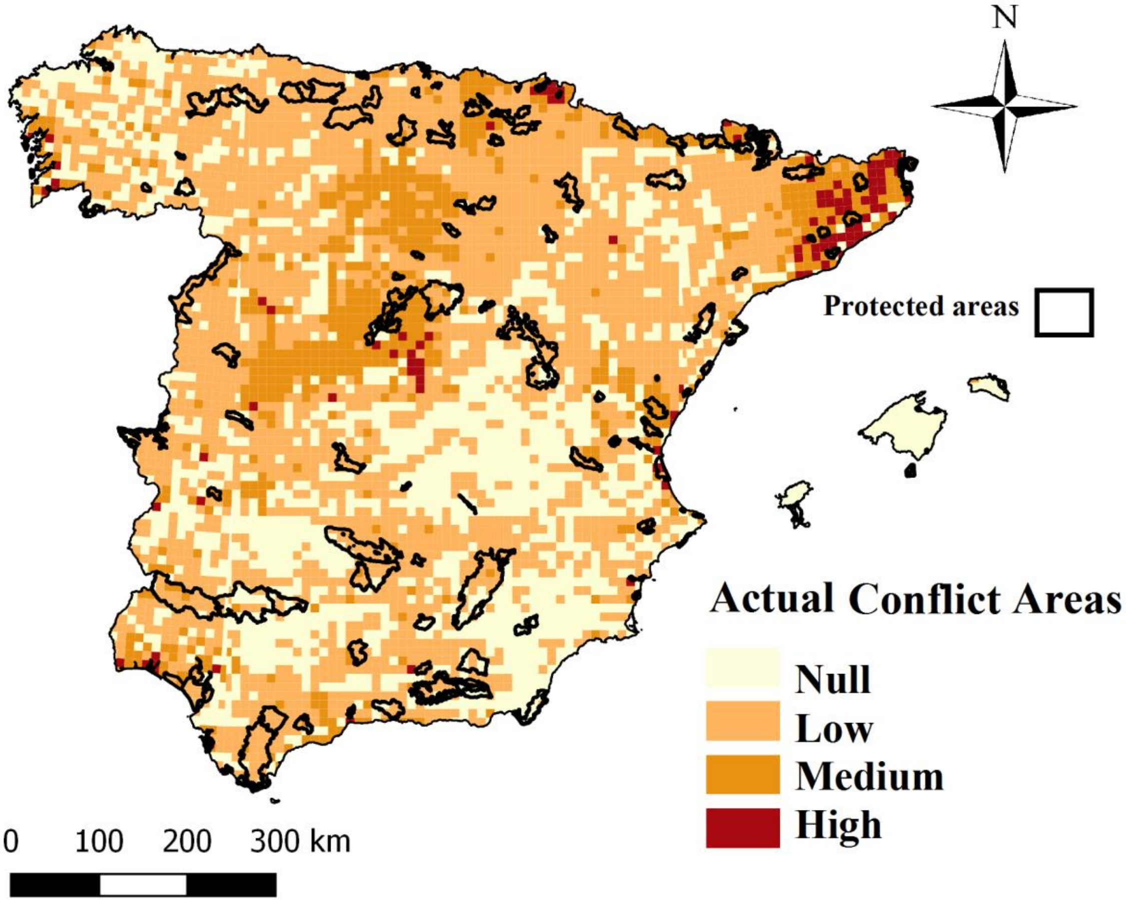

Figure 3. Overlap between Actual Conflict Areas and Protected areas (black).

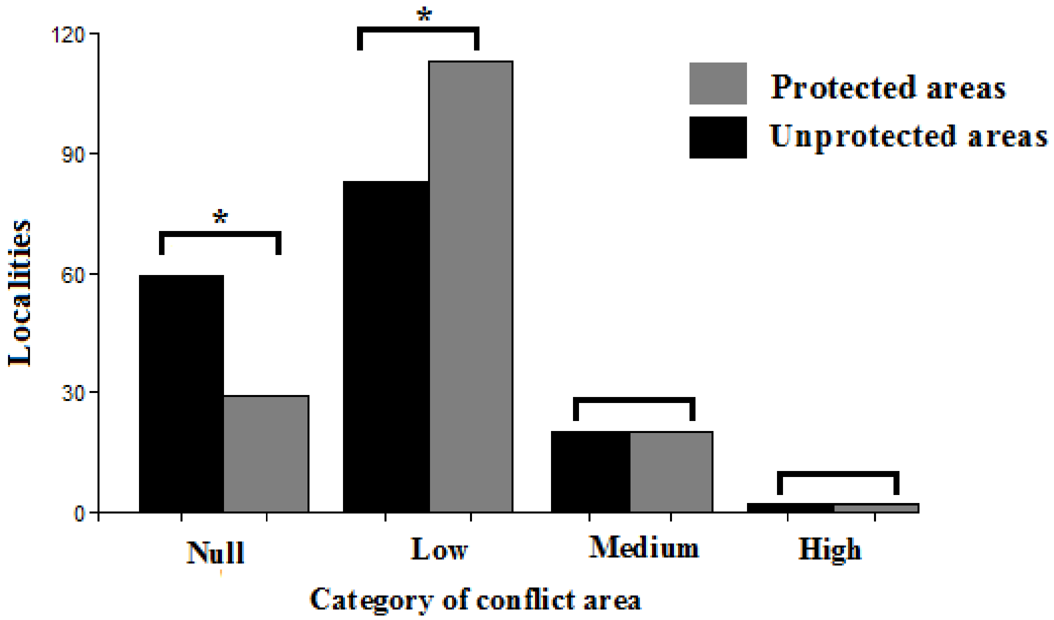

Figure 4. Histograms showing the frequency distribution of each category in protected (grey) and unprotected areas (black). * indicates significant differences for the same level of conflict category.

Discussion

The richness of alien species can be explained by a limited number of variables related to anthropic variables, climate and land use, and to a lesser extent also by the richness of native species. The main factor explaining the observed patterns of richness of alien species was the anthropic factor (79.5% of the total variation; Appendix 2). This factor included urban land use and the distance to cities, which are known predictors of alien species distribution patterns (Luck 2007; Spear et al. 2013). The anthropogenic variables are mainly related to the introduction step in the invasive process, which is more common in urban areas, as has recently been shown for various vertebrate groups (LePrieur et al. 2008; Blackburn et al. 2008; Chiron et al. 2009; Jeschke and Genovesi 2011). These results support the hypothesis that considers that the introduction step is very important in determining the geographic distribution of invasive processes, in contrast to the traditional hypothesis which makes reference only to the second step, establishment, and to some extent the third step, spread (Kolar and Lodge 2001; Jeschke and Strayer 2005, 2006; Jeschke 2008). Areas with dense human population are consequently relevant sources of alien species owing to: i) the release and escape of alien species kept as pets (Spear et al. 2013); ii) the intensity of tourism, which is directly associated with the pathways of introduction (e.g., ornamental trade and tourism, Hulme 2009), and iii) the intensity of anthropogenic disturbance, which can be considered as a proxy of risk of invasion (Hulme 2009; Spear et al. 2013; Dalmazzone and Giaccaria 2014).

Our results indicated that abiotic factors have a strong influence on the distribution of alien species richness; the abiotic factors were, independently of the others, able to explain 58.3% of the variation. The relevance of abiotic predictors as regards explaining distribution patterns of biodiversity on large spatial scales is well known (Peterson and Robins 2003; Thuiller et al. 2005; Loo et al. 2007). Firstly, they directly suppose the physical constraints for biological species persistence (e.g. Guisan and Zimmermann 2000). Secondly, they indirectly include spatial inertia in the models, since these gradients in nature are spatially structured (Peres-Neto and Legendre 2010). Abiotic factors therefore account for both physical requirements and spatial structure and are usually highly explanatory when studying distribution patterns, even when models are calibrated for alien species in invaded territories (Muñoz and Real 2006). What is more, this risk may increase because previous studies have shown that protected areas will probably undergo higher pressure from alien invasive species under future climatic conditions (Walther et al. 2009; Vicente et al. 2011). Indeed, our results showed that the alien species richness of terrestrial vertebrates was influence by several climatic variables such as isothermality, mean diurnal range or precipitation seasonality, which could be affected by climate change and thus favour the spread of alien species.

According to previous studies, the distribution of alien species is positively related to the number of native species (Stohlgren et al. 2003, 2005, 2006; Jeschke and Genovesi 2011). Although the pure effect of native species richness on alien species was low, the mixed model indicated a significant effect of native species richness. This result is consistent with “The rich get richer” pattern (Lonsdale 1999; Fridley et al. 2007; Tilman et al. 2014) which, on a large scale, predicts that those areas with high native diversity have a higher number of microniches (or more spatial heterogeneity), which would therefore allow a greater number of alien species to be accommodated, even when interspecific competition is greater (Davies et al. 2005). According to this hypothesis, it is therefore necessary to protect native biodiversity against alien species, and this requires powerful methods with which to anticipate and monitor these invasions so as to protect native species (Vicente et al. 2011). Our results therefore highlight the informative character of the ACA approach as regards addressing practical issues in conservation and management programmes, particularly those aimed at mitigating the impact of future alien vertebrate species, focusing on the relation with native species in sensitive regions.

Although there is an overlap between native and alien species on the macro-ecological scale, not always alien species pose danger to native species, as the result of the existence of ‘phenotypic divergence’ (Ordonez et al. 2010). ‘Phenotypic divergence’ is based on the concept of limiting similarity and proposes that an introduced species will be more successful in a community that lacks species that are ecologically similar to it (Van Kleunen et al. 2010). Alternatively, others authors have argued that the opposite tendency, known as ‘phenotypic convergence’, may occur (Daehler 2003). This author suggested that when an alien species has similar traits to those of the native community, it is more likely to succeed in the introduced range as it will be better adapted to local conditions. Both mechanisms share the idea that the success of an alien species relies on how its traits match with those of co-occurring native species. Field research with which to experimentally assess the potential impact of alien species on native species on smaller scales would, therefore, be highly informative. In this respect, if harmful effects on native species in the form of competition, disease contagion or predation are detected, specific eradication or control programmes should be carried out to reduce the undesirable impact of alien species on native species.

The acceptance hypothesis implies the emergence of conflict areas. One way in which to assess these emergence pressures is by determining the geographic overlap of biological invasions and native species. In our study, ACAs are those with a high-medium number of native species and a high-medium number of alien species that are potentially harmful to native fauna. In other words, the spatial overlap of important areas for both groups of species delimits conflict hotspots (Farris et al. 2016). Moreover, as Figure 3 shows, some of these conflict areas are protected, as is the case of Natural or National Parks, suggesting that additional conservation concerns could arise as a result of alien species spreading into these priority conservation areas, which are often inhabited by endangered species. In this respect, our results show that protected areas tend to have higher ACAs mean values than unprotected areas, but with similar values of native species richness (Figure 4; Maironaro et al. 2015). This risk may also increase because, as previous studies have shown, protected areas will probably undergo a higher pressure from alien invasive species under future climatic conditions (Walther et al. 2009; Vicente et al. 2011). Preventive measures should, therefore, be focused on these conflict areas, thus making it possible to invest economic resources in those areas with a higher risk of conflict.

Areas near to big cities also require monitoring and preventive measures, since these areas are typically points for the spread or new entry (trade pathways, unintentional release events and population dynamics and local anthropogenic dispersal) of alien species (Chapman et al. 2016). For example, Veran *et al.* (2015) found that anthropogenic factors (urbanisation, agriculture, vineyards, and the presence/absence of highways) explained more variation in the diffusion process of the ladybird (*Harmonia axyridis)* than environmental factors. Identification and prevention are, therefore, the most cost-effective ways in which to minimise the impact of biological invasions, and our maps could therefore assist in the selection of those areas to which wildlife managers should pay most attention. This will provide managers with a powerful approach as regards prioritising management strategies.

In summary, our results showed that, on a macro-ecological scale, the distribution pattern of alien species of terrestrial vertebrates is affected by the combination of biotic and abiotic factors, together with the strong influence of human presence measured. Particularly, more alien species were detected in large areas covered by urban surfaces and close to large urban areas, showing a weak but statistically significant relationship with the native vertebrates' species richness. This entails that conservation efforts should be targeted towards two very different landscapes: urban areas close to big cities and areas with a high diversity of native vertebrate species which sometimes overlap with natural and national parks. In urban and semi-urban ecosystems which have not yet been colonised, preventive measures such as monitoring programmes designed for the early detection of new species, contingency plans, and environmental education campaigns targeted towards different stakeholders (farmers, hunters, pet shops and pet owners…) should be performed in order to avoid the release and spread of new alien species. Furthermore, eradication, control or mitigation programmes should be carried out in those areas with a high diversity of native species and which are prone to being colonised by alien species, in order to reduce the undesirable impact that alien species often have on native fauna.

Acknowledgements

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Appendix 1

Alien species in Spain and percentage of 10x10 km squares with recorded presence. * Species excluded from the analysis, both from the ONSR and the PSR, owing to their sparse distribution in Spain (<0.03%).

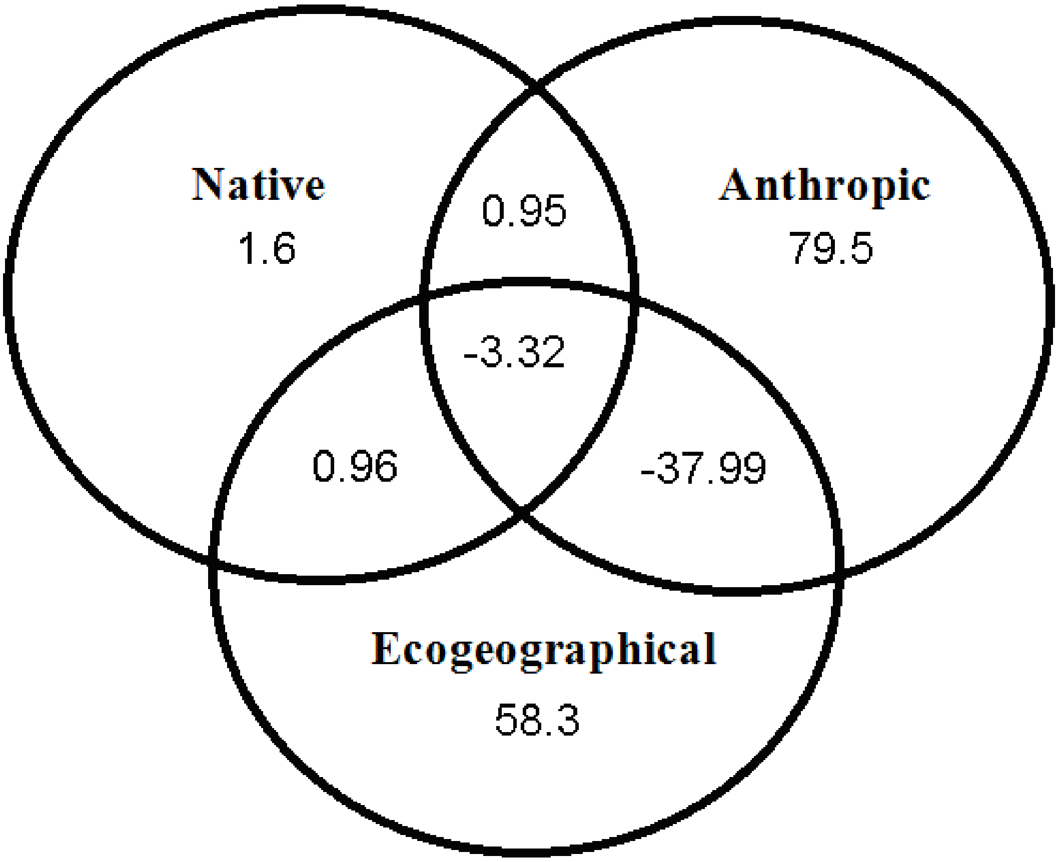
Exotic species name	% Squares	Exotic species name	% Squares
Bufo viridis	0.75	*Ammotragus lervia*	1.97
Discoglossus pictus	0.81	*Myocastor coipus*	0.38
Cynops pyrrhogaster	0.03	*Marmota marmota*	1.21
*Oophaga pumilio**	<0.03	*Neovison vison*	11.4
*Lithobates catesbeianus**	<0.03	*Ondatra zibethicus*	0.13
*Anolis carolinensis**	<0.03	*Ovies aries*	7.13
Chrysemys picta	0.05	*Agapornis fischeri**	<0.03
Crocodilus niloticus	0.03	*Agapornis personatus**	<0.03
*Elaphe guttata**	<0.03	*Alectoris barbara**	<0.03
Graptemys pseudogeographica kohni	0.07	*Alopochen aegyptiaca**	<0.03
Graptemys pseudogeographica pseudo.	0.03	*Amandava amandava*	1.08
Iguana iguana	0.09	*Amazona aestiva**	<0.03
Lacerta perspicillata	0.11	*Aratinga acuticaudata*	0.13
*Laudakia stellio**	<0.03	*Aratinga erythrogenys*	0.03
Macroprotodon mauritanicus	0.75	*Aratinga mitrata*	0.07
Pelodiscus sinensis	0.15	*Callipepla californica*	0.03
*Pelomedusa subrufa**	<0.03	*Coturnix japonica**	<0.03
Podarcis sicula	0.31	*Cyanoliseus patagonus*	0.09
Pseudemys floridana	0.03	*Cygnus atratus*	0.03

Trachemys scripta	3.81	*Dendrocygna autumnalis**	<0.03

Exotic species name	% Squares	Exotic species name	% Squares
Estrilda astrild	2.26	*Nandayus nenday*	0.07
Estrilda melpoda	0.18	*Oxyura jamaicensis**	<0.03
Estrilda troglodytes	0.46	*Phasianus colchicus*	3.96
Euplectes afer	0.15	*Ploceus cucullatus**	<0.03
Euplectes orix	0.07	*Poicephalus senegalus**	<0.03
*Lamprotornis caudatus**	<0.03	*Psittacula krameri*	1.77
*Lamprotornis chalybaeus**	<0.03	*Pycnonotus cafer**	<0.03
Leiothrix lutea	0.03	*Quelea quelea*	0.03
Lonchura malacca	0.03	*Threskiornis aethiopicus**	<0.03
Myiopsitta monachus	3.96		

Appendix 2

Venn diagram of variation partitioning results for three sets of explanatory variables (number of native species, anthropic and abiotic).



CAPÍTULO 5

Discusión general y conclusiones

Discusión general

Este apartado expone los contenidos más relevantes de la presente Tesis Doctoral, poniendo especial atención en resaltar los resultados más destacados, interacciones e implicaciones de diversa índole entre los diferentes elementos de los ecosistemas estudiados (agrícola y agro-forestal; Fig. 7). Esta sección se centra principalmente en los aspectos relativos a la interrelación de los resultados de los diferentes capítulos de la Tesis, ya que las discusiones individuales han sido ampliamente presentadas en cada capítulo (Tabla 2).

La actual crisis de pérdida de biodiversidad es consecuencia de la intensificación de los diferentes sectores primarios como el agrícola, cinegético o forestal. Ante esta situación se están demandado esfuerzos hacia la integración y sostenibilidad de estas actividades con la gestión del medio ambiente y la biodiversidad (Bengtsson et al. 2005; Henle et al. 2008; Di Minin et al. 2016). El área de estudio de esta tesis ejemplariza dos hábitats donde estos usos están presentes (Fig. 8). Parte de esta Tesis Doctoral se ha centrado en el estudio de las cubiertas vegetales como modelo de herramienta de gestión para frenar las actuales tasas de pérdida de biodiversidad en un gradiente de hábitats mediterráneos de la Península Ibérica. Este tema es de especial interés, ya que las cubiertas vegetales están incluidas en la nueva PAC (Pe’er et al. 2014, 2016), y particularmente porque incluye mucha de las actividades en la cuales existe un conflicto con la conservación de la biodiversidad, abarcando una multitud de hábitats y usos del suelo (Schipanski et al. 2014; Gómez et al. 2017).

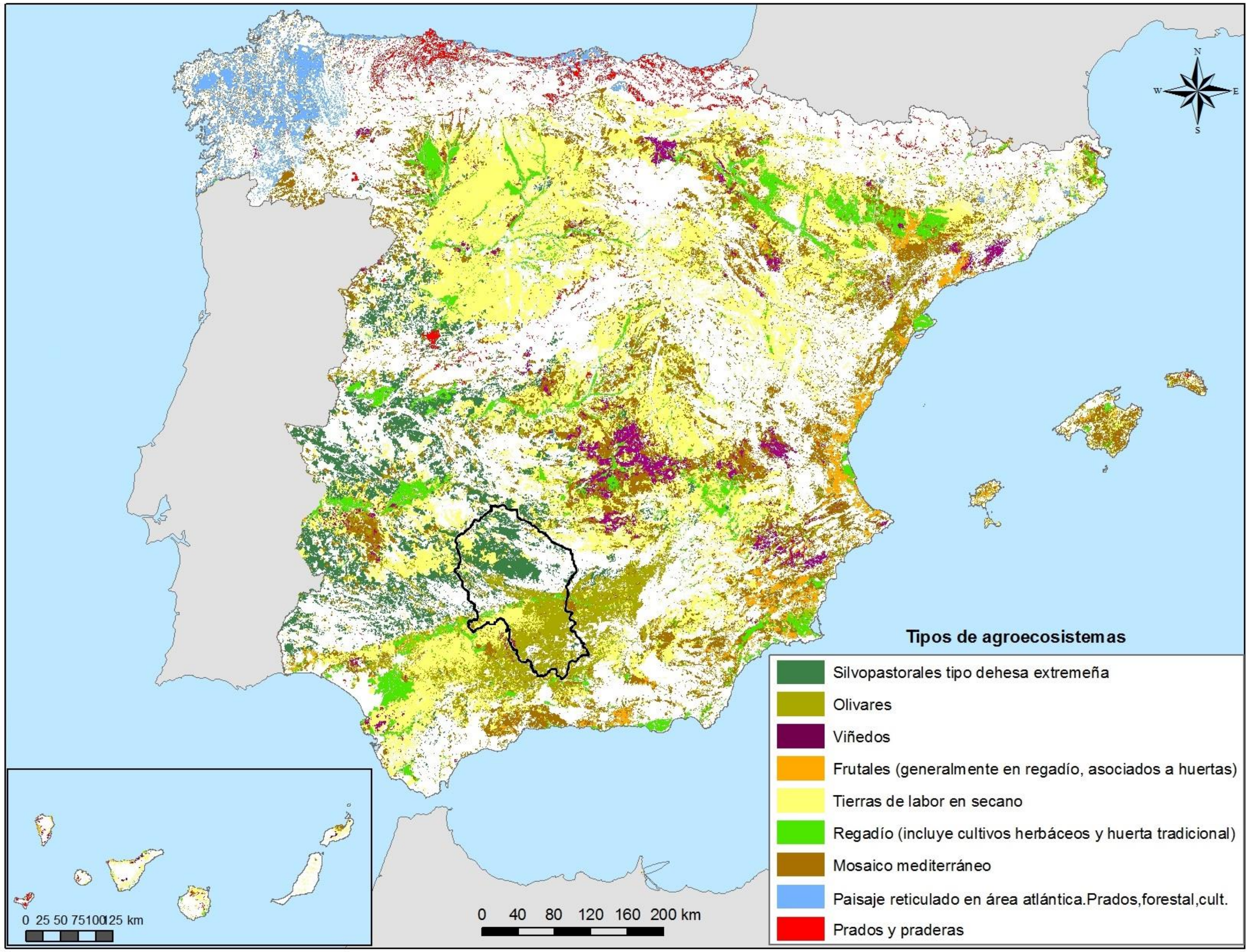

N
W
E
S
Tipos de agroecosistemas
Silvopastorales tipo dehesa extremeña
Olivares
Viñedos
Frutales (generalmente en regadío, asociados a huertas)
Tierras de labor en secano
Regadío (incluye cultivos herbáceos y huerta tradicional)
Mosaico mediterráneo
Paisaje reticulado en área atlántica.Prados,forestal,cult.
Prados y praderas
0 40 80 120 160 200 km
0 25 50 75100125 km

Figura 7. Distribución actual de los principales tipos de agroecosistemas en España. La provincia de Córdoba es delimitado con un trazo negro. Fuente: http://www.ecomilenio.es. En blanco se indican las áreas forestales.

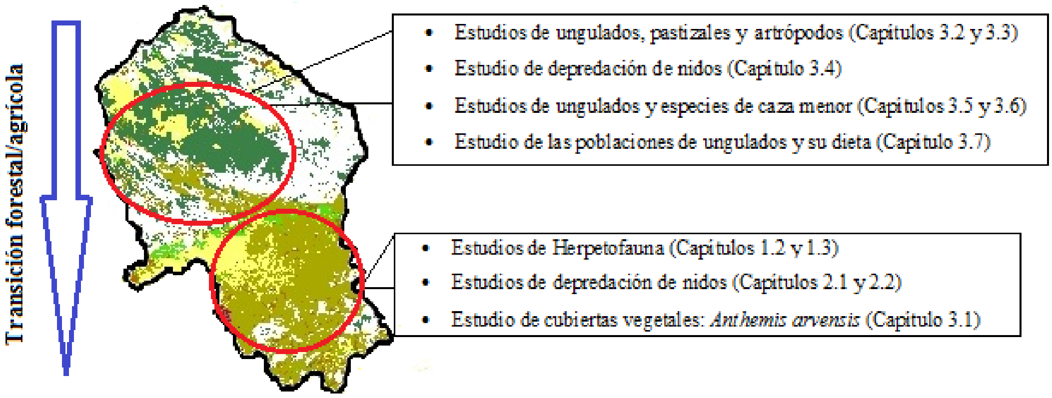
Tabla 2. Interrelación de los principales resultados de los diferentes capítulos de la Tesis e implicaciones de manejo en ambos agro-ecosistemas.

	Agro-ecosistema		
Efecto	**Agrícola/Olivar**	**Forestal/Cinegético**	**Interpelación**
Cubiertas vegetales	La abundancia de conejo puede limitar el establecimiento de cubiertas de especies como *Bromus rubens*, sin embargo especies no palatables como *Anthemis arvesis* son viables	Las densidades actuales de ungulados están alterando la composición de las comunidades herbáceas, favoreciendo a las especies nitrófilas	En ambas situaciones la abundancia de herbívoros limita y altera las comunidades herbáceas, ya sea de cubiertas sembradas o naturales (pastizales)
	Esto implica la utilización de especies no palatables en zonas con elevada abundancia de herbívoros	Esto implica la necesidad de controlar las abundancias de estas especies.	
Invertebrados	Las cubiertas vegetales favorecen la riqueza y diversidad de las comunidades de artrópodos, especialmente cuando se trata de cubiertas naturales (multiespecificas)	Las comunidades de invertebrados se vieron modificadas por las poblaciones de ungulados, especialmente por jabalí (reduciendo su riqueza)	La comunidad de invertebrados depende de la comunidad vegetal, viéndose favorecida por medidas que favorezca su crecimiento (como el control de ungulados o el establecimiento de cubiertas)
	Medidas de manejo como la siega mecánica, que permitan el establecimiento de cubiertas naturales pueden ayudar a frenar la	Las medidas deben ir encaminadas a controlar la densidad de ciervo y jabalí e implementar parcelas de exclusión de ungulados	

	pérdida de la biodiversidad de artrópodos	(islas de biodiversidad)	
Herpetofauna	Los olivares se asociaron negativamente con la riqueza y abundancia de hepertofauna, aunque las cubiertas vegetales ayudaron a disminuir la pérdida de reptiles en olivares El olivar fue el uso del suelo más perjudicial para la herpetofauna, por lo que reducir la intensidad de aplicación de agroquímicos, labranza… resulta esencial para conservar este grupo	No testado en esta tesis: A tratar en el futuro la situación de la herpetofauna en zonas de caza mayor. Atauri and Lucio 2001: Este estudio muestra que la composición de la vegetación y algunos tipos de hábitats adecuados son claves para este grupo, lo cual implica que no se disparen las abundancias de ungulados, y mantener un hábitat mínimamente heterogéneo.	La herpetofauna se ve directamente favorecida por una comunidad vegetal diversa y por una cierta complejidad estructural, de forma independiente al hábitat. A pesar de que ciertos hábitats son más favorables
Nidos aves	La complejidad estructural y la altura de la vegetación redujeron las tasas de depredación, mientras que la abundancia de conejos o la posición del nido (suelo) se asociaron con tasas más altas Permitir una mínima complejidad estructural (cubiertas vegetales) y reducir la abundancia de presas alternativas (conejos) puede ser crítico para reducir las tasas de depredación de nidos en olivares	La altura del pasto ayudo a reducir las tasas de depredación, las cuales fueron debidas principalmente a jabalí (Andalucía, contrastando con Suecia, donde fue el zorro) Es necesario reducir la abundancia de jabalíes, pero también de otros ungulados que limitan la altura del pasto, lo cual facilita la posibilidad de depredarlos	La complejidad estructural dismuye el riesgo de depredación de los nidos en todos los hábitas, independientemente de la naturaleza del depredador, la densidad de nidificación o la posición del nido.
Caza menor	No testado en esta tesis: A tratar en el futuro la situación de la	La abundancia de ungulados se relaciono negativamente con la	Pendiente para el futuro

	caza menor en el olivar Casas y Viñuela 2010 o Barrio et al., 2013: Estos trabajos muestran el papel negativo que tiene la intensificación del olivar sobre especies como conejo o perdiz. Esto es debido a labores como el arado y el control de la maleza con herbicidas de preemergencia, que limitan las fuentes alterativas de alimento	abundancia de perdiz y conejo, debido a limitación de alimento, refugio o depredación (jabalí) Limitar la abundancia de ungulados es clave para conservar especies como conejo y perdiz. Además el uso de parcelas de exclusión de ungulados puede ayudar a proporcionar alimento y refugio.	
Ungulados	No testado en esta tesis	Las densidades actuales de ciervos repercuten negativamente en su propia condición física, por limitar el alimento, además de aumentar la ingesta de taninos, los cuales precipitan las proteínas de la dieta Es necesario mantener las poblaciones por debajo de la capacidad de carga del ecosistema, y mantener una vigilancia continua del estado de las poblaciones	Pendiente para el futuro

Esta tabla muestra la importancia y complementariedad de ambos agro-ecosistemas para la biodiversidad (de distintos grupos taxonómicos) en la provincia de Córdoba (Fig. 8) y de forma general en los ecosistemas Mediterráneos (Fig. 7). Además es de destacar el papel que pueden desempeñar las zonas de transición, donde existe un gradiente de hábitats como los olivares de montaña o cultivos mixtos (viñedos, olivar).



- Estudios de ungulados, pastizales y artrópodos (Capítulos 3.2 y 3.3)
- Estudio de depredación de nidos (Capítulo 3.4)
- Estudios de ungulados y especies de caza menor (Capítulos 3.5 y 3.6)
- Estudio de las poblaciones de ungulados y su dieta (Capítulo 3.7)

- Estudios de Herpetofauna (Capítulos 1.2 y 1.3)
- Estudios de depredación de nidos (Capítulos 2.1 y 2.2)
- Estudio de cubiertas vegetales: *Anthemis arvensis* (Capítulo 3.1)

Figura 8. Áreas de estudio mostrando la transición de los dos agroecosistemas estudiados.

Por tanto, esta tesis trata de evaluar los efectos que los distintos usos del suelo tienen sobre la biodiversidad en dos agroecosistemas (agrícola-olivar/ agro-forestal). Para ellos los bloques de contenidos se desarrollan en uno, otro o ambos agroecosistemas (Tabla 2). El **Capítulo 1** contextualiza la situación actual de la herpetofauna bajo los diferentes usos del suelo que existen en Andalucía, con especial atención al papel del olivar. Dada la escasa información que existe tanto sobre este grupo taxonómico como su papel como bioindicador (Westgate et al. 2016), y la creciente intensificación del olivar (Amate et al. 2013), se ha abordado esta temática como punto inicial de esta Tesis Doctoral. En consonancia con un estudio previo que ha generalizado el efecto negativo de la agricultura sobre los reptiles (Ribeiro et al. 2009), el **Capítulo 1.1** evidencia como este efecto es dependiente del tipo de cultivo e, incluso, del tipo de manejo llevado a cabo dentro de un mismo cultivo (Ej. Olivar de regadío y de secano). Es decir, no todos los cultivos afectan de la misma forma ni en el mismo sentido a este grupo, pudiendo existir incluso cultivos o manejos agrícolas que pueden favorecer a este grupo como cultivos mixtos de olivar y vides (Carpio et al. 2016a). En relación a esto, el estudio muestra claramente como olivares de secano y regadío se corresponden con una menor riqueza de especies de reptiles y anfibios, respectivamente, de las esperadas. Por tanto, alguno o varios de los efectos derivados de la intensificación del olivar, como puede ser la simplificación del paisaje (abordado en el **Capítulo 3**) están repercutiendo negativamente sobre estos grupos tan amenazados.

Si bien el **Capítulo 1.1** presenta una aproximación completamente teórica en relación al papel del olivar sobre la herpetofauna. En este sentido, el **Capítulo 1.2** se centra en una aproximación más práctica, tratando de establecer el mejor método de cálculo de abundancia de reptiles en el olivar. Este estudio corrobora que los transectos son un método eficaz para calcular la abundancia de reptiles en este cultivo, lo cual coincide con algunos estudios de otras áreas (Rödel y Ernst 2004; Sung et al. 2011). Este trabajo nos ha sido útil como punto de partida para el **Capítulo 1.3**, en el cual ya únicamente se empleó el método validado del transecto. Como se ha mencionado anteriormente, la intensificación agrícola conlleva asociada un detrimento de la herpetofauna, por lo que en el **Capítulo 1.3**, se trató de clarificar el efecto que las cubiertas puedan tener sobre este grupo, ya que se han determinado como un factor clave para los reptiles (Michel et al. 2014). El estudio muestra como estas cubiertas pueden incrementar la abundancia y riqueza de especies de reptiles; a pesar de que las cubiertas naturales (más diversas) albergan una comunidad más rica que las cubiertas sembradas (monoespecificas). Este hecho está determinado por una mayor heterogeneidad estructural (abordado en el **Capítulo 2**) y riqueza de especie vegetales (Gómez et al. 2017), que repercuten en una mayor abundancia y riqueza de artrópodos (abordado en el **Capítulo 3.3**), proporcionando todo ello refugio y alimento a los reptiles.

Atendiendo a la simplificación del paisaje, el análisis de diversos factores ha revelado la complejidad de algunas de las interacciones que ocurren en estos agro-ecosistemas y que afectan a factores como las tasas de depredación de nidos. Por ello se plantea la evaluación de las tasas de depredación de nidos en hábitats forestales y agrícolas, tanto en la Península Ibérica como en Suecia, lo que nos permite comparar los resultados en ambas regiones. Los resultados han mostrado la existencia de complejas interacciones en un agroecositema de olivar, con la aparición de un fenómeno conocido como *hiperpredación* (Smith y Quin 1996; Courchamp et al. 2000), donde la alta abundancia de una presa (conejo en este caso) afecta negativamente a otra especie (aves) debido a que comparten depredadores comunes. En este estudio los depredadores generalistas (como zorros, perros o gatos asilvestrados) atraídos por una elevada abundancia de conejos, junto con la ausencia de una cubierta vegetal (abordado en el **Capítulo 2.2**), incrementaron la tasa de depredación, especialmente, de los nidos del suelo. Este fenómeno, además, se puede ver influenciado por la introducción de especies exóticas (abordado en el **Capítulo 4**), junto con procesos como la *competencia aparente* o la *depredación aparente* (Bate y Hilker 2012). Por otro lado, aspectos como la densidad de nidificación pueden tener consecuencias sobre las tasas de depredación de nidos, estando a su vez esto también modulado por características del paisaje. Nuestros resultados muestran que las tasas de depredación de nidos estuvieron relacionadas negativamente con la densidad de nidificación (**Capítulo 2.2)**, un resultado que es contrario al supuesto general de que las tasas de depredación de nidos aumentan con la densidad nidificación (Gunnarsson y Elmberg 2008). No obstante, ésto puede depender de la naturaleza del depredador, ya que en el caso de depredadores pequeños, éstos se pueden saciar o pueden ser repelidos cuando las aves crían en colonias (Ackerman et al. 2004; Ringelman et al. 2014), mientras que en el caso de depredadores de mayor tamaño este hecho no ocurre (siendo independientes las tasa de depredación y la densidad de nidos). Dicho efecto también se observa en otros hábitats de Suecia (**Capítulo 2.3)**, donde la tasa de depredación de nidos por zorro, tejón o jabalí fue similar en ambos tipos de nidificación (colonial o aislada). Además, pueden aparecer otras interacciones entre los propios depredadores (competencia o desplazamiento) que repercutan indirectamente en las tasas de depredación de los nidos (Söderström et al. 1998; Chase et al. 2000). Mientras que los resultados de depredación obtenidos en Suecia muestran al zorro como principal depredador, en la zona Meditérranea (**Capítulo 3.4)** los roedores fueron los principales depredadores de nidos en ausencia de carnívoros (dentro de parcelas valladas), con una depredación similar a la que ocurre en el exterior de las parcelas, donde el jabalí fue el principal depredador de nidos.

La mayor complejidad estructural de las cubiertas y del paisaje se asocio con unas menores tasas de depredación en todos los hábitats estudiados. Así, se ha encontrado que la simplificación de las cubiertas (por reducción de su altura) determina una mayor tasa de depredación por zorro en Suecia, por jabalí en los sistemas agrofoestales y por roedores en olivares. Por tanto, el conocimiento de estos patrones de depredación de nidos puede ser de gran importancia si se quiere abordar el riesgo que la intensificación agrícola y la simplificación del paisaje puede representar para la biodiversidad en las zonas agrícolas (Evans 2004; Donald et al. 2006).

Otro objetivo perseguido en esta Tesis fue la búsqueda de las causas externas que afectan al desarrollo o implementación de las cubiertas vegetales (tanto sembradas como naturales), especialmente la herbivoría, en los agroecositemas estudiados

(**Capítulo 3**). En esta línea, se han separado las zonas agrícolas, donde lo que se pretende es establecer cubiertas vegetales que ayuden a mitigar los problemas de erosión y la pérdida de biodiversidad (**Capítulo 3.1**), de las zonas forestales, donde el principal objetivo es conservar o mantener las cubiertas naturales existentes (**Capítulo 3.2**). En el primer caso, un estudio previo de Guerrero-Casado *et al.* (2015), mostró como la elevada presión de herbivoría causada por conejos, podía llegar a impedir el establecimiento de las cubiertas vegetales, lo cual estaba modulado por la diversidad vegetal existente. De acuerdo a nuestros resultados la cubierta de *Anthemis arvensis* resultó una alternativa eficaz, siendo lo suficientemente extensa para alcanzar su función de protección del suelo. Este estudio muestra como *Anthemis arvensis* bajo las condiciones de nuestro estudio se trató de una especie no palatable para el conejo. Esta cubierta, junto a un manejo adecuado, pueden ayudar a conservar la biodiversidad y la humedad del suelo en olivares, ya que cuando el balance hídricos es positivo evita la escorrentía y favorece la infiltración del agua, mientras que cuando el balance hídrico es negativo esta especie ya se ha marchitado, evitando la competencia hídrica con el cultivo (Simões et al. 2014; Gómez et al. 2017).

En ambientes agroforestales encontramos la necesidad de información de un problema reciente y creciente, como es la sobreabundancia de ungulados (Côté et al. 2004; Massei et al. 2015) en un hábitat típico del entorno Mediterráneo como es la dehesa, que aparece combinado o como una transición desde las zonas con predominio agrícola (olivar y secano) hasta el hábitat forestal. En la dehesa, los pastos herbáceos y forestales representan un recurso fundamental (Garrido et al. 2017). Los resultados de este trabajo mostraron que las actuales densidades de ungulados (ciervo y jabalí) están alterando la composición y diversidad de las comunidades herbáceas, por lo que es necesario diseñar medidas de gestión que tengan en cuenta la abundancia de ungulados si queremos conservar unas cubiertas mínimamente diversas, lo que repercutirá en el resto del ecosistema (Capítulo 3.3, 3.5, 3.6).

Ambos estudios coincidieron en mostrar un patrón negativo de la presión de herbivoría sobre las cubiertas vegetales tanto en ambientes agrícolas como forestales, que fue especialmente crítico en zonas agrícolas con escasa diversidad vegetal. En general, este efecto puede estar directamente mediado por la abundancia del herbívoro en cuestión, la productividad de la zona y el manejo histórico de la zona, incluyéndose en este último, por ejemplo, la aplicación de herbicidas (Guerrero-Casado et al. 2015).

En vista de los resultados obtenidos de los efectos sobre las cubiertas vegetales, posteriormente hemos evaluado las consecuencias de la sobreabundancia de los ungulados sobre un ecosistema agroforestal (3.3, 3.4, 3.5, 3.6 y 3.7) (Fig. 9), y el efecto cascada que puede tener la alteración de la cubierta vegetal sobre el resto del ecosistema (Côté et al. 2004). El primer nivel en verse afectado es la comunidad de artrópodos (**Capítulo 3.3**), ya que está directamente influenciada por la comunidad vegetal. De hecho según Schaffers *et al.* (2008), la composición de las especies de plantas es el mejor predictor de la comunidad de artrópodos. Por tanto, como muestra este estudio, la exclusión de ungulados afectó positivamente a la riqueza de invertebrados, encontrándose valores más bajos en zonas con una alta densidad de ungulados, especialmente de jabalí. Estos efectos se pueden producir a través de interacciones indirectas mediadas por plantas, tales como la competencia y cambios en la palabilidad y calidad de las plantas; así como a través de interacciones directas, tales como la depredación accidental (González-Megías et al. 2004). Tanto la alteración de la estructura y composición vegetal como los cambios en la comunidad de artrópodos terminan repercutiendo de forma negativa en otros niveles del ecosistema, por ejemplo sobre el conejo o la perdiz (abordado en el **Capítulo 3.5 y 3.6**). Esta Tesis ha considerado estas especies por su valor socio-económico (especies cinegéticas) y por ser especies claves del ecosistema Mediterráneo (presa de multitud de predadores) (Delibes-Mateos et al. 2007). En ambos casos (perdiz y conejo), dicho efecto negativo puede estar principalmente causado por la disponibilidad de alimento y la ausencia de refugio, derivados de una elevada presión de herbivoría (Fig. 9). En el caso concreto de la perdiz (**Capítulo 3.5**), la disponibilidad de artrópodos para los pollos es un factor crítico para su supervivencia (Borg y Toft 2000), al igual que las semillas para los adultos (Green 1984). En el caso del conejo (**Capítulo 3.6**), la disponibilidad de leguminosas resulta crítica para su reproducción (Villafuerte et al. 1997; Ferreira y Alves 2009), siendo esta herbácea una de las familias más afectadas por la sobreabundacia de ungulados (ver **Capítulo 3.2**). En cuanto a la disponibilidad de refugio, la excesiva presión de herbivoría reduce drásticamente la altura y biomasa del pasto, lo que aumenta el riesgo de depredación de estas especies presa (Díaz-Fernández et al. 2013). Todos estos parámetros se abordan en el **Capítulo 3.5**, poniendo de manifiesto que los actuales sistemas intensivos de gestión de la caza mayor en el centro-sur de España no son compatibles con la conservación de la perdiz roja; y por lo tanto, que estos efectos deben ser considerados a la hora de definir las políticas sobre la gestión de la caza mayor.

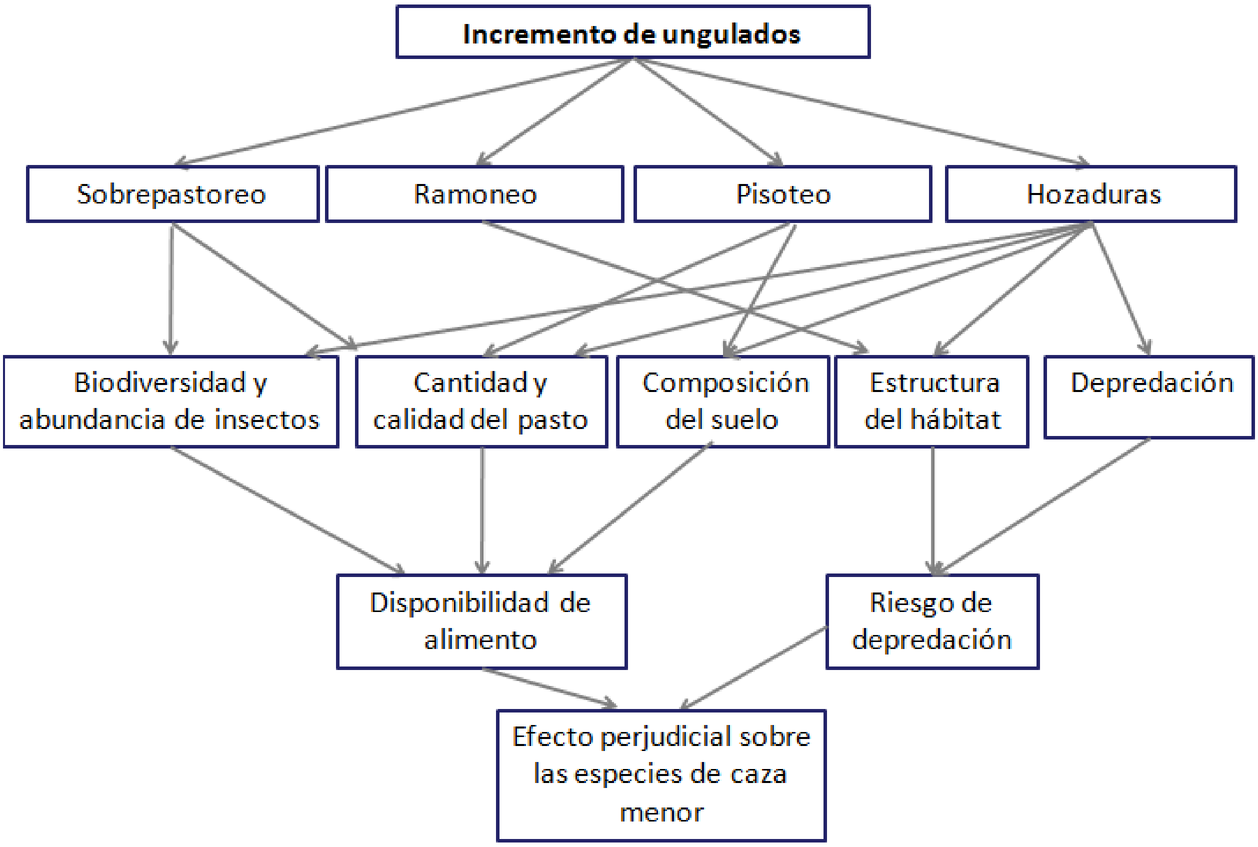


Figura 9. Mapa conceptual de las consecuencias de la sobreabundancia de ungulados.

Además de todos estos efectos sobre los diferentes estratos del ecosistema, en el **Capítulo 3.7** se mostró como otra de las consecuencias de estas elevadas abundancias es su repercusión sobre la propia población de ungulados debido a fenómenos denso-dependientes, que afectan a la condición corporal y a la reproducción (Stewart et al. 2005). Esto es especialmente grave en el centro-sur de la Península Ibérica debido al uso de vallado cinegético y a los manejos intensivos asociados (Torres-Porras et al. 2014). Por otro lado, estos manejos también pueden repercutir en la calidad del trofeo, lo cual representa un importante ingreso económico para estas fincas (Martínez-Jauregui et al. 2016). Este estudio mostró como los animales de áreas con mayor densidad presentaban una peor condición corporal (evaluada a través de la grasa renal), lo cual está correlacionado de forma directa con la calidad del alimento (abordado en el **Capítulo 3.2**). Por tanto, conocer los efectos de estas situaciones de sobreabundancia nos permite proponer actuaciones y prácticas, que permitan mejorar la gestión de la caza mayor, y por tanto obtener poblaciones más sostenibles.

Teniendo en cuenta la información generada en los capítulos anteriores, en el **Capítulo 4** se incorporó un nuevo factor que afecta a la biodiversidad, como es la introducción de especies exóticas, en este caso, con fines cinegéticos. Aunque esta variable no está directamente relacionada con la estructura global de la Tesis Doctoral, los efectos de estas especies pueden ser equiparables a la intensificación agrícola o la sobreabundancia de ungulados en términos de pérdida de biodiversidad (Gurevitch y Padilla 2004), por lo que es crítico tenerlo en cuenta a la hora de desarrollar cualquier actuación de conservación.

Sin menoscavo de la existencia de otras vías de introducción de especies exóticas que existen (Hulme 2009, 2015), el **Capítulo 4.1** se centró en el papel de la caza como razón para la introdución de especies exóticas, lo que resulta un enfoque novedoso. Además de la escasa información que existe sobre este tema (Jeschke y Strayer 2006), el papel de la caza como vía de introducción de especies exóticas se seleccionó en esta Tesis por su importancia económica y por su relación directa con el **Capítulo 3**. Este trabajo de revisión sugería como la caza ha sido una de las principales razones para la introducción de aves y mamíferos exóticos en Europa. Además, estas especies suelen tener mayores tasas de éxito tras su introducción (Jeschke y Strayer 2006) debido a que son manejadas para garantizar su supervivencia y alcanzar altas densidades (alimentación suplementaria, uso de fármacos…), igual que ocurre con las especies de caza nativas (Rodriguez-Hidalgo et al. 2010); por lo que sus efectos son, en muchos casos, similares a éstos (abordado en el **Capítulo 3**).

No obstante, para abordar el efecto que la introducción de especies exóticas tiene sobre la biodiversidad de especies nativa, esta Tesis Doctoral incorporó un último estudio (**Capítulo 4.2**) donde explicar cuáles son las principales variables predictoras de la aparición de especies exóticas. Así, se evidenció como factor primordial las variables antrópicas (véase también Spear et al. 2013), lo que está en concordancia con lo mostrado en el **Capítulo 4.1**. Un segundo factor, que también se consideró importante como predictor de las especies exóticas fue la riqueza de especies nativas, lo cual coincide con la hipótesis de ``los ricos se hacen más ricos´´ (Stohlgren et al. 2003). Los resultados mostraron la existencia de zonas de conflicto, identificadas como zonas con alta abundancia de especies nativas y un alto riesgo de invasión por un elevado número de especies exóticas (Vicente et al. 2011). Las áreas conflictivas son aquellas en las que nos encontramos simultáneamente mayor biodiversidad nativa y que a su vez serian más susceptibles de acoger más especies exóticas, lo que puede afectar a la biodiversidad de especies nativas.

Perspectivas de futuro y limitaciones

Aunque esta tesis evalúa algunos de los efectos que las cubiertas vegetales pueden tener sobre la biodiversidad, desde un punto de vista más general y mirando hacia el futuro, la implantación, tipos, cobertura y otros aspectos relacionados con las cubiertas vegetales van a depender de la PAC. Por tanto, las investigaciones futuras deberían ir evaluando el efecto de esas nuevas directrices de la PAC. No obstante, incluso actualmente, otros aspectos esenciales, tales como el posible efecto de trampa ecológica de las cubiertas o su beneficio sobre otros grupos taxonómicos, deben ser evaluados. Esta trampa ecológica se produce cuando existe un desacoplamiento entre el atractivo y la idoneidad de una hábitat (Robertson & Hutto 2006). Además la viabilidad de estas cubiertas va a depender de la presión de herbivoría a la que se vean sometidas, por lo que sería interesante determinar el papel que la abundancia de herbívoros, sean conejos en zonas agrícolas o ungulados en áreas agroforestales, puede tener a largo plazo sobre las comunidades de herbáceas y por consiguiente sobre el resto del ecosistema. Otro concepto importante en el que debe trabajarse de cara al futuro es la *gestión sostenible* de la caza mayor, no solo desde el punto de vista de sus efectos sobre el ecosistema (tratado en esta tesis), sino también en términos de rendimientos cinegéticos, tasas máximas de extracción sostenible, cargas óptimas…. Por último como se observa en la tabla 2, temas como la situación actual de la herpetofauna en áreas cinegéticas o el efecto de la intensificación del olivar sobre las especies de caza menor son temas que requieren de más investigaciones en un futuro inmediato.

CONCLUSIONES

1. Los olivares intensivos pueden actuar como un "enorme vacío" para la riqueza de especies de reptiles y anfibios; y particularmente para aquellas especies endémicas. Teniendo en cuenta que los olivares cubren 2.5 millones de ha en Andalucía, la tendencia actual en los olivares podría ser considerada como una de las principales amenazas para los anfibios y reptiles en la región mediterránea.
The olive groves may act as a "huge void" for reptilian and amphibian species richness, and particularly for those endemic species. Taking into account that the olive farmland covers 2.5 million ha in Andalusia, the current tendency in olive grove could be considered as the major large-scale threat to amphibians and reptiles in the Mediterranean region.

2. La presencia de cobertura vegetal herbácea (y sobre todo los cultivos de cobertura naturales) es importante en cuanto a la mejora de la diversidad de reptiles. En este escenario, el mantenimiento o aumento de la heterogeneidad del hábitat con un mosaico de parches con cultivos de cobertura naturales, es fundamental para la expansión de grupos de animales de baja movilidad como los reptiles, para los cuales el mejor método de muestro resulto ser el trasencto (debido al uso vertical del espacio).
The presence of herbaceous ground cover (and particularly natural cover crops) is important for enhancing reptile diversity. In this scenario, the maintenance or increasing of habitat heterogeneity with a mosaic of natural crop patches is essential for the expansion of low-mobility animal groups such as reptiles, for which the best method of sampling turned out to be the transect (due to the vertical use of space).

3. Se han encontrado relaciones positivas entre la tasa de depredación de nidos y la abundancia de conejos en las áreas estudiadas. Por lo tanto, los procesos de hiperpredación deben ser considerados al diseñar medidas de conservación para prevenir la depredación excesiva de los nidos de aves.
We found a positive relationship between nest predation rate and rabbit abundance in the studied areas. Therefore, hyperpredation processes should be considered when designing conservation measures to prevent the excessive bird nest predation.

4. La mayor complejidad estructural de las cubiertas vegetales y del paisaje se asoció con unas menores tasas de depredación en todos los hábitats estudiados, ya sea en hábitats de Suecia o en Andalucía. En el primer caso, el principal depredador fue el zorro, mientras que en la región Mediterránea fue principalmente el jabalí, por lo que las medidas de gestión en cada zona deberán ser especificas para estas especies.

The greater structural complexity of the vegetation covers and the landscape is associated with the small rates of predation in all the habitats studied, whether in habitats in Sweden or in Andalusia. In the first case, the main predator was the fox, whereas in the Mediterranean region it was mainly due to the wild boar, so the management measures in each area should be specific for these species.

5. Especies no palatables tales como *A. arvensis* podrían ser una herramienta adecuada para establecer cultivos herbáceos de cobertura en olivares en zonas con altas densidades de conejo, donde otras especies palatables (por ejemplo, *B. rubens*) son fuertemente consumidas.

Unpalatable species such as A. arvensis could be a suitable tool for establishing herbaceous cover crops in olive groves at high rabbit densities, where other palatable species (e.g., B. rubens) are strongly consumed.

6. Las altas densidades de ungulados silvestres reducen tanto la abundancia como la diversidad de las comunidades de plantas y de artrópodos, lo que resulta en un impacto indirecto sobre la conservación de otras especies, como conejo y perdiz o incluso sobre la propia población de ungulados. Este impacto puede ser mediado por la competencia con el alimento, la alteración del hábitat, la ausencia de refugio, el aumento del riesgo de depredación, como el jabalí sobre los nidos de perdiz. Por tanto las consecuencias para la biodiversidad deben tenerse en cuanta a la hora de regular las poblaciones de ungulados.

Wild ungulate at high densities reduce both abundance and diversity of plant communities and arthropods, resulting in an indirect impact on the conservation of other species such as rabbit and partridge or even on the own population of ungulates. This impact may be mediated by both to lack of food and to the absence of shelter, and increased risk of predation, such as wild boar on partridge nests. Therefore the consequences for biodiversity must be taken into account when regulating the populations of ungulates.

7. La caza puede ser considerada como una de las principales vías de introducción de especies de mamíferos y aves exóticas en Europa en el último siglo. La aparición de especies exóticas ha generado zonas de conflicto entre especies nativas y exóticas, especialmente en zonas protegidas, lo que puede dar lugar a problemas de conservación de especies.

Hunting can be considered as one of the main routes of introduction of exotic species of mammals and birds in Europe in the last century. The emergence of conflict overlaping zones between native and exotic species, especially in protected areas, may lead to species conservation problems.

8. Los resultados globales nos permiten concluir que la intensificación de los diferentes usos del suelo (agrícola, cinegético o forestal), junto con la introducción de especies exóticas, están repercutiendo negativamente sobre la biodiversidad y estructura de las comunidades de los grupos taxonómicos estudiados. El mantenimiento de complejidad estructural a través de elementos como las cubiertas vegetales o moderando las poblaciones de ungulados pueden ayudar a frenar las pérdidas actuales de diversidad.

The global results allow us to conclude that the intensification of the different uses of the soil (agricultural, hunting and forestry), along with the introduction of exotic species are negatively affecting the biodiversity and the structure of the communities of the taxonomic groups studied. Maintaining structural complexity through elements such as vegetation cover or moderating the populations of ungulates can help to slow the current losses of diversity.

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ANEXOS

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SHORT COMMUNICATION

The role of rabbit density and the diversity of weeds in the development of cover crops in olive groves

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Abstract

Cover crops are an effective means to reduce soil erosion and to provide food and shelter for wildlife. However, in areas of intensive farming, which are characterised by the scarcity of weed communities, wild herbivores may focus their grazing on cover crops, which could make their implementation difficult. In this work, we test whether rabbit grazing can prevent the growth of herbaceous cover crops in olive groves in Southern Spain in addition to assessing the role of rabbit abundance and diversity of weeds in the development of cover crops. This question has been addressed by sowing *Bromus rubens* between the rows of five olive groves in Cordoba province (Spain). We then monitored the surface covered by *B. rubens,* along with both diversity of weed communities and rabbit abundance. Two rabbit exclusion areas were also placed in each olive grove in order to assess the impact of rabbits on the development of cover crops. Our results showed that the surface occupied by *B. rubens* was considerably higher in the rabbit exclusion areas (mean 56.8 ± 5.65 %) than in those areas in which they could feed (mean 35.6 ± 4.32 %). The coverage occupied by cover crops was higher in areas with lower rabbit density, although this relationship was modulated by the weed diversity index, since in areas with the same rabbit abundance the coverage was higher in those with a richer weed community. These findings suggest that high rabbit abundances can prevent the development of herbaceous cover crops in olive groves, particularly in areas in which alternative food resources (measured as weed diversity) are scarce.

Additional key words: agriculture; *Bromus rubens*; crop damage; human-wildlife conflict; grazing; *Olea europea*; *Oryctolagus cuniculus*.

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Olive (*Olea europaea* L.) groves cover a vast surface of the Mediterranean basin, and are an important resource in terms of income and employment in some areas like southern Spain (Gómez *et al.*, 2004) in which agricultural intensification has also taken place, as has occurred on much farmland worldwide. This intensification includes an exhaustive weed control to prevent water competition by the use of herbicides and frequent ploughing that keeps the ground weed-free and bare, thus leading to severe soil erosion (Gómez *et al.,* 2003) and an overall decrease in both plant and animal diversity (McLaughlin & Mineau, 1995). Nonetheless, sustainability is one of the key priorities defined in the new Common Agricultural Policy (Pe'er *et al.,* 2014), and if this goal is to be achieved, it is essential to reduce soil erosion and enhance both plant and animal biodiversity on farmland.

In the light of these considerations, cover crops could be an appropriate tool with which to achieve the aforementioned objectives in woody crops. For instance, and taking olive groves as a model, different studies have evidenced that, in comparison with conventional tillage, cover crops increase soil carbon sink (Marquez-Garcia *et al.,* 2013); significantly reduce soil erosion and runoff (Gómez et *al.,* 2004); improve soil water conservation (Simoes *et al.,* 2014); and harbour higher songbird, soil microbial, pollinators and arthropod species richness (Saunders *et al.,* 2013; Castro-Caro *et al.,* 2014; McDaniel *et al.,* 2014). Furthermore, cover crops can provide an alternative food resource in woody croplands in order to satisfy herbivorous requirements and thereby reducing agricultural damage caused by wildlife. For instance, Barrio *et al.* (2012) suggest that cover crops can reduce crop damage by the European rabbit (*Oryctolagus cuniculus*) in Southern Spanish vineyards, since rabbits find an alternative food resource in cover crops. This means that, in areas characterised by high rabbit densities and a poor weed community resulting from intensive control, rabbit grazing could be also targeted towards the herbaceous cover crops, thus making their implementation difficult. Our objective was therefore to assess the development of cover crops in areas with different rabbit abundances and with varying alternative food resources measured as the diversity of weed species in order to understand in which situations the development of cover crops is viable.

Fieldwork was conducted in Córdoba province, Southern Spain, which is characterised by a dry Mediterranean climate (an average annual rainfall of 500 mm and monthly mean temperatures of 8-26 °C). The main crops are olives, grapes (*Vitis vinifera*), wheat (*Triticum* sp.) and sunflowers (*Helianthus annuus*). Rabbit hunting is very popular in the area, and they are also considered to be a pest species owing to the significant crop damage caused and the relative high density that they may attain in some areas (Barrio *et al.*, 2012). We selected five olive grove estates with an area ranging between 2 and 12 ha that were at least 20 km apart from each other. In autumn 2013, *Bromus rubens* (25 kg seeds/ha) was sown between every two consecutive rows in the entire orchard (mean row width 3 m). *B. rubens* has previously been used as a cover crop in Mediterranean regions (Linares *et al.,* 2014), since it is an annual grass which germinates in winter and withers before the dry season (late spring), thus avoiding water competition with olives. In all cases, herbaceous plants growing under trees were killed by herbicides after sowing and before *B. rubens* growth to prevent water competition. Two rabbit exclusion areas (6 × 3 m), fenced 0.5 m below ground and 1 m above ground, were placed in two sown rows on every estate (50 m apart), and located in the middle of the sown area to avoid edge effects.

Rabbit abundance was estimated at the olive grove estate level by counting the number of latrines per kilometre by walking transects of 1 km in length (mean 1.12 ± 0.03 S.E.). This method has been widely used in the literature on rabbits (Virgós *et al.,* 2003; Guerrero-Casado *et al.,* 2013), and it provides a good approximation of rabbit density at least at local scale. The surveys were performed in April, May and June 2014. Since other herbaceous species apart from *B. rubens* grew in the sown rows, the diversity of non-crop herbaceous plants (weed) was assessed by creating two linear sampling transects (100 m in length) in two sown rows, in which 10 points (0.5 m^2) separated by 10-m were sampled in each row. All weed species at these sampling points were identified (see Suppl. Table S1 [pdf online]), and we counted the number of individuals of each species and the coverage occupied by *B. rubens* visually as a proportion of an area, which was calculated by the same three people (J.G.C., A.J.C., and L.M.P), being the final data a mean value of the three fieldworkers. The mean values of the Shannon diversity index (Shannon & Weaver, 1963) for the weed community and the surface covered by *B. rubens* were calculated at the row level per month. Moreover, the coverage of *B. rubens* in the rabbit-proof areas was estimated at two survey points (0.5 m^2).

With regard to statistical analyses, a Wilcoxon paired test was used to check the difference in the average coverage of *B. rubens* between fenced and unfenced areas in the rows in which the fenced area was located (data recorded in May; n=10 pairs). A linear mixed model was then applied using the row as the experimental unit and the coverage occupied by *B. rubens* in each row (excluding the rabbit proof areas) as the response variable. In this model, rabbit abundance, expressed as the number of latrines per kilometre, and the Shannon weed diversity index were included as explanatory continuous variables, whereas 'month' was considered as a three level categorical variable (April, May and June) and plot was included as random factor. The interaction between rabbit abundance and Shannon index was also included in the model in order to evaluate whether the effect of rabbit abundance on cover crops depends on weed diversity. Assumptions of normality and independence were confirmed, and variance structure (varIdent) was added to the model to ensure homogeneity in residual spread. This allowed the residuals to have different spreads across the levels of a categorical variable (in our case, the variance covariate was 'month'). InfoStat software was used in all analysis procedures.

The surface covered by *B. rubens* was considerably higher (Wilcoxon's test, $p<0.001$) within rabbit exclusion plots (mean 56.8% ± 5.65 S.E.) than in those areas in which rabbits could feed (mean 35.6% ± 4.32 S.E.). In each pair, the differences ranged from 2 to 78% (mean 20.5%). The mixed model showed that the surface occupied by cover crops outside the rabbit exclusion plots depended on date, with the lowest values being obtained in June (Table 1). The interaction among rabbit abundance and the Shannon weed diversity index was significant ($p = 0.001$), meaning that the effect of rabbit abundance on cover crops depended on the diversity of the weed community (Table 1). More specifically, in areas with similar values of rabbit abundance, the coverage occupied by cover crops was higher in the presence of higher weed diversity (Fig. 1).

Table 1. Parameter estimates (± S.E.), *t* and *p* values of the variables included in the mixed model explaining coverage of cover crops. DF shows the degree of freedom of the denominator. The parameter estimate for the level of the fixed factor 'Month' was calculated using 'April' as a reference value

Parameter	Estimate	S.E.	DF	*t*–value	*p*–value
(Intercept)	110.13	15.64	20	7.04	<0.0001
May	3.46	2.16	20	1.61	0.1236
June	–28.96	2.53	20	–11.42	<0.0001
Shannon index	–88.91	20.18	20	–4.41	0.0003
Rabbit abundance	–4.32	1.12	20	–3.85	0.001
Shannon index * Rabbit abundance	6.23	1.61	20	3.85	0.001

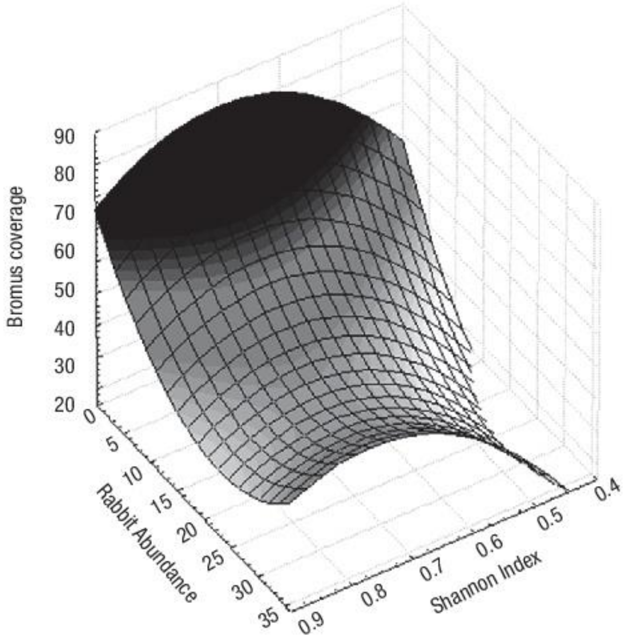

Figure 1. 3D graph showing the relationship between the coverage of cover crops (%), the rabbit abundance (latrines/km) and the Shannon index of weeds. Darker areas represent higher values of *Bromus rubens* coverage.

Agricultural intensification has led to an impoverishment of herbaceous weed communities, which may be problematic in agro-ecosystems in which weeds are important food resources for wildlife (Barrio *et al.*, 2013). The aforementioned authors suggest that the scarcity of alternative food resources can promote rabbit damage to woody crops, since they are almost the only resource available, and are thus more susceptible to rabbit damage. Concerning cover crops, we have found similar results, since, as expected, rabbits caused more damage to cover crops in areas with lower weed diversity. In fact, although the highest damage occurred in high rabbit density areas, in areas with similar rabbit abundance, the development of cover crops was much higher in those with a richer weed community (Fig. 1). The grazing exclusion areas allowed quantifying the use of cover crops by rabbits: as the rabbit is the main herbivorous mammal in the study area, the differences probably result solely from rabbit grazing. Indeed, in some pairs, the differences in the coverage of cover crops between fenced and unfenced areas was as much as 78%, which highlights the agricultural damage that rabbit can cause in the context of food scarcity, when they might be forced to consume crops.

Agro-environmental measures should therefore be applied to maintain weed species on farmland and thus increase food resources and overall orchard biodiversity. Simoes *et al.* (2014) recently proposed that cover crops controlled by mowing before water shortage could be an environmentally friendly management tool, since this practice may favour plant communities and soil water conservation without negatively affecting olive production. Furthermore, the lack of negative effects of cover crops on olive yield would make their implementation optimal in terms of cost-benefits from both an environmental and agronomic point of view as a consequence of its ecosystem services such as soil and water conservation (Duarte *et al.,* 2014; Simoes *et al.,* 2014).

Although cover crops have agro-environmental advantages, in this work we showed that high rabbit abundance can prevent their development. However, rabbit grazing is shown to be modulated by rabbit abundance and weed diversity. This entails that the implementation of cover crops in areas of high rabbit abundance and low weed diversity may be not viable, and it would thus be advisable to select plots with low rabbit density and/or a weed community with high diversity. Our results argue in favour of agricultural practices that are compatible with wildlife conservation, in which the development of a diverse weed community fulfils wildlife requirements, which in turn allow the development of cover crops and their intended benefits.

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Herbaceous ground cover reduces nest predation in olive groves

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Capsule Bare ground increases artificial nest predation in olive groves.

Aims To assess the effect of different soil management regimes on nest predation rates in olive groves.

Methods We performed nest predation experiments with artificial nests during the breeding season in 2013, in two areas of southern Spain. Each artificial nest ($n = 300$) contained three quail *Coturnix* eggs, two of which were unmanipulated and the third one was emptied and injected with plaster. Predators were identified by marks on eggs filled with plaster.

Results Ground nests were significantly more depredated, irrespective of the presence of ground cover; tree nests were less depredated in fields with ground cover. There was a clear difference in nest predators of ground and tree nests. Rodents were the most frequent predators of tree nests.

Conclusion Lower predation rates of tree nests in orchards with ground cover are probably linked to a change in the foraging behaviour of rodents, which in these more complex habitats might be restricted by rodents' own risk of predation. This study underscores the important role of agricultural practices in preserving farmland bird communities, particularly tree-nesting species, suggesting that for this group, implementation of ground cover in olive groves might enhance breeding success by reducing nest predation rates.

In recent decades, many farmland songbirds have experienced population declines in Europe (Donald *et al.* 2006). Degradation of habitats, particulary the simplification and homogenization of agricultural landscapes, has been suggested as the main factor affecting the decline of these bird populations (Benton *et al.* 2003, Tscharntke *et al.* 2005). The alteration of farmland ecosystems has created an environment in which prey populations might be more sensitive to predation, i.e. habitat change may interact with predation rates (Evans 2004). Nest predation is the primary cause of nest losses for a wide range of bird species, in different habitats and geographic locations (Ricklefs 1969, Martin 1993, Schmidt & Whelan 1999), and it has probably contributed to the decline of passerine populations in landscapes heavily modified by agriculture and other human developments (Robinson *et al.* 1995, Bayne & Hobson 1997, Donovan *et al.* 1997, Willson *et al.* 2001). For example, in Spain most farmland birds favour fallow fields for nesting; however, due to the intense use of herbicides, fallow fields are nowadays a rare habitat type and the few favourable patches have high nest densities, attracting predators, and thus exposing nests to very high predation rates (Pescador & Peris 2001). A similar situation occurs with Sky Larks *Alauda arvensis*, which preferentially nest in set-aside fields, but suffer high nest predation rates owing to high nest densities in this habitat type (Donald 1999). Such decoupling of habitat attractiveness from suitability may lead to the development of an 'ecological trap' (Robertson & Hutto 2006).

In the Mediterranean Basin, olive orchards are one of the primary agro-ecosystems and they are important winter quarters and breeding areas for numerous European bird species (Rey 2011). In Europe, the largest area of olive farming is in Spain, where 2.5 million ha are dedicated to this crop. In recent decades, agricultural intensification and changes in land use have replaced the traditional mosaic structure of olive groves interspersed with other crops, with extensive monocultures, resulting in a more homogeneous landscape (Sokos *et al.* 2013). Conventional farming, involving the intensive use of agrochemicals, is the traditional and most common production system (85% of the crop area), which has

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*Correspondence author. Email: jucacaca@hotmail.es lead to significant negative environmental consequences including water pollution and, especially, soil erosion (Gómez *et al.* 2009). However, to prevent erosion, many farmers are now maintaining (or implementing) herbaceous ground cover within crops, which likely increases and provides structural complexity and resources for foraging birds (Wilson *et al.* 1999, Vickery *et al.* 2009). For instance, Castro-Caro *et al.* (2014) have shown that herbaceous ground cover consistently favoured the abundance and richness of songbirds in the olive groves of southern Spain. In addition, breeding birds select their territories in olive orchards according to the availability of food resources such as seeds and arthropods (Muñoz-Cobo 2009). As a result, birds prefer to settle on fields with herbaceous ground cover, and songbird density in these fields can be at least twice as high compared to bare ground in conventional olive groves (Muñoz-Cobo 2009, Castro-Caro *et al.* 2014).

According to theoretical models (see patch use theory; Stephens & Krebs 1986) the foraging effort of predators may be directed towards patches with the highest cumulative prey availability. In Mediterranean farmland, isolated good-quality olive orchards with ground cover embedded in a bare-ground-dominated olive matrix are expected to attract breeding birds, but also their predators. Empirical data have shown that land use intensification in Mediterranean farmland is associated with an increase in the abundance of generalist predators, such as foxes, feral dogs and cats, which exert a significant predatory pressure on some farmland species, particulary ground-nesting birds (Yanes & Suárez 1996, Pita *et al.* 2009). Therefore, olive groves with ground cover may act as an ecological trap for birds, because they may not experience an increase in fitness in terms of reproductive success from settling in these preferred habitats (Robertson & Hutto 2006).

On the other hand, there is a debate as to whether nest predation rate is related to spatial structural complexity. Some studies have shown higher nest predation rates in agricultural landscapes compared to those in contiguous forests (Bayne & Hobson 1997, Hannon & Cotterill 1998), while others have found a higher risk predation in the more structurally complex habitats (Zuria *et al.* 2007). However, these studies focused mostly on field-forest areas, and little work has addressed nest predation in non-forested habitats (but see Ludwig *et al.* 2012). In the present study, we compared nest predation in olive orchards of southern Spain under two different soil management regimes (herbaceous ground cover vs. bare ground) using artificial ground and tree nests. If orchards with herbaceous ground cover are attracting predators, and thus acting as an 'ecological trap' we should predict that (1) predation rates could be higher in olive orchards with ground cover and (2) ground nests will suffer from higher predation pressure than tree nests, because ground nests are exposed to a greater diversity of predators.

METHODS

Study area and study design

The study was conducted in 2013 in three study sites of Southern Spain from mid-April to early June, coinciding with the breeding period of most common nesting species birds in the area (Muñoz-Cobo *et al.* 2001). Two sites were located in Villa del Río (37° 58′ N, 4° 17′ W), and the other in Montilla (37° 34′ N, 4° 37′ W), Córdoba province. All sites were embedded in an olive-dominated landscape, where agricultural intensification has eliminated most of the natural vegetation (Rey 2011). A more detailed description of the study area is provided by Castro-Caro *et al.* (2014). In each study site, we selected two independent plots of 4 ha each, one with ground cover and the other with bare ground. The distance between plots was at least 500 m. The herbaceous ground cover comprised annual species that are adapted to Mediterranean climate and set their seeds before the summer drought. Cover was present throughout the groves except in the area below tree crowns, which was kept plant-free by the application of contact and systemic herbicides. The amount of area covered by ground cover varied among plots (50–75%). Ground cover was not mown during the experiment. All experimental plots were olive orchards that were managed under conventional olive grove farming practices and were selected at random, although an effort was made to choose olive groves of the same age and tree density. All of the olive orchards had trees >100 years old at a density of ~100 trees/ha, and were subjected to the same pruning schemes.

The community of tree-nesters in the studied olive groves was dominated by Cardueline finches, mainly European Serin *Serinus serinus*, European Greenfinch *Carduelis chloris* and Common Linnet *Carduelis cannabina*, while Crested Larks *Galerida cristata* and Woodlarks *Lullula arborea* represent the ground-nesting community (Muñoz-Cobo 2009, Castro-Caro *et al.* 2014; Castro-Caro *et al.* unpubl. data).

The assemblage of potential nest predators includes corvids like Ravens *Corvus corax*. The most common mammalian carnivores are Red Fox *Vulpes vulpes*, feral dogs and cats (Duarte & Vargas 2001). Small mammals have been reported to be one of the main predator guilds of nests (e.g. Rats *Rattus* sp. and Garden Dormouse *Eliomys quercinus*; Gil-Delgado *et al.* 2010): see Supplemental Material.

Nest predation experiment

Artificial nests resembled those of Crested Larks, which build ground nests, and of Serins, which build open-cup nests on the outer parts of olive tree branches. Both bird species breed in olive agro-ecosystems in Spain; their breeding season extends from March to early June, and two or three broods per year are common. Clutch size for Crested Larks ranges between three and seven, and for Serins between two and five eggs; incubation time is around 13 days for both species (Cramp & Perrins 1994).

We exposed 100 artificial nests in every study site, 50 of them in the plot with ground cover and 50 in the plot with bare ground. In each plot, half of the nests were placed on the ground and the other half were placed on trees, following a 30 × 30 m grid in alternating positions (following Ludwig *et al.* 2012). Therefore, the distance between two nests of the same type was 60 m. Ground nests were placed in a small hollow dug on the ground at the border of the tree canopies and were oriented north, while tree nests were fixed to branches at a height of about 2 m and oriented randomly (see Supplemental Material). Altogether, 300 nests were exposed to predators for a two-week period and were checked every three or four days. The first period of exposure took place in the study site of Villa del Río from 18 April to 2 May, the second period was in Montilla from 6 to 20 May and the third period was in Villa del Río again, from 23 May to 6 June. A nest was considered as depredated, if any of the eggs was damaged or lost. Nest predation rate was estimated as the percentage of nests depredated in every plot.

We used artificial nests to overcome the extreme difficulty of finding real nests in the study area (Castro-Caro unpubl. data), thereby obtaining sufficiently large sample sizes to test ecological hypothesis. The use of artificial nests is an indirect method to estimate the impact of predation and has been widely used in bird studies (Zanette 2002, Beja *et al.* 2013). We used commercially available open-cup nests made of hempen braid 8 cm in diameter and 5 cm deep. Nests were exposed to the weather for at least 14 days before use, to dispel any artificial scent (Zuria *et al.* 2007). In each nest we placed three quail *Coturnix coturnix* eggs, two were unmanipulated and the third one was emptied and injected with plaster. In this way the three eggs had the same external appearance (Yanes & Suárez 1997), and plaster eggs could be used to identify teeth marks left by the predator (Major 1991, Willson *et al.* 2001, Carpio *et al.* 2013). Quail eggs have been useful to estimate spatial variation in nest failure risk for ground-nesting passerines (Cortés-Avizanda *et al.* 2009, Vögeli *et al.* 2011). Latex gloves and clean footwear were used during the placing of the nests to prevent scents that might be attractive to predators (Beja *et al.* 2013). Predators were identified by marks on eggs filled with plaster (Yanes & Suárez 1997, Duarte & Vargas 2001). In addition, four automatic cameras (Bushnell Trophy Cam) were placed in each plot to identify predators and were moved to another nest if the nest was depredated. Automatic camera systems have been used extensively to identify potential predator species (Laurance & Grant 1994). Photographic evidence was used to confirm the identification based on marks on the plaster moulds (Herranz, Suárez *et al.* 2002, Herranz, Yanes *et al.* 2002); identification was correct in 100% of cases (see Supplemental Material).

Statistical analysis

Predation level of a plot or nests inside each plot may be influenced by the presence of landscape features that promote landscape heterogeneity, such as hedges, ditches or roads (Chalfoun *et al.* 2002, Whittingham & Evans 2004, Zuria *et al.* 2007). To account for these effects we calculated the distance from each nest to the nearest hedge, ditch and road using ArcGIS 9.3.

Chi-squared tests were used to compare nest predation rate between groups of predators depending on the vegetation cover (ground cover vs. bare ground), and on the type of nest (ground vs. tree). To evaluate the relationships between the level of nest predation and several experimental variables we used a generalized linear mixed model, in which 'site' was considered a random variable and 'plot' was nested within 'site' for the random effect. In this model, nest site (categorical as ground vs. tree), vegetation cover (categorical as ground cover vs. bare ground), and the distance to road and the distance to hedge–ditch were included as explanatory variables. The dependent variable used in the model was whether the nest was depredated or not. We used a binomial distribution, with a logit-link function.

Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson 2002) was used to perform a backward model selection; the model with the lowest AICc was considered the best one (Zuur *et al.* 2009). The statistical software INFOSTAT proposed by Balzarini *et al.* (2001) was used.

RESULTS

A total of 300 nests were exposed during the breeding season, of which 157 nests were depredated (52%). In orchards with ground cover, 65 nests were depredated (41%) vs. 92 nests (59%) in plots with bare ground. Ground nests were significantly more depredated, either in bare ground or with ground cover (Mann–Whitney *U* test, $Z = -0.1$, $P > 0.05$), whereas tree nests were less depredated with ground cover (Mann–Whitney *U* test, $Z = -4.8$, $P < 0.01$; Fig. 1).

The full model was the best model, which included nest site, ground cover, distance to road and distance to hedge–ditch and the interaction between ground cover × nest site (Table 1). Finally, we found that the most frequent predators of tree nests were rodents (65% of nests predated, $\chi^2 = 23.2$, df = 6, $P < 0.001$). However, no single type of predator of ground nests was predominant ($\chi^2 = 1.8$, df = 6, $P = 0.11$) – see Fig. 2. When considering all plots (ground cover and bare ground) rodents turned out to be the main predator group ($\chi^2 = 3.8$, df = 6, $P < 0.001$ and $\chi^2 = 3.8$, df = 6, $P < 0.001$, respectively; Fig. 2).

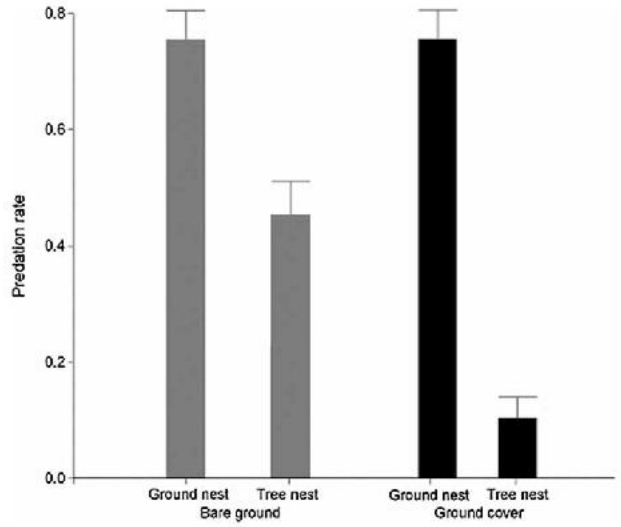

Figure 1. Nest predation rate as a function of the interaction between cover type (ground cover vs. bare ground) and nest site (ground vs. tree) based on the 25 nests in each of the treatments ± sd.

Table 1. The best model to predict nest predation. The intercept for the variable vegetation cover is 'Bare ground' and for the nest site is 'Ground nests'.

Variable	df	Estimate ± se	*F*	*P*
Intercept		1.53 ± 0.41	70.1	<0.001
Ground cover	1	−0.02 ± 0.38	7.1	<0.01
Nest site	1	−1.31 ± 0.36	72.9	<0.001
Distance to road	1	−0.02 ± 0.02	0.4	0.48
Distance to hedge–ditch	1	−0.01 ± 0.01	0.9	0.33
Ground cover × nest site	1	−1.95 ± 0.58	11.8	<0.01

DISCUSSION

Our results show that nest predation was lower in plots with ground cover than in those placed in the bare ground plots. However, these results may be attributed to the lower predation rate on tree nests in fields with herbaceous cover, while similar predation rate was found on ground nests when soil management regimes were compared. Rodents were the most frequent predator on tree nests and we found that predation rate on tree nests was relatively low in orchards with ground cover. It has been shown that ground cover increases the structural complexity in perennial woody systems (Arlettaz *et al.* 2012, Castro-Caro *et al.* 2014), which benefits invertebrates, particularly if the sward is species-rich and structurally complex (Wilson *et al.* 1999, Vickery *et al.* 2009). Potentially, such patches constitute a suitable habitat for small farmland mammals such as rodents. For instance, the total autumn small mammal biomass found in a UK farmland was three times higher on 6-m wide field margins than on arable field without such margins (Shore *et al.* 2005). Rodents select microhabitats where they can optimize their anti-predation and foraging requirements (Mandelik *et al.* 2003, Macdonald *et al.* 2007). In southern Spain, Boulay *et al.* (2009) showed that rodents preferred to forage in covered microhabitats, where they consumed a larger proportion of seeds, probably because they were less visible to potential predators.

Some studies have shown that the observed variations in patterns of nest predation are determined by the distribution, abundance or species composition of nest predators and their specific foraging behaviours in different landscapes and habitats (Martin 1987, Ricklefs 1989, Andrén 1995). For instance, seasonal

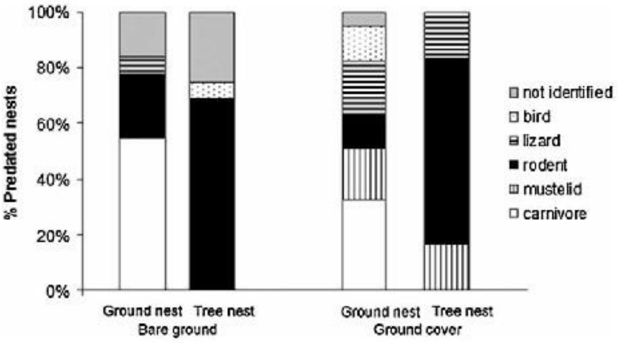

Figure 2. Percentage of nests depredated for each predator group in each cover type (ground cover vs. bare ground), and at each nest site (ground vs. tree).

patterns in habitat use by rodents appeared to be largely a response to seasonal disturbance and the availability of cover in the fields (Todd *et al.* 2000). In fields with ground cover, rodents could extend their foraging areas beyond the olive trees to the ground which provides food resources and shelter from their predators. Therefore, predation pressure on tree nests is likely to be lower in the more structurally complex olive orchards, whereas this pressure might be higher in bare ground orchards where the foraging effort of rodents could be more intensive in the olive trees.

An alternative explanation for the lower nest predation rate on tree nests when ground cover occurs is through what is known as the 'mesopredator release hypothesis' which states that larger predators reduce density of smaller predators with concomitant decreases in predation pressure on their prey (Terborgh *et al.* 1999, 2001). This hypothesis has been used to explain the decline in nest success of many tropical migrants (Soulé *et al.* 1988, Ritchie & Johnson 2009). In our study, ground cover is likely to be more suitable habitat for some predators such as mustelids and reptiles which consume mainly rodents (McDonald *et al.* 2000). In fact, in our study, these predators only depredated nests in orchards with ground cover. As a result, higher predation pressure on rodents in ground cover orchards may decrease their predation rates on nests.

Artificial nests placed on the ground were more depredated than those placed in trees regardless of the type of soil management regime. This result agrees with established patterns of nest predation noted in the literature (Ricklefs 1969, Wilcove 1985, Melampy *et al.* 1999) which postulates that ground nests have higher rates of predation because of the presumed greater diversity of terrestrial predators. Furthermore, in this study, carnivores were the main predators of ground nests (Fig. 2), particulary red foxes *Vulpes vulpes* and feral dogs. Nevertheless, experimental studies carried out with captive foxes have shown that aural cues (e.g. chick alarm calls) are particulary important in stimulating and directing search behaviour (Österholm 1964). For instance, captive foxes and trained hunting dogs were unable to find nests without chicks unless in close proximity (<1 m) to the nest (Österholm 1964, Storaas *et al.* 1999). When chicks are present, mammalian predators can detect them from a much greater distance (Storaas *et al.* 1999), suggesting that in real nests the predation pressure on ground nesters may be even greater because chicks are more susceptible to mammalian predator than their clutches (Storaas *et al.* 1999). On the other hand, if foxes are relatively inefficient predators of nests when only eggs are present, we suggest that in our experimental study, ground nest losses to foxes are expected to be 'incidental' (*sensu* Vickery *et al.* 1992). Incidental predation occurs when secondary prey items are encountered and subsequently consumed, not through directed search for such prey, but through their casual encounter by a predator engaged in search for primary prey (Schmidt *et al.* 2001). In Mediterranean farmland, rabbits are primary prey for most of the carnivores (Delibes-Mateos *et al.* 2008); however, carnivores may depredate ground nests as secondary prey when found during their foraging bouts. Incidential predation because of rabbit abundance has been used to explain, for example, the declining population of larks in an Iberian semiarid shrubsteppe (Yanes and Suárez 1996). Interestingly, Carpio *et al.* (unpub. data) found high density and abundance of rabbits in the olive groves under study here.

The idea that complex habitats have lower predation rates was supported by this study, which may be the result of a greater biodiversity of either predators or microhabitats. Indeed, the variety of predators may promote intraguild competition and mesopredator release, with larger predators controlling smaller ones, which may be an important factor in structuring predator communities (Ritchie & Johnson 2009). Herbaceous ground cover may effectively increase microhabitat diversity and niche availability in the olive orchards, making them more suitable for foraging and shelter for both rodents and their potential predators (Kisel *et al.* 2011). Olive orchards with ground cover are known to be preferred by birds when compared to those having bare ground (Muñoz-Cobo 2009, Castro-Caro *et al.* 2014). Therefore, the lower nest predation rates of tree nests in groves with ground cover provides some evidence that, at least for tree-nesting songbirds, these orchards are not acting as ecological traps. This might increase the intrinsic value of this practice in enhancing biodiversity in olive groves, in addition to their agronomic benefits and soil erosion protection. Nevertheless, more research is needed to disentangle the magnitude of predator–prey interactions, which should be taken into account as a tool to promote biodiversity in farmland systems.

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SUPPLEMENTAL MATERIAL

A supplementary online appendix giving predation rates by predator type, nest position and with/without herbaceous cover (Table S1) and showing examples of artificial nests, photo-trapped predation attempts and the marks left on artificial and real eggs by different predator species (Figs S1–S8) can be accessed at http://dx.doi.org/10.1080/00063657.2014.961894.

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Spring evaluation of three sampling methods to estimate family richness and abundance of arthropods in olive groves

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Abstract

Spring evaluation of three sampling methods to estimate family richness and abundance of arthropods in olive groves.— The intensification and expansion of agriculture is currently one of the greatest threats to biodiversity worldwide. Olive groves are one of the most extensive and diverse agroecosystems in the Mediterranean region. However, the efficiency of the methods used to sample arthropods in olive crops remains unclear. We compared the effectiveness of pan traps, sweep net and bait traps used to sample arthropods in olive groves. The pan traps collected 19 orders and 182 families, with an abundance that was 76% and 86% higher than that of sweep nets and bait traps, respectively. The composition of families differed significantly according to the method used; from a total of 234 families, 23% were sampled only by pan traps, 16% only by sweep net and 5% only by bait traps. The sampling method was the best predictor of arthropod abundance and number of families, followed by the vegetation and landscape diversity indexes. As pan trap, sweep net and bait trap methods do not obtain the same results when sampling arthropods, we recommend a combination of pan traps and a sweep net, depending on the goal of the studies and the arthropod groups targeted.

Key words: Agro–ecosystems, Arthropod surveys, Bait traps, Pan traps, Sweep net

Resumen

Evaluación en primavera de tres métodos de muestreo para estimar la riqueza de familias y la abundancia de los artrópodos en olivares.— En la actualidad, la intensificación y expansión de la agricultura es una de las mayores amenazas para la biodiversidad mundial. El cultivo de olivo es uno de los agroecosistemas más extensivo y diverso de la región mediterránea. Sin embargo, aún no está clara la eficiencia de los métodos empleados para muestrear artrópodos en cultivos de olivo. Hemos comparado la efectividad de las trampas de bandeja, la red de barrido y las trampas de cebo que se emplean para muestrear artrópodos en olivares. Con las trampas de bandeja se capturaron 19 órdenes y 182 familias, cuya abundancia fue un 76% y un 86% superior a la de los artrópodos capturados por las redes de barrido y las trampas de cebo, respectivamente. La composición de familias taxonómicas fue significativamente diferente según el método de captura empleado: de un total de 234 familias, un 23% fue capturado únicamente con las trampas de bandeja; un 16%, únicamente con las redes de barrido; y un 5%, únicamente con las trampas de cebo. Además, el método de muestreo fue el mejor factor para predecir la abundancia y el número de familias de artrópodos, seguido por los índices de vegetación y de diversidad del paisaje. Debido a que las trampas de bandeja, la red de barrido y las trampas de cebo no obtuvieron los mismos resultados en los muestreos de artrópodos, recomendamos el uso combinado de trampas de bandeja y una red de barrido, dependiendo del propósito de la investigación y del grupo de artrópodos objetivo del estudio.

Palabras clave: Agro–ecosistema, Muestreo de artrópodos, Trampas de cebo, Trampas de bandeja, Red de barrido

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Introduction

The intensification of agricultural practices has led to a dramatic decline in the biodiversity of agro–ecosystems (Matson et al., 1997; Tilman et al., 2001; Nentwig, 2003; Pfiffner & Luka, 2003). The survival of the arthropods in these intensive agro–ecosystems depends on the suitability of the habitat, which is in turn influenced by both agricultural management and the surrounding landscape (Jeanneret et al., 2003) in which arthropods are part of important functional groups in food webs (Gonçalves & Pereira, 2012). The diverse agricultural landscapes provide several available niches and micro–niches (canopy–ground: soil, grass, roots) in different types of management regimes, which could be used by arthropods.

Assessing the effects of these different managements and micro–niches on arthropod and plant communities is essential for the management and preservation of biological diversity (Bardgett, 2002). The evaluation, protection and management of biodiversity in agro–ecosystems have been identified as a major challenge of the future in Europe (Jerez–Valle et al., 2014). Methods to sample arthropod assemblages must be efficient, repeatable and representative because they are commonly used in environmental monitoring (Rubene et al., 2015). Monitoring and biodiversity inventories require survey methods that will permit the most efficient and comprehensive completion of study aims (Hutchens & DePerno, 2009; Popic et al., 2013). However, the effectiveness of each method may depend on a range of factors, including the location of the study plots, the type of vegetation (Pedigo & Buntin, 1993), the availability of resources (such as flowering), the sampling season, and the composition of the arthropod community (Baum & Wallen, 2011; Gollan et al., 2011). The most appropriate sampling methods will, moreover, depend on the aims and the target taxa of the study, in addition to resources and time consumption (Popic et al., 2013).

Previous studies have compared different sampling methods in different habitats (see Spafford & Lortie, 2013), such as those in Australia (Popic et al., 2013), New Zealand (Larsen et al., 2014), North America (Shapiro et al., 2014; Joshi et al., 2015), Central and North Europe (Niedobová & Fric, 2014; Rubene et al., 2015) and South America (Nemesio & Morato, 2005). However, few studies have compared their effectiveness in Mediterranean regions (Nielsen et al., 2011; Ponce et al., 2011).

One of the main crops in the Mediterranean basin is the olive tree (*Olea europaea*) (Sokos et al., 2013). The olive culture is deeply rooted in Mediterranean countries, which produce 99% of olive oil throughout the world (Loumo & Giourga 2003). Spain occupies the first place as regards surface and olive production and its production represents 60% of the European olive production and 45% of the world olive production (MAGRAMA, 2016). The large surface area occupied by olive crops in the Iberian Peninsula, particularly in the south, means these agro–ecosystems play a crucial role in biodiversity conservation, but this role varies according to key factors such as the use of pesticides, the presence of natural and semi–natural features (such as scrub, woodland, dry–stone walls, etc) and the age of the trees (Beaufoy, 2000). The flora present in olive crops is similar to that in a natural Mediterranean ecosystem (Margaris, 1980; Giourga et al., 1994), providing suitable conditions for arthropod communities, which are, together with the plant communities, the key factors on which mammal and bird communities depend (Beaufoy, 2000).

Olive groves have currently reached record levels in terms of area and production in the Mediterranean region. Intensive agriculture has simultaneously impoverished the arthropod fauna in the agro–ecosystem of olive orchards (Ruano et al., 2004; Allen et al., 2006; Santos et al., 2007; Castro–Caro et al., 2014; Jerez–Valle et al., 2014). However, little is as yet known about the effect of different olive orchard management regimes (organic production, conventional non–tillage, traditional farming), with different uses of agrochemicals, irrigation, tree density or cover ground, on arthropod diversity (Ruano et al., 2004; Gkisakis et al., 2015, 2016). Little is therefore known about the simultaneous effectiveness and repeatability of the different methods in this habitat.

Our objective was to compare and evaluate the three commonly used arthropod survey methods (pan traps, sweep nets and bait traps) in terms of capture rates, arthropod richness and the family composition of arthropod communities in olive groves, and to determine the influence of landscape and the diversity of herbaceous plants on the efficiency of the three sampling methods.

Material and methods

Study area and sampling design

The study was conducted in Andalusia (37° 30'–37° 58' N, 4° 17'–4° 56' W; between 159–369 m a.s.l.), which is located in the south of the Iberian Peninsula (fig. 1). We selected 123 study sites in a representative geographical range of olive groves in Guadalquivir valley. All the sites were located in an olive–dominated landscape, in which agricultural intensification has eliminated most of the natural vegetation (Rey, 2011).The mean distance between study sites was 15 ± 17 km.

Sampling was conducted in the middle of May 2014. Data from three meteorological stations close to the orchards were used to obtain mean humidity, mean temperature and mean rainfall during the sampling period. The climatic conditions in the study sites were similar during the sampling period: 54.37% ± 0.95% (mean humidity ± SE.), 20.56 ± 0.27ºC (mean temperature ± SE.) and 12.67 ± 4,31 mm (rainfall ± SE). The study sites were managed with similar farming system methods (conventional tillage, mineral fertilization, and planting using a traditional framework), but plant communities differed. To take the plant biodiversity on arthropod captures into account, we calculated two landscape indices and the vegetation Shannon index at each study site (see below).

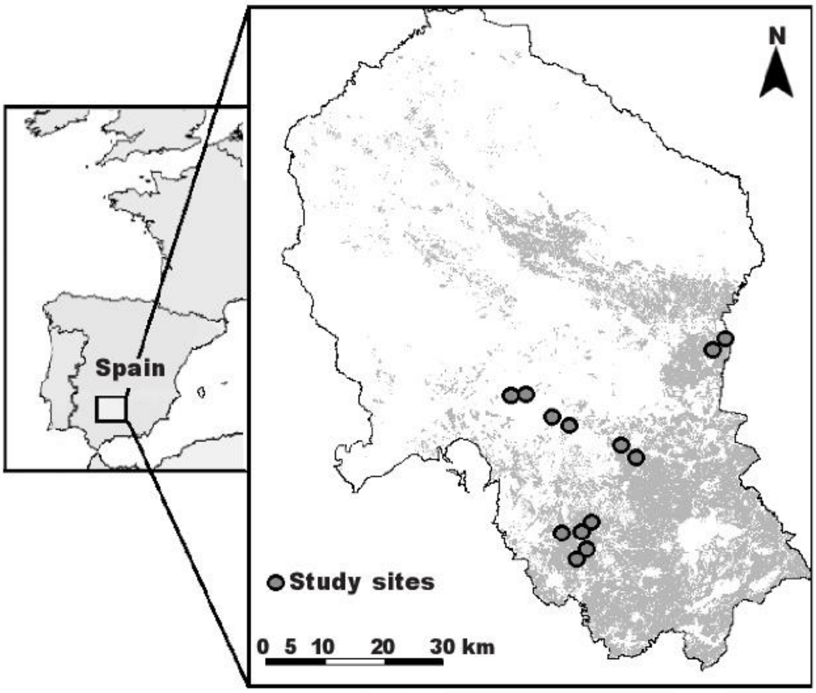

Fig. 1. Study area showing distribution of study sites (circles) and olive groves (shaded areas) in the province of Córdoba.

Fig. 1. Área de estudio en la que se muestra la distribución de los lugares de estudio (círculos) y los cultivos de olivo (zonas sombreadas) en la provincia de Córdoba.

We tested three arthropod survey methods: pan traps, sweep netting and bait traps. These sampling surveys are appropriate to sample canopy and flying arthropods, but not soil arthropods, which were not therefore included in this research. Each survey method was deployed in two transects on each study site for three consecutive days (78 transects per method). The arthropods collected on different days in the same transect were pooled to compare the arthropods captured by pan and bait traps with arthropods captured in sweep netss. To avoid the edge effect (the major vegetal complexity or simultaneous availability of one or more elements, Yahner, 1988) all the transects were surveyed at > 30 m from the nearest edge (fig. 2), and a distance of 100 m was established between the transects to ensure their independence and avoid pseudoreplication.

Arthropod sampling

Pan traps

The traps were placed in two transects (each of which was 90 m in length) with 10 traps (spaced every 10 m) per transect (fig. 2). The traps were set at each study site for three consecutive days; they were placed above the ground and between olive trees to be seen easily by arthropods. The trap–trays were made from polyethylene plastic bowls (400 ml, 110 mm in diameter, 70 mm high) and painted in UV fluorescent yellow (Popic et al., 2013). One hundred ml of soapy water was placed in each pan (to break the superficial tension). There were a total of 260 (10 traps x 2 transects x 13 study sites) pan traps per day (780 pan traps in total, 260 x 3 days). The pans were checked and cleared of captures daily and the arthropods were transferred to plastic bottles with 70% ethanol for transportation to the laboratory. As mentioned above, the arthropods collected on different days in the same transect were pooled to allow comparison of the three methods (n = 26 transect data).

Sweep netting

Flower–visiting arthropods and arthropods that live or feed on vegetation were sampled along two sweep–net transects on each site. One collector (always the same person, A. J. C.) carried out the sampling of both transects for three consecutive days on each site. The sweep net transects were 90 m in length and 5 m in width (fig. 2; Popic et al., 2013) and the collector sampled arthropods from all the plant species along both transects for 1 h (each transect was sampled for 30 minutes). Sweep netting took place in morning sessions (11:00–12:00 h) in order to match the activity patterns of arthropods and to avoid the extreme midday heat (Popic et al., 2013). Sampling only took place during fine weather (days without wind or rain) so as to minimise any potential effects of weather on captures. The arthropods were transferred to 5 ml vials for transportation. As in the case of the pan traps transects, the arthropods captured in the same transect on three different days were pooled for comparison with the pan trap and bait trap transects (n = 26 sweep net transects data). A total of 39 hours were spent on sweep net sampling.

Bait traps

Bait traps were set in the same way as pan traps (two transects on each site with 10 bait traps spaced every 10 meters for three consecutive days; fig. 2). The traps were made from 1.5 L plastic bottles (Allemand & Aberlenc, 1991). The top of the plastics bottles were cut off to increase the entrance opening (98 mm in diameter approximately) and were placed upside down (as funnels) to avoid arthropod escapes. The plastic bottles were filled with natural flowers from the surrounding area and 100 ml of soapy water per bottle. Many substances can be used as bait depending on the target arthropod group, but to compare this method with the pan trap and sweep netting sampling methods (non–specific sampling method), natural flowers from the surrounding area were used as bait (mainly species belonging to asteraceae, brassicaceae and fabaceae families). According to Basset et al. (1997), this method is the most appropriate for the sampling of arthropods in tree canopies. The traps were collected each day and the bait (flowers) was replaced daily. A total of 260 bait traps per day (780 in total) were used. As with pan traps and sweep netting, we pooled the numbers of arthropods captured by bait traps on the different days in the same transect (n = 26 transect data) to allow comparison with arthropods captured by sweep netting.

Plant and landscape diversity

The study sites presented different levels of plant biodiversity. To take this difference into consideration we laid out an additional two transects in two separate rows of olive trees on each site. The transects were 90 m in length, and 10 hoops (0.5 m^2) spaced 10 m apart were used as sampling points for herbaceous plants (fig. 2) (Guerrero–Casado et al., 2015). All the weed species at these sampling points were identified. The mean values of the Shannon diversity index (Shannon & Weaver, 1963) for the weed community were calculated at the site (n = 13). The transects for plant and arthropod surveys were sampled simultaneously on each site. The effect of the surrounding landscape was estimated by recording two environmental variables at the site level (Schweiger et al., 2005): the Shannon index of the landscape (SHDI) and the edge density of the landscape (ED). The SHDI quantified the diversity of the countryside on the basis of richness (the number of different patch types) and evenness (the proportional area distribution among patch types).

The SHDI is calculated according to the formula:

$$\mathrm{SHDI} = \sum_{i=1}^{m} (Pi * \ln Pi)$$

where m is the number of patch types and *Pi* is the proportion of area covered by patch type (land cover class).

The ED is a measurement of the complexity of the shapes of patches and an expression of the spatial heterogeneity of a landscape mosaic. The index is calculated as:

$$\mathrm{ED} = \frac{\sum_{K=1}^{m} e_{ik}}{A} (10{,}000)$$

where e_{ik} is the total length (in m) of edge in a landscape involving patch type (class) *i*, and includes the landscape boundary and background segments involving patch type *i*, whereas A is the total landscape area in m^2.

Both landscape indices were obtained using FRAGSTATS 4.1 software (McGarigal et al., 2002). The landscape diversity index and edge density were recorded in a buffer of approximately 500–m radius around the centre of the sampling site. In each buffer, different land cover classes present were recorded (urban land uses, rivers and natural streams, arable crops, olive groves, vineyard, irrigated crops, citrus and dense scrub). Information concerning land cover classes was obtained from aerial photographs (Ortofotografía digital de Andalucía).

Arthropod identification

The arthropods captured were identified at family level. Classification at species level was unnecessary because the purpose of this study was to assess the effectiveness of each sampling method as regards capturing specific arthropod families. A binocular microscope (Nikon SMZ–U) and several guides were used to identify the arthropods (Barrientos, 1988; Dindal, 1990; Chinery, 2005), but keys were used for Hymenoptera families (Goulet & Huber, 1993).

The PRIMER package, version 6 (Clarke & Gorley, 2006), was used to calculate the number of families (N_F) and Pielou´s evenness index (J´) for each sampling method.

Data analysis

The sampling unit used for statistical analysis was 'transect' because sweep netting has no 'trap' unit to compare with bait and pan traps. Relative abundance and total abundance of arthropod families were calculated for each sampling method. The estimation of diversity can be strongly dependent on differences in inventory completeness (Chao & Jost, 2012). We estimated the inventory completeness for each method using the sample coverage estimator recommended by Chao & Jost (2012) using the iNEXT online software (Chao et al., 2016).

Comparison of family composition obtained using each sampling method

Comparison analyses of the arthropod community were performed using the Bray–Curtis similarity index (Bray & Curtis, 1957) following square root transformation

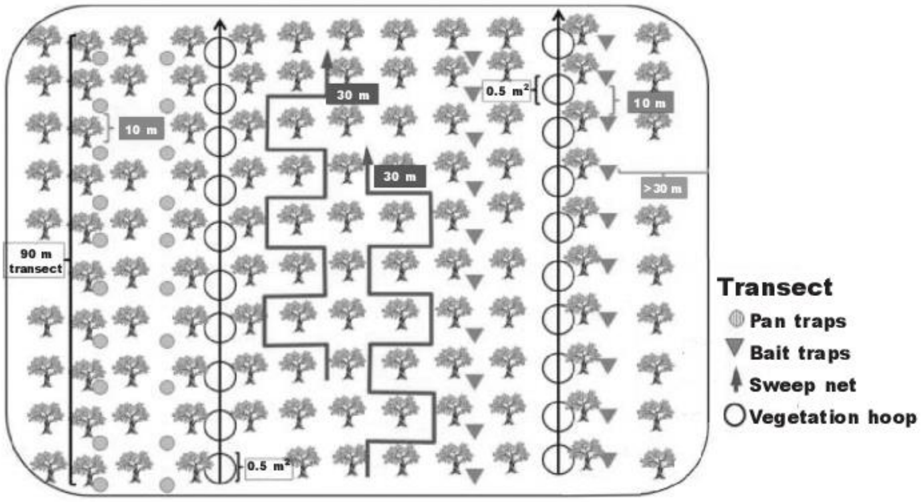

Fig. 2. Sample design and arthropod and vegetation sampling methods used at each sampling site. A total of 13 olive orchards were sampled. The distance between olive trees was less than 10 m. The vegetation hoops indicate the surface used for plant sampling.

Fig. 2. Diseño de muestreo y métodos de muestreo de artrópodos y vegetación empleados en cada lugar del estudio. En total se muestrearon 13 cultivos. La distancia entre los olivos fue inferior a 10 m. Los aros de vegetación indican la superficie empleada para el muestreo de plantas.

of transect data. Dummy values (= 1 specimen) were added to avoid a collapse in subsequent multidimensional scaling (MDS) representation resulting from empty samples. The differences in the sampling methods used in terms of arthropod composition were assessed using MDS. A permutational multivariate ANOVA (PERMANOVA) was then used to check for significant differences between the arthropod assemblages sampled using each method. The MDS and PERMANOVA were performed on the basis of the Bray–Curtis similarity index matrix. PERMANOVA constructs an *F*–ratio from the sums of squared distances within and between groups that are analogous to Fisher´s *F*–ratio (Anderson, 2001). Pair–wise comparisons of the sampling methods were subsequently performed to determine which arthropoda communities differed. The PERMANOVA test was performed with 9999 permutations with the objective of increasing the power and precision of the analysis (Hope, 1968; Anderson et al., 2008). A Similarity Percentage (SIMPER, Clarke, 1993) was used to identify the arthropod families principally responsible for the dissimilarity among the sampling methods. PRIMER package, version 6 (Clarke & Gorley, 2006) was used to perform the MDS plot, PERMANOVA and SIMPER procedure.

Predictive factors of N_F and arthropod abundance

We tested the relationships between each type of sampling method, N_F and abundance using two univariate analysis of varianza (UNIANOVA). In the first UNIANOVA, the number of arthropods is considered as a response variable, while in the second UNIANOVA, N_F was used as the response variable. In both models, the method (three levels: pan trap, sweep netting, and bait trap) was used as a factor, whereas the Shannon index of vegetation, the SHDI and the ED of the landscape were included as explanatory variables (co–variates). For these analyses, we used the sum of squares type III. UNIANOVA were performed using IBM SSPS Statistics 20 software.

Results

Descriptive results

We captured a total of 19,990 arthropods belonging to 25 orders and 234 families. The pan traps captured 14,476 individuals, 22 orders and 179 families. Sweep netting captured 3,571 specimens, 15 orders and 141 families, and the bait traps captured 1,943 specimens, 20 orders and 105 families (table 1). The effectiveness of pan traps was particularly evident in the case of Diptera, Hymenoptera, Homoptera, Collembola and Thysanoptera, for which the number of individuals was greater than 1,000 (table 1). The greatest numbers of Coleoptera, Heteroptera, and Lepidoptera (with 996, 773 and 154 individuals, respectively) were collected using sweep netting (table 1). The lowest abundance values were recorded for bait traps. Some orders were present only in bait traps (*e.g.,* Scutigeromorpha and some Hymenoptera families, see supplementary material) but in low abundance. The order with the largest number of specimens captured by bait trap was Homoptera, with 590 individuals.

The results show that 54 arthropods families (23.07%) were collected exclusively by pan traps, 37 families (15.8%) solely by sweep netting, and 12 families (5.12%) only in bait traps. In other cases, arthropod families were collected by two of the three sampling methods (fig. 3; appendix 1).

The inventory completeness analysis indicated that all three sampling methods had high and similar values of inventory completeness (0.99, 0.98 and 0.97 for pan traps, sweep netting and bait traps, respectively). The similar values of these coverage estimators indicate that the three methods are sufficiently and similarly exhaustive to be compared.

Comparison of abundance, number of families and evenness among sampling methods

The highest arthropod abundance (mean ± SE; 595.5 ± 247.7) was recorded for the pan traps, followed by the sweep net (mean ± SE; 134.9 ± 17.2). The bait trap, meanwhile, was the method with which least arthropods were captured (mean ± SE; 76.6 0 ± 11.8). With regard to the N_F, the highest mean value was also recorded for pan traps (mean ± SE; 30.7 ± 3.9), followed by sweep nets (mean ± SE; 23.1 ± 2.5) and bait traps (mean ± SE; 12.9 ± 1.2). Finally, in the case of the J index, the mean values for the sweep nets and bait traps were similar (mean ± SE; 0.80 ± 0.02 and 0.79 ± 0.02 respectively), while the value of this evenness index (mean ± SE; 0.7 ± 0.02) was lowest for pan traps.

Comparison of family composition between sampling methods

The PERMANOVA indicated that the family composition of arthropods captured using was different for the three sampling methods (Pseudo $F = 6.52$; $p < 0.001$). Sweep netting was significantly different from pan traps (Pseudo $F = 2.67$; $p < 0.001$) and bait traps (Pseudo $F = 3.04$; $p < 0.001$) in the case of arthropod family composition. The PERMANOVA also showed differences in composition of families as regards the pan traps and bait traps (Pseudo $F = 1.84$; $p < 0.001$).

The differences in arthropod family composition obtained using the different sampling methods are shown by means of an MDS ordination plot (fig. 4). The MDS plot supports the PERMANOVA results. The figure shows a differentiation between the fauna collected using the sweep nets with regard to the other two sampling methods (fig. 4), while there was no clear difference between the pan traps and bait traps in the MDS plot, although they can be grouped into subgroups (fig. 4, groups B, C, D, and E). In the case of the sweep net, most transcets (less than one of them) can be grouped into a 16% similarity–level group (fig. 4, group A). There are another two subgroups in this group with a higher similarity level: 40% and 29% (fig. 4, groups A.1 and A.2).

The MDS plot did not show any distinctive grouping for pan traps and bait traps (no more than five transects, fig. 4). The pan trap transects are grouped into two groups, located at different points in the MDS plot. These sets include transects with a similarity of 25% (one net transect is also included) and 33%, respectively (fig. 4, groups B and C). Most bait trap transects, however, are grouped in another two similarity groups (closer to each other than the pan trap groups) with a similarity of 40% and 16%, respectively (fig. 4, groups D and E).

In the SIMPER procedure, in the case of similarity between methods, families that contributed to 70% of cumulative similarity are shown, whereas in the case of dissimilarity between sampling methods, only families which contributed to more than 2% are shown owing to the high number of families needed to achieve 70% of cumulative dissimilarity. The SIMPER procedure showed that the pan trap transects had a similarity of 23.78%, the lowest similarity value. The highest contributions to similarity in the pan trap transects were made by Thripidae, Adelgidae, Formicidae and Aeolotrhipidae, while the sweep netting transects proved to be more similar than the pan traps and bait traps (31.53%). The most important families responsible for similarity in the sweep–netting sample family composition were Nabidae, Apidae, Pyrrhocoridae, Thripidae, Cantharidae and Mesovelidae. The similarity for bait trap transects was 27.23%, and only five families contributed to more than 5% of similarity in the case of this sampling method: Thripidae, Adelgidae, Formicidae, Aeolothripidae and Cantharidae (appendix 2).

The dissimilarity between the three methods was, in contrast, high (no less than 77%). The SIMPER indicated that Thripidae, Apidae, Formicidae, and Nabidae were the most important families as regards the dissimilarity between pan trap and sweep netting sampling (overall dissimilarity = 81.12%). Furthermore, pan traps and bait traps had a lower dissimilarity value (overall dissimilarity = 77.88%), and five families of dipterans (Mycetophilidae, Muscidae, Phoridae, **Sciaridae** and Chyronomidae) contributed to more than 2% of dissimilarity (appendix 3). The highest dissimilarity value was between sweep netting and bait traps (overall dissimilarity = 82.12%), and in this case, 11 families contributed to more than 2% (appendix 3), with the most numerous taxa being Apidae and Nabidae.

Predictive factors of arthropod richness and abundance

With regard to first UNIANOVA analysis (abundance as the response variable, table 2), only the sampling method and the Shannon diversity of vegetation were significantly related to abundance. The Shannon index for vegetation was positively associated with the number of arthropods, whereas the sampling method had a significant effect on the abundance of arthropods, since pan traps and sweep netting captured more arthropods than bait traps.

However, in the second UNIANOVA (N_F as the response variable, table 3), only the sampling method and the SHDI were significantly related to N_F. The SHDI was positively associated with arthropod richness, whereas the sampling method had a significant effect on the N_F value, and pan traps and the sweep captured more families than bait traps.

Table 1. Abundance (N) and number of families (N_F) of arthropods sampled using pan traps, sweep net and bait traps. Percentages are shown in brackets.

Tabla 1. Abundancia (N) y número de familias (N_F) de los artrópodos muestreados usando trampas de bandeja, red de barrido y trampas de cebo. Los porcentajes se indican entre paréntesis.

	Pan traps		Sweep nets		Bait traps		Total	
	N	N_F	N	N_F	N	N_F	N	N_F
Actinedida	0 (0)	0 (0)	0 (0)	0 (0)	1 (< 1)	1 (< 1)	1 (<1)	1 (< 1)
Araneae	125 (< 1)	14 (7.8)	122 (3.4)	18 (12.7)	23 (1.2)	11 (10.4)	270 (1.4)	22 (9.4)
Coleoptera	396 (2.7)	32 (17.8)	996 (27.9)	24 (17)	130 (6.7)	18 (17.1)	1,522 (7.6)	37 (15.8)
Collembola	5,272 (36.4)	5 (2.7)	2 (< 1)	1 (< 1)	97 (5)	3 (2.8)	5,371 (26.9)	5 (2.1)
Dermaptera	5 (< 1)	1 (< 1)	2 (< 1)	1 (< 1)	2 (< 1)	1 (< 1)	9 (< 1)	2 (< 1)
Diptera	2,902 (20)	42 (23.4)	238 (6.7)	31 (21.9)	319 (16.4)	20 (19)	3,459 (17.3)	50 (21.3)
Dyctioptera	1 (< 1)	1 (< 1)	0 (0)	0 (0)	1 (< 1)	1 (< 1)	2 (< 1)	1 (< 1)
Embioptera	5 (< 1)	2 (1.1)	0 (0)	0 (0)	2 (< 1)	2 (1.9)	7 (< 1)	2 (1.2)
Ephemeroptera	0 (0)	0 (0)	1 (< 1)	1 (< 1)	0 (0)	0 (0)	1 (< 1)	1 (< 1)
Heteroptera	58 (< 1)	6 (3.3)	763 (22.1)	15 (10.6)	16 (< 1)	5 (4.7)	847 (4.2)	17 (7.2)
Homoptera	2,571 (17.8)	13 (7.2)	167 (4.7)	7 (4.9)	590 (30.4)	9 (8.5)	3,328 (16.6)	13 (5.5)
Hymenoptera	1,225 (8.5)	35 (19.5)	834 (23.4)	15 (10.6)	311 (16)	19 (18)	2,370 (11.9)	38 (16.2)
Isopoda	3 (< 1)	2 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	3 (< 1)	2 (< 1)
Ixodida	1 (< 1)	1 (< 1)	2 (< 1)	2 (1.4)	1 (< 1)	1 (< 1)	4 (< 1)	2 (< 1)
Lepidoptera	47 (< 1)	11 (6.1)	154 (4.3)	17 (12.7)	8 (< 1)	6 (5.7)	209 (1)	21 (8.9)
Mesostigmata	13 (< 1)	1 (< 1)	0 (0)	0 (0)	1 (< 1)	1 (< 1)	14 (< 1)	1 (< 1)
Neuroptera	1 (< 1)	1 (< 1)	5 (< 1)	2 (1.4)	1 (< 1)	1 (< 1)	7 (< 1)	3 (1.2)
Orthoptera	10 (< 1)	2 (1.1)	21 (< 1)	3 (2.1)	1 (< 1)	1 (< 1)	32 (< 1)	3 (< 1)
Pseudoescorpionida	3 (< 1)	2 (1.1)	0 (0)	0 (0)	1 (< 1)	1 (< 1)	4 (< 1)	2 (< 1)
Psocoptera	4 (< 1)	3 (1.6)	0 (0)	0 (0)	3 (< 1)	1 (< 1)	7 (< 1)	4 (1.7)
Raphidioptera	8 (< 1)	1 (< 1)	6 (< 1)	1 (< 1)	0 (0)	0 (0)	14 (< 1)	1 (< 1)
Sarcoptiformes	5 (< 1)	1 (< 1)	0 (0)	0 (0)	0 (0)	0 (0)	5 (<1)	1 (< 1)
Scutigeromorpha	0 (0)	0 (0)	0 (0)	0 (0)	1 (< 1)	1 (< 1)	1 (< 1)	1 (< 1)
Thysanoptera	1,820 (12.6)	2 (1.1)	248 (6.9)	3 (2.1)	434 (22.6)	3 (2.8)	2,502 (12.5)	3 (1.2)
Zygentoma	1(< 1)	1 (< 1)	0 (0)	0 (0)	0 (0)	0 (0)	1 (< 1)	1 (< 1)
Total	14,476	179	3571	141	1,943	105	19,990	234

Discussion

In this study, climatic conditions (humidity, temperature and rainfall) and management practices (such as tillage or fertilizer) during the sampling period were similar in all study plots. These factors were considered to avoid introducing noise into the models or influencing captures rates.

Our results show that the three methods are strongly biased towards certain taxa, highlighting the importance of combining various sampling methods if the aim of the study is to monitor the biodiversity or complete community of superior arthropod taxa. We found that pan traps were more effective than bait traps and sweep netting as regards detecting arthropods (for abundance and N_F), although this may depend on the taxon.

Other studies have also found that pan traps are highly effective when sampling arthropod species richness (Nielsen et al., 2011; Spafford & Lortie, 2013) and that they are an unbiased method (Westphal et al., 2008). However, although passive sampling methods such as pan traps and bait traps avoid collector bias (present in the sweep net), they are

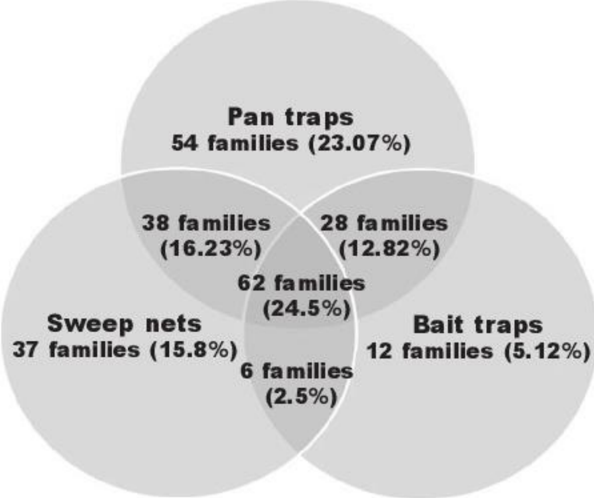

Fig. 3. Venn diagram representing the number and percentage, in brackets, of families captured using the sampling methods.

Fig. 3. Diagrama de Venn que representa el número y el porcentaje, en paréntesis, de las familias capturadas por los métodos de muestreo.

associated with other biases, as they capture species with an unequal probability owing to specific visual or olfactory attractors (Cane et al., 2000; Roulston et al., 2007). Nevertheless, our findings contrast with those of other studies in which sweep netting has been found to capture a greater species richness and abundance of arthropods (Popic et al., 2013), although this observation depended on the taxonomic group. For example, we found that pan traps sampled a greater abundance of Diptera, Hymenoptera, Collembola, Homoptera or Thysanoptera, while sweep netting collected a higher abundance of Coleoptera, Heteroptera or Lepidoptera, and bait traps captured a mixture of both, with a greater abundance of Homoptera and Thysanoptera. The richness of the families captured using each sampling method shows that the group from which the most families were captured was Diptera, followed by Hymenoptera (in pan traps and bait traps) and Coleoptera (in sweep nets). The poor abundance of flowers and vegetation in olive groves may contribute to the superiority of pan traps when compared to the other two methods (Roulston et al., 2007).

Although pan traps captured the highest number of families –followed by sweep netting and bait traps– the combination of pan traps and the sweep netting proved to be more effective, capturing 95% of total families. This further emphasizes the importance of including more than one method when conducting arthropod species richness inventories. The various methods have advantages and disadvantages. Pan traps and bait traps (static methods) may not reveal the spatial variation in arthropod assemblages between sites and communities (Nielsen et al., 2011). Furthermore, in the case of pan traps, different colours may significantly affect the capture rate for different arthropod taxa (Yi et al., 2012). For example, yellow pans are used in studies of diverse groups of pollinators (Kitching et al., 2001; Popic et al., 2013), while blue pan traps are more effective as regards catching Stephanidae (Aguiar & Sharkov, 1997) and red pans are attractive to Amphicoma beetles (Dafni et al., 1990). This should be taken into consideration during general surveys. It should also be kept in mind that a large number of families were not collected by bait traps. These traps are effective sampling methods for live catches of arthropods. However, the selection of the food source is vitally important, and a basic knowledge of the feeding habits is therefore a prerequisite when using this method (Yi et al., 2012). Sweep netting offers several advantages.It is not only a highly cost–effective and fairly non–intrusive method (Yi et al., 2012), but is also particularly useful when comparing relative species abundance and richness of arthropods in different areas with similar vegetation types (Siemann et al., 1997), as is the case of olive groves. However, the capture rate of sweep netting, depends to a great extent on the collector's skills and the method is relatively time–consuming. Furthermore, it is mainly suitable for open habitat types such as grassland or agriculture land and not easy to standardise in forest environments with a high vegetation density (Yi et al., 2012).

The different assemblages captured by the survey methods suggest the need for complementary sampling methods if the objective is to describe the invertebrate community (Spafford & Lortie, 2013). Our findings suggest a combination of sweep netting

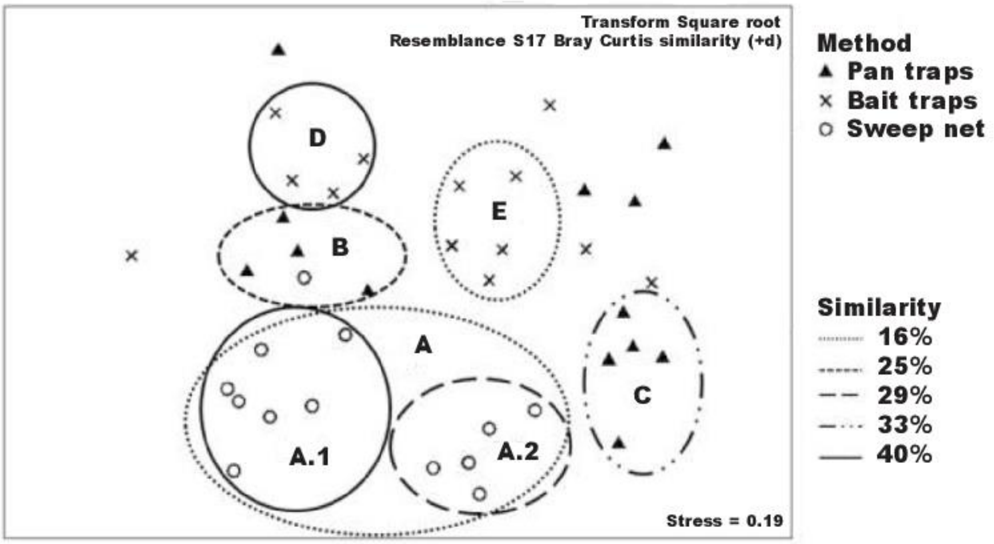

Fig. 4. MDS plot for arthropod community captured in the pan trap, sweep net and bait trap transects. Arthropod abundance data for the same study site and captured by using the sampling method were pooled. Groups are delineated according to the results of the cluster analysis.

Fig. 4. Gráfico MDS para la comunidad de artrópodos capturados en las trampas de bandeja, la red de barrido y las trampas de cebo. Se agrupan los datos relativos a la abundancia de los artrópodos capturados con el mismo lugar del estudio y con el mismo método de muestreo. Los grupos se definieron según los resultados del análisis de conglomerados.

and pan traps could be an appropriate approach to determine arthropod diversity. The low similarity in family composition within the pan trap transect is evidence of the effectiveness of this method when used to sample diverse arthropod taxa. A single sampling method should be selected to sample a

Table 2. UNIANOVA results considering the abundance of arthropods as a response variable and showing the degree of freedom (df), type III sum of square (SS), mean square (MS), Fisher statistic (*F*) and *p*–values: [a] R^2 = 0.136 (adjusted R^2 = 0.076).

*Tabla 2. Resultados de UNIANOVA que considera la abundancia de los artrópodos como variable de respuesta y de los valores de los grados de libertad (df), la suma de cuadrados tipo III (SS), el cuadrado medio (MS), el parámero de Fisher (*F*) y los valores de *p*: [a] R^2 = 0,136 (R^2 ajustado = 0,076).*

	df	SS	MS	*F*	*p*
Corrected model	5	5,186,594.5[a]	1,037,318.91	2.26	0.057
Intercept	1	797,265.1	797,265.10	1.74	0.192
SHDI	1	127,849.4	127,849.39	0.28	0.599
ED	1	823,540.3	823,540.27	1.79	0.185
Vegetation Shannon index	1	1,285,260.2	1,285,260.20	1.93	0.049
Sampling method	2	3,564,859.5	1,782,429.78	3.88	0.025
Error	72	33,049,909.3	459,026.52		
Total	78	43,240,344			
Corrected total	77	38,236,503.8			

Table 3. UNIANOVA results considering the number of families (N_F) as a response variable and showing the degree of freedom (df), type III sum of square (SS), mean square (MS), Fisher statistic (F) and *p*–values: ᵃ $R^2 = 0.348$ (adjusted $R^2 = 0.303$).

Tabla 3. Resultados de UNIANOVA que considera el número de familias (N_F) como variable de respuesta y los grados de libertad (df), la suma de cuadrados tipo III (SS), el medio cuadrado (MS), el parámero de Fisher (F) y los valores de p*:* ᵃ *$R^2 = 0,348$ (R^2 ajustado = 0,303).*

	df	SS	MS
Corrected model	5	6,142.9ᵃ	1,228.59
Intercept	1	18,543.5	18,543.59
SHDI	1	837.9	837.99
ED	1	134.1	134.19
Vegetation Shannon index	1	166.8	166.82
Sampling method	2	3,853.4	1,926.70
Error	72	11,505.4	159.80
Total	78	54,569.0	
Corrected total	77	17,648.4	

specific arthropod group. Some examples of this might be pan traps for Hymenoptera (Westphal et al., 2008), pit fall traps for ants (Wang et al., 2001), baiting techniques for wireworms (Coleoptera, Elateridae, Parker, 1996) or live–bait traps for *Rhodnius* (Hemiptera, Reduviidae) (Abad–Franch et al., 2000). The table of supplementary material presented in this study can be considered as a guide when choosing an effective sampling method for specific families.

The UNIANOVA results indicate the importance of vegetation and landscape diversity as regards abundance and number of families, respectively. However, the sampling method had a great influence for arthropod abundance and the number of families. This result highlights the importance of appropriately selecting sampling methods to describe arthropod communities, and the scope of any research could be limited by the sampling method chosen (Marshall et al., 1994).

Conclusion

Our results showed that the pan traps were the most effective method for sampling a large abundance of arthropod families in olive groves. However, the high number of families not found in pan traps suggests that a combination of methods is recommended. As sweep netting caught different family compositions to those obtained in bait traps and pan traps, a combination of sweep netting and pan traps may be a more effective approach for arthropod community monitoring in olive orchards. However, the selection of the sampling method depends greatly on the target taxa. The limitation of the sampling period made this research a first approximation to survey method effectiveness. Our conclusions should be evaluated in olive orchards with other management systems and climatic and seasonal variations should be considered. Further research including environmental variations is clearly needed.

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