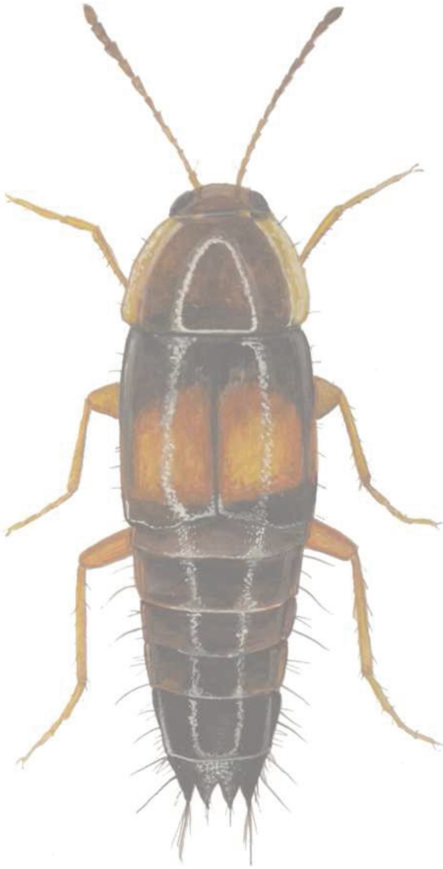
Efecto de las perturbaciones antropogénicas sobre carábidos y estafilínidos (Coleoptera: Carabidae, Staphylinidae) en paisaje forestal de *Quercus pyrenaica* del noroeste de España



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León 2015

Universidad de León
Departamento de Biodiversidad
y Gestión Ambiental

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Effect of human disturbances on ground and rove beetles (Coleoptera: Carabidae, Staphylinidae) in *Quercus pyrenaica* woodlands of north-west Spain

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Memoria presentada para optar al grado de Doctor en Biología

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León, 2015

La realización de esta Tesis Doctoral ha sido posible gracias a una beca de investigación concedida por la Junta de Castilla y León (EDU/918/2006) y a financiación recibida del proyecto de investigación LE008A06, subvencionado por la Junta de Castilla y León.

Todos los artrópodos han sido muestreados con los correspondientes permisos de captura concedidos por la Junta de Castilla y León.

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Ilustraciones de la portada (de arriba a abajo):

Izquierda: Bosque quemado al mes, al año y a los dos años del incendio (I)

Derecha: Dehesa abandonada (II, III), desbrozada (II, III) y pastada (II, III y IV)

Centro: Estafilínido (*Tachyporus hypnorum* Fabricius, 1775). Thom Dallimore, acuarela

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SERGIO GARCÍA TEJERO

Esta tesis se basa en las siguientes publicaciones, indicadas en el texto mediante números romanos:

I. García-Tejero, S., Taboada, A., Tárrega, R., Salgado, J.M., Marcos, E. 2013. Differential responses of ecosystem components to a low-intensity fire in a Mediterranean forest: a three-year case study. – Community Ecology 14, 110-120.

II. Tárrega, R., Calvo, L., Taboada, A., García-Tejero, S., Marcos, E. 2009. Abandonment and management in Spanish dehesa systems: Effects on soil features and plant species richness and composition. – Forest Ecology and Management 257, 731-738.

III. García-Tejero, S., Taboada, A., Tárrega, R., Salgado, J.M. 2013. Land use changes and ground dwelling beetle conservation in extensive grazing dehesa systems of north-west Spain. – Biological Conservation 161, 58-66.

IV. García-Tejero, S., Taboada, A. The role of microhabitats and their management in the functioning of wood-pastures. – Manuscrito.

RESUMEN

Los ecosistemas de *Quercus pyrenaica* han sido modificados por el hombre durante milenios, principalmente a través del pastoreo, que ha ido acompañado de perturbaciones como la corta y el uso del fuego para favorecer los pastos de herbáceas y evitar el crecimiento de la vegetación leñosa. El fuego ha sido la herramienta más utilizada y su uso continuado ha dado lugar a ecosistemas resilientes, que se recuperan con rapidez tras los incendios de baja intensidad. Las dehesas supusieron un método alternativo de gestión que proporcionaba pastos para el ganado, mientras permitía mantener altos valores de biodiversidad y conservación en el medio. Sin embargo, el reciente abandono de los usos tradicionales supuso una masiva proliferación de matorral en muchos bosques y dehesas, que, en ocasiones, son desbrozadas para disminuir el riesgo de incendios. Las perturbaciones antrópicas tienen un fuerte efecto sobre los distintos elementos del ecosistema, y, especialmente, sobre la estructura de la vegetación que influye, a su vez, en las condiciones ambientales y los recursos disponibles para la fauna de artrópodos del suelo, entre la que destacan los coleópteros carábidos y estafilínidos. En esta tesis se estudian los cambios producidos por distintas perturbaciones antrópicas en masas forestales de *Quercus pyrenaica* (incendio forestal de superficie en un bosque maduro, y pastoreo, abandono de los usos del suelo y desbroce mecanizado tras el abandono en sistemas adehesados), analizando su efecto sobre la fauna de carábidos y estafilínidos, y relacionando su respuesta con las alteraciones que sufren el suelo superficial y la vegetación. El incendio de superficie estudiado apenas afectó al suelo superficial del bosque, pero consumió la mayor parte del sotobosque, lo que disminuyó la competencia permitiendo un aumento de la riqueza de plantas y carábidos, gracias a la presencia de especies herbáceas anuales y de especies de carábidos granívoros durante los dos años siguientes al fuego. Además, las especies leñosas rebrotaron con rapidez, ayudando a recuperar la estructura de la vegetación y la cobertura de la capa de hojarasca, y contribuyendo a que las comunidades de plantas y estafilínidos se asemejasen, en apenas dos años, a las del bosque sin quemar. En las dehesas, la composición de especies de plantas, carábidos y estafilínidos difirió entre los distintos usos (pastoreo, abandono y desbroce). Las dehesas pastadas destacaron por su elevada riqueza de especies exclusivas, por la abundancia de grupos funcionales característicos, ligados a la actividad del ganado extensivo (dispersión de semillas y heces), tales como herbáceas anuales, carábidos granívoros y estafilínidos coprófilos, y por una mayor diversidad de la fauna de carábidos. Sin embargo, la diversidad de la fauna de estafilínidos fue alta en las dehesas abandonadas, donde una mayor cobertura de hojarasca pudo beneficiar a esta familia de coleópteros. En las dehesas desbrozadas, el aporte de nutrientes desde los restos de corta en descomposición enriqueció el suelo y posiblemente favoreció la abundancia de artrópodos detritívoros, que forman parte de la dieta de carábidos y estafilínidos, lo que explicaría la mayor abundancia de estos grupos de coleópteros en estas dehesas. No obstante, aunque el desbroce mecanizado redujo la diversidad de

la fauna de carábidos, logró que la composición de las comunidades de los dos grupos de coleópteros fuera similar a la de las dehesas pastadas, constituyendo un primer paso para la restauración de las dehesas tras el abandono. Sin embargo, el pastoreo puede ser necesario después del desbroce para impedir la proliferación de los arbustos, recuperar una composición de herbáceas similar a la de las dehesas pastadas, a través de las semillas dispersadas por las heces, y preservar los grupos funcionales de carábidos granívoros y estafilínidos coprófilos característicos de estas dehesas. En las dehesas pastadas, la gestión tradicional de baja intensidad dio lugar a un mosaico de distintos microhábitats (pastizales, árboles aislados, arbustos dispersos, arbustos bajo árbol y montones de restos de poda) que potenció la diversidad de la fauna de carábidos y estafilínidos a pequeña escala, al proporcionar una gran variedad de condiciones ambientales y recursos para los diferentes grupos funcionales de artrópodos (detritívoros, herbívoros y depredadores). Entre los microhábitats estudiados, destacaron los arbustos y los montones de restos de poda, al retener la hojarasca arrastrada por el viento en las dehesas pastadas, contribuyendo al reciclaje de nutrientes y proporcionando el hábitat óptimo para una comunidad de estafilínidos diferente. Los arbustos dispersos constituyeron, además, estructuras clave para los dos grupos de coleópteros estudiados, al servir de refugio para las especies depredadoras de gran tamaño que se alimentan en el pastizal; mientras que los arbustos bajo árbol albergaron una abundancia total y una biomasa de carábidos dos veces mayor que el resto de microhábitats, lo que puede ayudar a la conservación de niveles tróficos superiores en las dehesas. Estos resultados confirman la importancia de la gestión tradicional para mantener la elevada biodiversidad y heterogeneidad de los paisajes alterados por perturbaciones antrópicas, como es el caso de los bosques maduros y las dehesas de *Quercus pyrenaica*.

Índice

Publicaciones

INTRODUCCIÓN

La elevada biodiversidad que caracteriza la cuenca Mediterránea es el resultado de factores biogeográficos y geológicos, de la ecología del paisaje y de la larga historia de modificaciones antrópicas (Blondel *et al*. 2010). Los seres humanos han ocupado la cuenca Mediterránea durante milenios, alterando profundamente el paisaje, siendo el pastoreo uno de los principales usos del medio (Perevolotsky y Seligman 1998). Las especies de plantas mediterráneas, adaptadas a la sequía estival, al herbivorismo y al fuego desde la más remota antigüedad, se muestran muy resilientes al uso humano, recuperándose con rapidez tras las perturbaciones antrópicas, entre las que destaca el uso del fuego (Fox y Fox 1986, Lloret 1996, Pausas *et al*. 2008). El fuego ha sido tradicionalmente la principal herramienta de gestión, usada para potenciar la cobertura de las especies herbáceas a costa de las leñosas a fin de favorecer la caza ya en el Paleolítico y los pastos para el ganado tras la revolución Neolítica (Blanco Abril 2002).

La llegada de la agricultura empujó al pastoreo a zonas más infértiles, como las áreas de montaña y zonas marginales (Fillat 2002) y permitió un aumento en la densidad de población y, con ello, una mayor presión sobre el medio ambiente (Blanco Abril 2002). Además del pastoreo, la explotación de los montes también incluía la extracción de leña, que ha sido la fuente de combustible más usada hasta tiempos recientes (Blanco Castro *et al*. 1997, Blanco Abril 2002). La presión humana, mantenida y en aumento durante siglos, ha llevado, en muchos casos, a la degradación de los bosques hasta convertirlos en monte bajo (Blanco Castro *et al*. 1997, Luis *et al*. 2000, Consejería de Fomento y Medio Ambiente 2002).

Éste es el caso de los montes del roble melojo o rebollo (*Quercus pyrenaica* Willd.), en los que sólo un 14,75% de superficie se encuentra bien conservado (Maldonado *et al*. 2001). El melojo está prácticamente restringido a la Península Ibérica y representa un 6,5% (aproximadamente 950.000 ha) de la superficie forestal española (Maldonado *et al*. 2001). Los melojares se localizan en la zona de transición entre los bosques típicos mediterráneos (sobre todo de *Quercus ilex*) y los bosques eurosiberianos, asentándose sobre suelos silíceos y principalmente en zonas de umbría, ya que tienen una resistencia moderada a la sequía estival (Blanco Castro *et al*. 1997). El melojo es un árbol marcescente, es decir, conserva las hojas ya muertas protegiendo las yemas foliares, lo que puede suponer una adaptación para resistir el frío invernal (Blanco Castro *et al*. 1997).

El melojo resiste bien la explotación para leña y el pastoreo (ver Pardo y Gil 2005), ya que rebrota desde las raíces superficiales con gran facilidad al ser perturbado (Blanco Castro *et al*. 1997), lo que ha dado lugar a un mosaico paisajístico de zonas arboladas con diferentes estructuras de copa y sotobosque (Tárrega *et al*. 2006, 2007). Su resiliencia a la presión humana le ha permitido aumentar su área de distribución a costa del retroceso de otras especies más sensibles a las perturbaciones (Consejería de Fomento y Medio Ambiente 2002, García Antón *et al*. 2002). El abandono de las prácticas tradicionales en los bosques de melojo supone una proliferación de matorral de brezo (*Erica* spp.) y escoba (*Cytisus* spp.) que gracias a su alta capacidad de rebrote (favorecida por los siglos de uso humano) puede ocupar rápidamente el sotobosque (Calvo *et al*. 2002a, Tárrega *et al*. 2007).

Los efectos del fuego sobre la vegetación y el suelo han sido ampliamente estudiados en zonas mediterráneas (por ejemplo, Trabaud 1987, Pausas *et al*. 2008). Sin embargo, apenas se ha investigado su efecto en otros elementos del ecosistema, como los artrópodos del suelo (García-Villanueva *et al*. 1998, Antunes *et al*. 2009), y la información existente procede principalmente de los bosques boreales (por ejemplo, Gandhi *et al*. 2001, Buddle *et al*. 2006, Gongalsky *et al*. 2006). Los cambios que produce el fuego en el ecosistema dependen en gran medida del régimen de incendios, es decir, de su intensidad, estacionalidad y recurrencia (Pausas *et al*. 2008). Si los incendios son de baja intensidad, permiten la recuperación de nutrientes del suelo (Certini 2005) y potencian la presencia de herbáceas mientras se recupera la vegetación leñosa (Luis y Tárrega 1993, Calvo *et al*. 1999). En ecosistemas con una larga historia de incendios, la comunidad de especies de las masas forestales inflamables está muy adaptada a esta perturbación y se recupera a través de un proceso de autosucesión en el que, en poco tiempo, vuelven a dominar las especies presentes antes del fuego (Trabaud 1987, Lloret 1996).

Una alternativa de gestión que favorece los pastos, sin recurrir al fuego, es el adehesamiento, en el que se clarea el bosque para lograr pastos arbolados (“wood-pastures”) donde se combinan el pastoreo, la extracción de leña y, en ocasiones, el uso agrícola, al tiempo que se mantienen altos valores ambientales (Moreno y Pulido 2008, Bergmeier *et al*. 2010, Bugalho *et al*. 2012). Las dehesas son el tipo de pasto arbolado más abundante de Europa, siendo su cobertura arbórea de roble o encina (*Quercus* spp.) (Moreno y Pulido 2008, Plieninger *et al.* 2015). Las dehesas actuales son el resultado de la gestión tradicional mantenida durante siglos que, al realizarse con una intensidad moderada, aumenta la heterogeneidad espacial a diferentes escalas (Diacon-Bolli *et al*. 2012).

Dentro de las dehesas, la variedad de microhábitats existente permite una alta biodiversidad y la presencia de especies que necesitan distintas condiciones ambientales dentro de un mismo ecosistema (Hartel *et al*. 2014). El pastoreo, si la carga ganadera es adecuada, supone una perturbación intermedia que potencia la riqueza y la densidad de especies en los pastizales, tanto de plantas (Bergmeier *et al*. 2010) como de animales (Martins da Silva *et al*. 2008, Taboada *et al*. 2011). Los árboles proporcionan sombra para el ganado en los momentos de más calor y son esenciales para el flujo de materia en las dehesas, ya que sus raíces les permiten bombear nutrientes desde capas profundas del suelo donde las herbáceas no llegan, y devolverlos al sistema principalmente en forma de hojarasca (Blanco Castro *et al*. 1997, Vetaas 1992). Los árboles proveen un

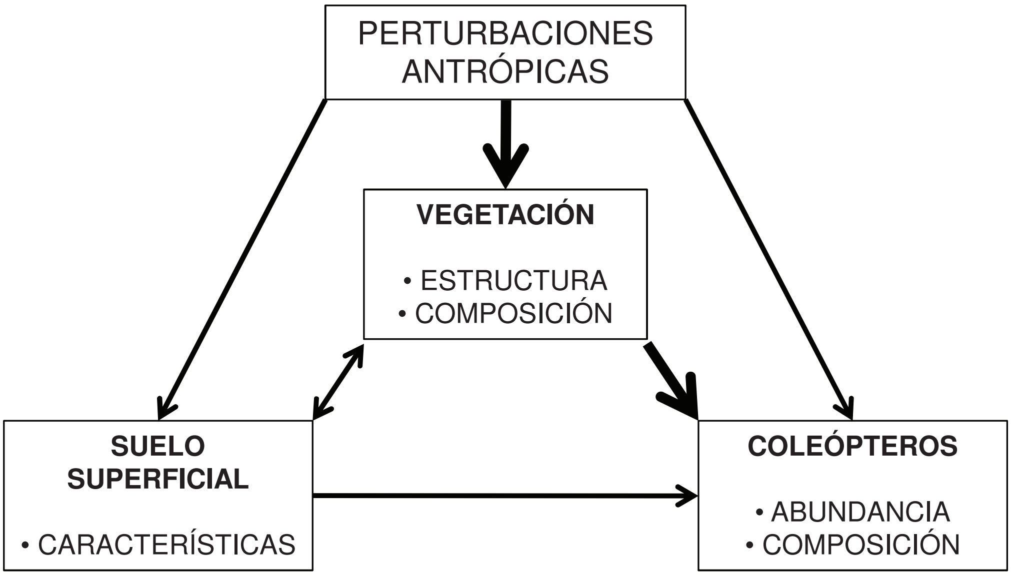

Figura 1. Modelo conceptual de los efectos de las perturbaciones antrópicas sobre los distintos elementos estudiados en los ecosistemas de *Quercus pyrenaica*. Las flechas gruesas indican mecanismos de acción más evidentes y/o comprobados.

microclima más suave bajo su copa (Blanco Castro *et al*. 1997) y suponen una estructura clave (*sensu* Tews *et al*. 2004) para numerosos animales tales como aves, murciélagos e insectos saproxílicos (Fischer *et al*. 2010, Robles *et al*. 2011, Sebek *et al*. 2013).

Además del pastizal y los árboles aislados, los arbustos constituyen otro componente del mosaico de microhábitats en muchos pastos arbolados y paisajes de tipo 'sabana' (Vetaas 1992, Bergmeier *et al*. 2010, Bugalho *et al.* 2011, Plieninger *et al.* 2015). Sin embargo, su importancia en el funcionamiento de estos ecosistemas se ha estudiado poco, aunque se sabe que son utilizados por las aves para descansar, cantar, refugiarse y anidar (Hartel *et al.* 2014) y que proporcionan un hábitat apropiado para diversos reptiles (Martín y López 2002, Godinho *et al*. 2011). Además, en zonas abiertas y expuestas como las dehesas, los arbustos pueden retener la hojarasca que arrastra el viento (Facelli y Pickett 1991), evitando que desaparezca del ecosistema e influyendo en el ciclo de nutrientes a través de la cadena de los descomponedores (Sayer 2005). La densidad de arbustos en la dehesa depende de las labores de desbroce y sobre todo de la intensidad del pastoreo, que limitan la expansión del matorral en favor del pasto (Moreno y Pulido 2008).

En las últimas décadas, el despoblamiento rural y la sustitución de la leña por combustibles fósiles han supuesto una disminución de la intensidad de las prácticas tradicionales o incluso el abandono de las mismas, permitiendo la continuación de la sucesión secundaria y causando un aumento de la densidad de arbustos en las masas forestales anteriormente gestionadas (Blanco Castro *et al*. 1997, Tárrega *et al*. 2006). La

Tabla 1. Esquema indicando el tipo de hábitat, intervención, concepto clave y elementos del ecosistema analizados en cada estudio.

Hábitat	Perturbación	Concepto clave	Elementos del ecosistema
Bosque	Fuego	Sucesión secundaria	Suelo superficial, vegetación, coleópteros
Dehesa	Gestión tradicional Abandono Desbroce	Cambio de uso del suelo	Suelo superficial, vegetación
			Coleópteros
	Gestión tradicional	Microhábitats	Suelo superficial, coleópteros

acumulación de biomasa en el sotobosque contribuye a aumentar el riesgo de incendios, especialmente los de gran extensión (San-Miguel-Ayanz *et al*. 2012), que pueden tener consecuencias dramáticas tanto para la vida silvestre como para los seres humanos (Hernández 2015). En el caso de las dehesas, el abandono conlleva la proliferación de los arbustos y una disminución de la riqueza de especies vegetales y de su diversidad funcional (Peco *et al*. 2006, 2012). Aunque, en ocasiones, la continuidad del estrato arbustivo puede beneficiar a los reptiles (Godinho *et al*. 2011) y mejorar la regeneración del arbolado (Plieninger *et al*. 2003, Moreno y Pulido 2008, Ramírez y Díaz 2008), a largo plazo no preserva el funcionamiento y la provisión de servicios de las dehesas (Moreno *et al*. 2013). Recientemente se ha promovido el uso del desbroce mecanizado para reducir la cantidad de combustible en el sotobosque (Baeza 2004), pero esta práctica de gestión utilizada en las dehesas puede tener efectos negativos para la diversidad de aves (Camprodon y Brotons 2006) y para la regeneración del arbolado (Pinto-Correia y Mascarenhas 1999).

Estas perturbaciones antrópicas (incendios forestales, pastoreo, abandono de los usos del suelo y clareo por desbroce mecanizado) afectan al conjunto del ecosistema, siendo su efecto más marcado sobre la estructura de la vegetación, que repercute, a su vez, en multitud de procesos ecológicos. Las plantas son los productores primarios y por ellas pasa todo el flujo de energía del ecosistema, del cual, hasta un 90% entra en la cadena de descomposición en los ecosistemas arbolados (Chen y Wise 1999). Esta energía mantiene a descomponedores y detritívoros que se relacionan entre sí a través de complicadas redes tróficas (Begon *et al*. 2006), dando como resultado una alta biodiversidad a nivel del suelo superficial (Giller 1996). Dentro de los detritívoros se encuentran numerosos artrópodos entre los que se incluyen los colémbolos (Collembola) y los dípteros (Diptera) (Hövemeyer 1992, Rusek 1998), que sirven de alimento a multitud de depredadores, incluidas dos familias de coleópteros muy abundantes y diversas

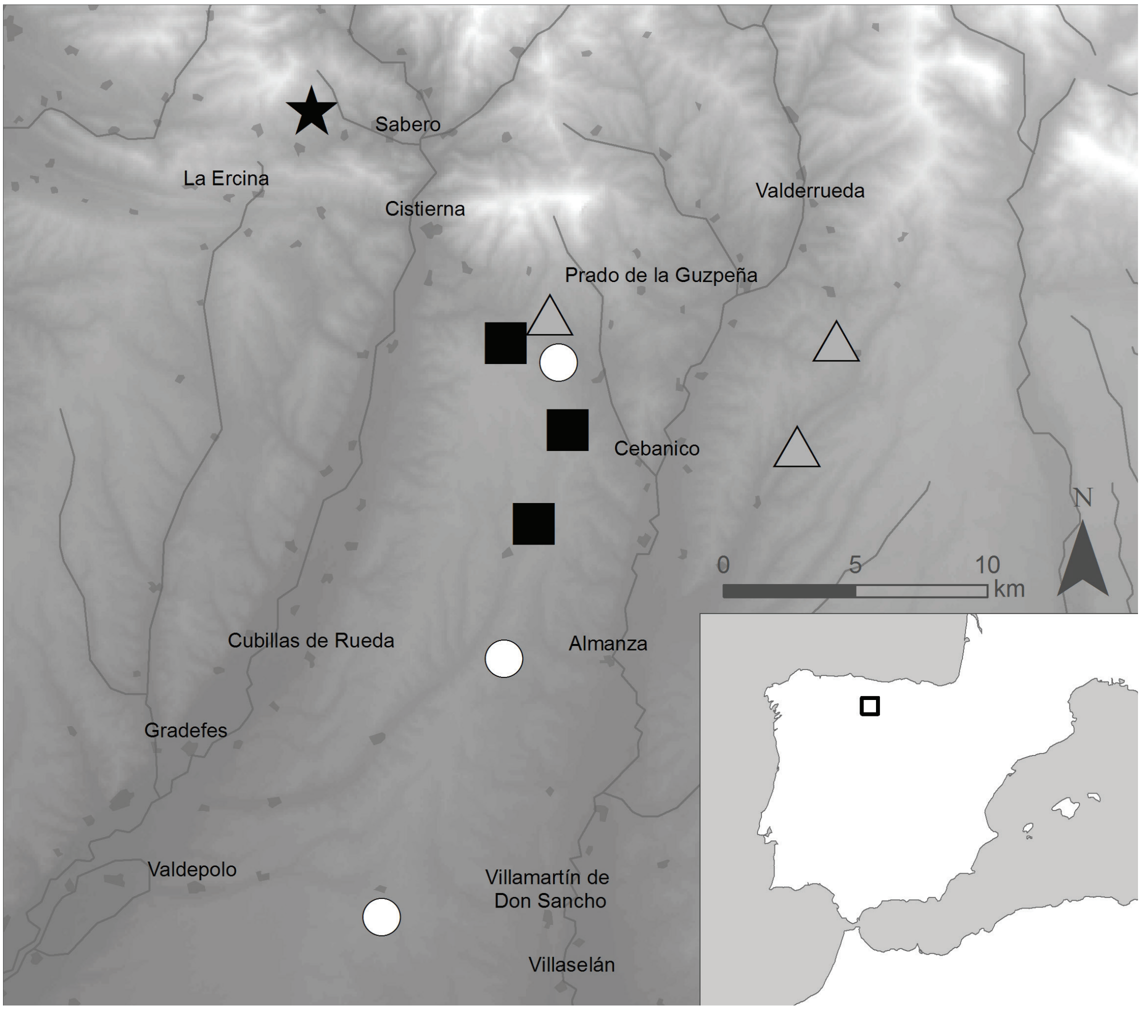

Figura 2. Localización del área de estudio, indicando mediante símbolos las zonas muestreadas en cada estudio. Estrella: estudio I; triángulos: dehesas abandonadas (II y III); cuadrados: dehesas desbrozadas (II y III); círculos: dehesas pastadas (II, III y IV). Se muestran también las principales localidades.

en el suelo: los carábidos (Coleoptera: Carabidae) y los estafilínidos (Coleoptera: Staphylinidae) (Thiele 1977, Thayer 2005).

Tanto los carábidos como los estafilínidos se ven afectados por factores abióticos como las condiciones microclimáticas, que dependen en gran medida de la estructura de la vegetación (Chen *et al*. 1999), o la composición del suelo, y también por factores bióticos como la disponibilidad de presas y la presencia de competidores (Thiele 1977, Thayer 2005). Los carábidos son principalmente depredadores o carroñeros (Lövei y Sunderland 1996), aunque algunas especies complementan su dieta con semillas o son exclusivamente granívoras (Thiele 1977, Honek *et al*. 2003). Los estafilínidos son particularmente diversos sobre materia en descomposición, como hojarasca, setas, excrementos o carroña, donde la mayoría de especies son depredadoras, aunque también las hay saprófagas y micófagas (Hammond 1976, Newton 1984, Thayer 2005). Ambas familias de coleópteros compiten (y se depredan) entre sí y con otros artrópodos depredadores del suelo como las hormigas, las arañas y los opiliones, y son al tiempo presas importantes para niveles tróficos superiores (Thiele 1977), constituyendo un eslabón clave en la red trófica del suelo (Lövei y Sunderland 1996). La importancia de los carábidos y los estafilínidos en el ecosistema del suelo, su diversidad y sensibilidad a los cambios del medio y el grado de detalle con que se conoce su ecología, les convierte en buenos bioindicadores de los efectos de las prácticas de gestión y las perturbaciones antrópicas (Bohac 1999, Rainio y Niemelä 2003, Taboada Palomares 2007).

OBJETIVOS

En esta tesis se estudian las respuestas de dos grupos de coleópteros, carábidos y estafilínidos, a diferentes perturbaciones antrópicas en masas forestales de *Quercus pyrenaica*, y su relación con los cambios que tienen lugar en las condiciones del suelo superficial y en la vegetación. Las perturbaciones pueden afectar a los coleópteros de manera directa o a través de cambios en la vegetación y en las características del suelo, que están a su vez interrelacionados (Figura 1). En total, se estudiaron cuatro perturbaciones antrópicas, entendidas en un sentido amplio como aquellos cambios originados por las prácticas de gestión tradicional y reciente o por el abandono de los usos del suelo. Las perturbaciones consideradas fueron un incendio forestal de superficie en un bosque maduro, y el pastoreo, el abandono del uso del suelo y el desbroce mecanizado tras el abandono en sistemas adehesados.

En el estudio I se analizó la sucesión secundaria (definida como el proceso de recuperación del ecosistema tras una perturbación) después de un incendio superficial, de baja intensidad y de primavera. En los estudios II y III se evaluaron los efectos de los cambios de uso del suelo en las dehesas, comparando dehesas pastadas, abandonadas y aquéllas que han sido recientemente desbrozadas después del abandono. Las dehesas pastadas están sometidas a la gestión tradicional, principalmente mediante el pastoreo que resulta en una perturbación intermedia, que puede contribuir a potenciar la diversidad de especies (Grime 1973, Connell 1978). Las dehesas abandonadas son el resultado de la sucesión secundaria, mientras que el desbroce mecanizado es una perturbación que reinicia de nuevo este proceso y que podría servir como un primer paso para la restauración de las dehesas. En el estudio IV se analizó el efecto de la gestión tradicional en las dehesas a pequeña escala, que da lugar a una gran variedad de microhábitats que contribuyen a aumentar la biodiversidad por dos vías distintas. Por una parte, los microhábitats potencian la heterogeneidad espacial al diferir en sus condiciones ambientales y en los recursos que aportan al ecosistema, dando cabida a más riqueza de especies dentro de la misma área. Por otra parte, algunos microhábitats pueden suponer estructuras clave (“keystone structures”) en el ecosistema, definidas como elementos del paisaje distintivos que proveen recursos, refugio o bienes y condiciones ambientales cruciales para otras especies (Tews *et al*. 2004). La Tabla 1 resume los conceptos clave y los elementos del ecosistema analizados en cada estudio.

Las hipótesis de las que partimos son: (1) las comunidades de carábidos y estafilínidos de las masas forestales de *Quercus pyrenaica* son muy resilientes a las perturbaciones antrópicas y se recuperan con rapidez, especialmente tras un incendio forestal de baja intensidad (Estudio I); (2) el abandono de las prácticas de gestión tradicional puede actuar en detrimento de la diversidad de plantas, carábidos y estafilínidos en los ecosistemas adaptados a las perturbaciones antrópicas (Estudios II y III); (3) la gestión tradicional potencia la diversidad de carábidos y estafilínidos a pequeña escala, al mismo tiempo que permite un uso sostenible del medio (Estudio IV).

MATERIAL Y MÉTODOS

1. Área de estudio y diseños experimentales

Los estudios se realizaron en masas arboladas de roble melojo (*Quercus pyrenaica*) asentadas en las estribaciones de la Cordillera Cantábrica, en el noroeste de España (42°33' – 42°50'N, 4° 55' – 5°10'W) a una altitud de 975–1230 m sobre el nivel del mar (Figura 2). El clima es de tipo mediterráneo sub-húmedo (temperatura media anual 10,9 °C, precipitación media anual 927 mm, sequía estival en julio y agosto) (Ministerio de Agricultura 1980) y el tipo de suelo es cambisol húmico (Forteza *et al*. 1987). La tesis se compone de cuatro estudios, de los cuales uno de ellos (estudio I) se realizó en un bosque maduro y los otros tres (estudios II, III y IV) en dehesas. Los estudios II y III comparten el mismo diseño experimental, centrándose el primero en las características del suelo y la vegetación y el segundo en la fauna de carábidos y estafilínidos.

Estudio I: Efectos de un incendio forestal

En este trabajo se analizaron las respuestas del suelo superficial, la vegetación y los dos grupos de coleópteros (carábidos y estafilínidos) a lo largo de tres años tras un incendio de superficie. En mayo de 2006 un incendio quemó 13 de las 55 ha de un melojar maduro (altura media del arbolado = 7 m, perímetro medio = 34 cm). Fue un incendio de superficie que consumió el sotobosque y parte de las copas, pero que permitió la supervivencia de la mayoría de los árboles. Un mes después del fuego, se establecieron cuatro transectos de 50 m de longitud separados al menos 75 m en la zona quemada (B1, B2, B3 y B4) y otros cuatro en la no quemada (control; C1, C2, C3 y C4). Los transectos siguieron la dirección de la pendiente (aproximadamente 15%) con orientación sur en B1, B2 y B4, este en B3, sudeste en C1 y C2, y sudoeste en C3 y C4. A lo largo de cada transecto se recogieron cinco muestras de suelo superficial y se seleccionaron tres puntos de muestreo en los que se caracterizó la estructura de la vegetación y la cobertura de cada especie de planta, y se capturaron carábidos y estafilínidos mediante dos trampas de caída.

El muestreo se llevó a cabo durante tres años (2006 a 2008): el suelo superficial se muestreó en septiembre, la vegetación en julio y los coleópteros de junio a octubre. Para cada año y transecto se obtuvo una muestra de suelo, se calculó la media de las coberturas de vegetación y se sumó el total de individuos de cada especie de carábido y estafilínido, resultando en cuatro réplicas para cada tratamiento (quemado, control) y año de muestreo (2006, 2007, 2008).

Estudios II y III: Efectos del cambio de uso del suelo en las dehesas

Se escogieron tres tipos de dehesas sometidas a diferentes prácticas de gestión: (1) dehesas pastadas en la actualidad, (2) dehesas abandonadas en las que el ganado no ha pastado en los últimos 20 años, y (3) dehesas desbrozadas, que fueron abandonadas durante al menos 20 años, y cuyo sotobosque arbustivo fue cortado en su totalidad 1-2 años antes del estudio por medios mecánicos. Las zonas de estudio son planas o con menos de un 10% de pendiente, con árboles de 10-12 m de altura y 1-1,5 m de perímetro a la altura del pecho. Las dehesas abandonadas están dominadas por arbustos de *Calluna vulgaris* y *Erica australis* que cubren un 30% de la superficie. En las dehesas pastadas los arbustos se encuentran dispersos pero bien desarrollados (altura 50-110 cm, anchura 100-200 cm), mientras que en las desbrozadas se encuentran en forma de pequeños rebrotes desde las raíces de los arbustos cortados. Se seleccionaron tres zonas de dehesa de cada tipo y en cada zona se situaron cinco puntos de muestreo separados al menos 25 m entre sí y de los bordes de la parcela. Para el estudio II, en cada punto de muestreo se tomó una muestra de suelo superficial y se estimó la cobertura de cada especie vegetal en tres unidades de muestreo cuadradas de un metro de lado; mientras que para el estudio III se caracterizó la estructura de la vegetación en esas mismas unidades y se colocaron dos trampas de caída para capturar carábidos y estafilínidos de mayo a octubre.

Estudio IV: Microhábitats de las dehesas pastadas

En el estudio IV se analizaron los principales microhábitats creados por las prácticas de gestión tradicional en las dehesas, y se investigó su influencia en las características del suelo superficial y en la fauna de coleópteros (carábidos y estafilínidos) y sus presas (colémbolos y dípteros). Se seleccionaron las tres dehesas pastadas incluidas también en los estudios II y III. Mientras que en estos estudios sólo se muestreó en la zona de pastizal, el microhábitat más extenso que conforma las dehesas pastadas, en el estudio IV se diferenciaron cinco microhábitats característicos de estas dehesas: (i) los pastizales, que son pastados por rebaños de tamaño moderado que suman en total unas 900-1250 ovejas por dehesa (García-Tejero, observación personal); (ii) los árboles aislados, de 10-12 m de altura y 1-1,5 m de perímetro a la altura del pecho, que son

Tabla 2. Esfuerzo de muestreo y número de individiuos y de especies de carábidos y estafilínidos capturados en cada estudio.

	Esfuerzo de muestreo					**Carábidos**		**Estafilínidos**	
Estudio	Tratamientos x réplicas	Puntos de muestreo	Trampas totales	Días de trampeo	Pérdida de trampas (%)	Individuos	Especies	Individuos	Especies
I	2 x 4 (x 3 años)	3	144	148*	2,8	2532	42	3073	99
III	3 x 3	5	90†	142	7,0	3632	55	1046	86
IV	5 x 3	4	120†	142	3,2	5128	51	2981	116
Total						11292	80	7100	179

* Promedio de días de trampeo por año. † Los estudios III y IV comparten 24 trampas, situadas en los pastizales de las dehesas pastadas.

Tabla 3. Tabla de contingencia indicando las técnicas estadísticas utilizadas para analizar las principales variables de suelo superficial, vegetación y coleópteros en los distintos estudios. Las técnicas marcadas en negrita son análisis multivariantes.

		Suelo superficial	Vegetación		Coleópteros		
Cuestión a resolver	Técnica estadística	Características	Cobertura y riqueza	Composición de especies	Abundancia	Riqueza	Composición de especies
Diferencias entre tratamientos	ANOVA	II	II				
	GLM				III		
	GLMM	I, IV	I		I, IV	I	
	Rarefacción					III, IV	
	PERMANOVA (+ MRT)	I, IV		I			I, III, (IV)
Efecto de otras variables	**RDA (+ varpart)**						I, (III)
Representación patrones generales	**PCA (DCA)**	I, II		(II)			I, III

ANOVA = análisis de la varianza; GLM(M) = modelos lineales generalizados (mixtos); PERMANOVA = análisis de varianza multivariante permutativo; MRT = árboles de regresión multivariantes; RDA = análisis de redundancia; varpart = partición de la varianza; PCA = análisis de componentes principales; DCA = análisis de correspondencias corregidas.

podados, o más bien trasmochados (poda en la que se corta la mayor parte de la copa), para mantener una copa ancha; (iii) los arbustos dispersos, distribuidos por el pastizal y formados por uno o varios matorrales juntos y que ocupan de media 1,8 m^2 (± 0,3 error estándar); (iv) los arbustos bajo árbol que consisten en grupos de arbustos o rebrotes de roble melojo que ocupan de media 16,1 m^2 (± 1,8) situados alrededor del tronco de uno o dos árboles muy próximos y; (v) los montones de restos de poda, donde se acumulan ramas finas procedentes de la poda de árboles cercanos, y que se extienden de media 15,1 m^2 (± 0,8). En estas dehesas la mayor parte de la hojarasca (de hojas de roble) es arrastrada por el viento y se acumula bajo los arbustos (tanto dispersos como bajo árbol) y los montones de restos de poda. En cada dehesa pastada se seleccionaron cuatro réplicas de cada tipo de microhábitat como puntos de muestreo, separados al menos 25 m entre sí y del borde de la parcela. En cada punto de muestreo se recogieron cinco muestras de suelo separadas entre 1 y 2 m que se homogeneizaron en una sola, se caracterizó la estructura de la vegetación en una unidad de muestreo de 5x5 m y se colocaron dos trampas de caída para capturar carábidos y estafilínidos y sus presas.

2. Toma de datos

Las técnicas empleadas para muestrear el suelo superficial, la vegetación y los coleópteros fueron las mismas a lo largo de la tesis.

Suelo superficial

En cada transecto (estudio I), parcela (estudio II) y microhábitat (estudio IV) se tomaron cinco muestras de los cinco primeros centímetros del suelo y se homogeneizaron en una sola para cada transecto (estudio I), parcela (estudio II) y microhábitat muestreado (estudio IV). La muestra de suelo se secó y tamizó (luz de malla de 2 mm) antes de ser analizada usando los métodos oficiales de análisis de suelo (M.A.P.A. 1994) para determinar el valor de pH, el contenido en materia orgánica (M.O..), el nitrógeno total (N), la relación carbono/nitrógeno (C/N) y el fósforo (P), calcio (Ca^{2+}), potasio (K^+), magnesio (Mg^{2+}) y sodio (Na^+) asimilables.

Vegetación

La estructura de la vegetación se caracterizó en cada punto de muestreo en tres unidades de muestreo de 1 m de lado separados entre sí 2 m en los estudios I y II, y en una unidad de 5 m de lado en el estudio IV. En cada unidad se estimó visualmente el porcentaje de suelo descubierto y el de la cobertura de hojarasca y de los estratos herbáceo (0 - 50 cm de altura), arbustivo (50 - 200 cm) y arbóreo (> 200 cm) y se midió la profundidad de la hojarasca. En los estudios I y II también se estimó visualmente el porcentaje de cobertura de cada especie vegetal, que se clasificaron según la nomenclatura de Flora Europaea (Tutin *et al*. 1964-1980).

Carábidos y estafilínidos

En cada punto de muestreo se colocaron a ras de suelo dos trampas de caída (recipientes de plástico de 86 mm de altura y 60 mm de diámetro) separadas entre 0,5 y 2 m y cubiertas con tejadillos de madera prensada de 10 x 10 cm, para capturar los artrópodos del suelo. Las trampas se llenaron parcialmente con propilenglicol al 25% como líquido conservante y se reemplazaron cada tres semanas hasta un total de siete muestreos. El propilenglicol tiene la ventaja de ser poco atrayente e inocuo para aves y mamíferos, a diferencia de otros conservantes como el etilenglicol (Woodcock 2005). Las trampas de caída son un método pasivo de captura que refleja tanto la densidad como la actividad de los artrópodos (Thiele 1977, Woodcock 2005), la cual puede verse afectada por numerosos factores como la estructura y densidad de la vegetación, la temperatura y el comportamiento de las especies capturadas (Thiele 1977, Guillemain *et al*. 1997, Melbourne 1999). Los artrópodos se capturaron de manera continuada desde principios de junio a finales de octubre coincidiendo con el periodo en el que el melojo mantiene su follaje. Los puntos de muestreo se separaron al menos 25 m para lograr que los datos de las capturas fueran estadísticamente independientes (Digweed *et al.* 1995). En la Tabla 2 se muestra el esfuerzo de muestreo y el número total de especies e individuos de carábidos y estafilínidos capturados en cada estudio. Del material recogido en las trampas de caída se separaron los carábidos y los estafilínidos para su posterior identificación y se contó el número de potenciales competidores (hormigas, arañas y opiliones) en el estudio III y de presas (colémbolos y dípteros) en el estudio IV. Los carábidos y estafilínidos se identificaron hasta el nivel taxonómico de especie usando las claves disponibles (Jeannel 1941-1942 para carábidos; Bordoni 1982, Coiffait 1972, 1974, 1978, 1984, Freude *et al*. 1964, 1975, Outerelo y Gamarra 1986, Palm 1948, 1961, 1968, 1970, 1972, Porta 1926, Zanetti 1987 para estafilínidos) y se siguió la nomenclatura de Serrano (2003) y Smetana (2004) respectivamente para cada grupo. Debido a la ausencia de claves de identificación apropiadas, unos pocos estafilínidos no pudieron ser identificados hasta el nivel de especie y sólo se incluyeron en los análisis de abundancia. A partir de la bibliografía existente, se recopilaron algunas de las características específicas más importantes de las especies de ambos grupos de coleópteros, como la longitud media del cuerpo, el tipo de alimentación en el caso de los carábidos (granívoro/depredador/omnívoro) y la preferencia por distintos recursos en el de los estafilínidos (coprófilo/micófilo/fitodetritícola), a fin de discutir mejor los resultados obtenidos.

3. Análisis de datos

En la Tabla 3 se resumen las herramientas estadísticas utilizadas para cada cuestión a analizar, grupo de estudio (suelo superficial, vegetación o coleópteros) y tipo de datos respuesta, según estuvieran conformadas por una (análisis univariantes) o más variables (análisis multivariantes), y se indica, además, en qué estudios de la tesis fueron empleadas.

Para analizar la influencia del fuego y el año de muestreo (estudio I), del tipo de uso (estudios II y III) o de los microhábitats (estudio IV) en las características del suelo superficial de manera individual, en la cobertura y riqueza de la vegetación y en la abundancia y riqueza de coleópteros se emplearon modelos de regresión lineal. Los modelos lineales suponen una relación entre el valor medio de la variable respuesta y una combinación lineal de las variables explicativas (Quinn y Keough 2002). A lo largo de la tesis se usaron modelos de distinta complejidad dependiendo del tipo de distribución de las variables respuesta y del diseño experimental de cada estudio.

En el estudio II se usaron modelos lineales clásicos (que suponen una distribución normal para la variable respuesta) y que al ser la variable explicativa de tipo categórico (tipo de uso del suelo), se conocen como análisis de varianza (ANOVA). En los estudios I, III y IV se usaron modelos lineales generalizados (GLM). Los GLM permiten tener en cuenta el tipo de distribución de la variable respuesta, mejorando la modelización de los datos (Quinn y Keough 2002). Se empleó la distribución normal para las variables continuas (pH, contenido de materia orgánica y de nutrientes del suelo, y longitud corporal media de los coleópteros), Poisson para la riqueza de especies, quasi-Poisson para la cobertura de los distintos tipos de vegetación (estudio I) y binomial negativa para la abundancia de artrópodos. Las distribuciones Poisson, quasi-Poisson y binomial negativa son discretas (no continuas) y apropiadas para datos en los que se cuenta el número de individuos o de especies y que por tanto se restringen al valor 0 y a números naturales. La distribución de Poisson supone una dispersión *moderada* de los datos en los que la media es igual a la varianza, por lo que es apropiada para modelar la riqueza, que no suele tomar valores extremos. Por su parte, las distribuciones quasi-Poisson y binomial negativa tienen en cuenta la sobredispersión de los datos propia de los muestreos en los que se cuenta el número de individuos (coleópteros) o se estima la cobertura de diferentes especies vegetales (White y Bennetts 1996, Ver Hoef y Boveng 2007). En los estudios I y IV los modelos lineales generalizados fueron de tipo mixto (GLMM), que permiten incorporar variables explicativas aleatorias con las que se tiene en cuenta que se ha utilizado un diseño de muestreo en el que los datos están agrupados. Esto sucedió en el estudio I al muestrear las mismas parcelas a lo largo de los años (diseño de medidas repetidas; variable aleatoria: transecto) y en el estudio IV al muestrear todos los microhábitats en tres dehesas separadas (diseño de bloques aleatorios completo; variable aleatoria: dehesa). Los modelos mixtos permiten dilucidar con más claridad cuál es el efecto de las variables explicativas fijas (tratamiento/microhábitat) ya que descartan la variabilidad debida a las variables explicativas aleatorias.

En los estudios III y IV se usaron curvas de rarefacción para comparar la riqueza de especies de carábidos y estafilínidos entre tipos de uso y microhábitats respectivamente. La rarefacción es una técnica que permite comparar los valores de riqueza entre distintas zonas teniendo en cuenta las diferencias en esfuerzo de muestreo y/o en el número de individuos capturados (Magurran 2004). Por el tipo de datos recogidos se utilizó “rarefacción basada en muestras” (“sample-based rarefaction”), ya que modela mejor el hecho de que los artrópodos terrestres se distribuyan de manera agrupada (Colwell *et al*. 2012). Además, se calcularon intervalos de confianza del 95% no condicionados por los datos muestrales, lo que permite una comparación válida entre curvas de rarefacción (Colwell *et al.* 2012). En el estudio III se estimó el “número efectivo de especies” como medida de diversidad, que se calcula con la función exponencial (e^x) del índice de Shannon $(H' = -\sum_{i=1}^{R} p_i \ln p_i)$ e indica cuántas especies habría en una comunidad si todas ellas fuesen igual de abundantes (Jost 2006). Los valores de diversidad tienen en cuenta tanto la riqueza de especies como lo “equilibradas” que están sus abundancias (uniformidad) y se compararon los distintos tipos de dehesa mediante GLM.

Para estudiar los patrones de composición de los nutrientes del suelo y de las especies vegetales y animales en su conjunto se emplearon técnicas multivariantes. El análisis de componentes principales (PCA; estudios I, II y III) y el de correspondencias corregidas (DCA; estudio II) permiten representar gráficamente la variabilidad de los datos en un número reducido de dimensiones (normalmente dos), para poder comparar visualmente las distintas zonas de muestreo respecto a las características del suelo o a la composición de especies. El análisis de varianza multivariante permutativo (PERMANOVA; estudios I, III y IV) permite saber si la composición (de nutrientes del suelo o de especies vegetales o animales) difiere significativamente entre clases establecidas (tratamientos, tipos de dehesas o microhábitats). Este análisis permite elegir el tipo de distancia multivariante calculada entre sitios muestreados, por lo que se eligieron distancias euclídeas para el suelo y Hellinger para la vegetación, los carábidos y los estafilínidos. La significación de los resultados se evaluó mediante 9999 permutaciones de Monte Carlo, apropiadas cuando el número de réplicas es bajo (Anderson 2001). En el estudio IV se usaron árboles de regresión lineal multivariante (MRT) para analizar qué grupos de microhábitats eran más parecidos entre sí y más diferentes del resto, en cuanto a composición de especies de carábidos y estafilínidos. Esta técnica subdivide el conjunto de los datos de tal forma que la variabilidad dentro de cada nuevo grupo sea la menor posible y las diferencias entre grupos sean lo mayores posibles (De’Ath 2002). En este caso, el tamaño del árbol de regresión se limitó de manera que todas las divisiones entre pares de grupos fueran estadísticamente significativas ($p<0{,}05$) de acuerdo a PERMANOVA.

El análisis de redundancia (RDA; estudios I y III) combina la regresión lineal con el análisis de componentes principales (PCA) y permite trabajar con variables explicativas categóricas y continuas (Legendre y Legendre 2012). En este caso, las variables explicativas se fueron añadiendo de una en una comprobando su significación (p<0,05) mediante 9999 permutaciones. En el estudio III, los resultados de varios RDA se combinaron mediante una técnica llamada partición de la varianza ("variation partitioning") para saber qué porcentaje de la variación total en la composición de las comunidades de carábidos y estafilínidos explicaban en común el tipo de uso, las características del suelo, la estructura de la vegetación y la abundancia de artrópodos competidores, y cuánto explicaba cada grupo de variables por separado. Antes de los análisis multivariantes, las variables del suelo se estandarizaron a media 0 y desviación estándar 1 para que todas tuvieran la misma importancia en los análisis. Los datos de composición de plantas y de coleópteros se adecuaron a técnicas que usan distancias euclídeas (PCA, MRT, RDA) mediante la transformación de Hellinger, que consiste en calcular la raíz cuadrada de la abundancia relativa de cada especie en cada sitio muestreado (Legendre y Gallagher 2001). Los resultados así obtenidos corresponden a distancias Hellinger, que son apropiadas para este tipo de datos (Legendre y Legendre 2012) y fueron las elegidas también en PERMANOVA. Las distancias chi cuadrado, preservadas en el DCA, también son apropiadas para analizar los datos de composición de la comunidad vegetal, aunque dan bastante peso a las especies poco abundantes (Legendre y Legendre 2012).

Finalmente, dos análisis se usaron de manera puntual en los estudios I y III. En el estudio I, se calculó el valor de indicación de cada especie (Dûfrene y Legendre 1997) para detectar qué especies fueron características de la zona quemada durante el primer, segundo o tercer años, o de la zona control en su conjunto. Este valor combina una medida de la especificidad y de la fidelidad de cada especie por cada tipo de hábitat y se evaluó la significación de los resultados (p<0,05) mediante 1000 permutaciones. En el estudio III, para comparar la composición de especies entre los distintos tipos de dehesas de manera cualitativa (es decir, usando sólo datos de presencia/ausencia), se utilizó el índice de complementariedad de Colwell y Coddington (1994). Con él se calcula qué porcentaje del total de especies está presente sólo en uno de cada par de tipos de uso, por lo que sus valores van del 0% (todas las especies están presentes en ambos tipos de uso) al 100% (los usos no comparten ninguna especie).

Los análisis se llevaron a cabo usando principalmente software libre y gratuito, en particular R (R Core Team 2015), PERMANOVA (Anderson 2001) y EstimateS (Colwell 2006). En el estudio II se emplearon los programas Statistica 6.0 y Community Analysis Package III (CAP3).

PRINCIPALES RESULTADOS Y DISCUSIÓN

1. Efectos de las perturbaciones antrópicas

Las perturbaciones antrópicas estudiadas afectan de manera directa al suelo superficial y a los coleópteros, pero su efecto más evidente es sobre la estructura de la vegetación, que a su vez repercute en el resto de elementos del ecosistema. Tanto el fuego superficial como el desbroce mecanizado eliminan la gran mayoría del sotobosque, reduciendo la competencia y aumentando la insolación, lo que permite que proliferen las herbáceas anuales a corto plazo, hasta que los arbustos rebrotan y alcanzan valores altos de cobertura. El pastoreo limita la expansión del matorral en favor de las herbáceas, y supone una perturbación intermedia que proporciona espacios abiertos y gran variedad de microhábitats mientras se mantiene el uso extensivo. El abandono de los usos del suelo permite que la sucesión secundaria siga su curso y los arbustos invadan la dehesa en detrimento de las herbáceas y retengan la hojarasca procedente de los árboles.

1.1. Suelo

El incendio analizado en el estudio I fue de poca intensidad, por lo que tuvo un efecto poco marcado sobre el suelo superficial del bosque (Luis *et al*. 2000), y el fuego apenas redujo la cantidad de materia orgánica del suelo (Certini 2005). En cambio, tras el incendio aumentó el contenido en materia orgánica y fósforo, probablemente debido a la incorporación de restos parcialmente quemados al suelo y al aporte de nutrientes de las cenizas (Romanya *et al*. 1994, Sánchez *et al*. 1994, Johnson y Curtis 2001, Antunes *et al*. 2009). Por lo demás, el incendio no tuvo efectos claros en el suelo superficial y no se apreciaron otros patrones de respuesta importantes en sus características.

En el estudio II la proliferación de arbustos en las dehesas abandonadas afectó al reciclaje de nutrientes a través de la descomposición de la hojarasca y de la renovación de las raíces de los arbustos (Gallardo 2003, Moreno *et al*. 2007), lo que aumentó el contenido en calcio respecto a las dehesas pastadas. Por su parte, las dehesas desbrozadas tuvieron un mayor contenido en materia orgánica, nitrógeno y fósforo que las pastadas, lo que puede explicarse mediante el retorno de nutrientes procedentes de los restos del desbroce mecanizado. En las dehesas pastadas, la constante regeneración del pasto consume rápidamente los nutrientes del suelo (Otieno *et al*. 2011), mientras que en las desbrozadas el secuestro de nutrientes por parte de la vegetación, que ha sido recientemente cortada, es mucho menor. El retorno de nutrientes desde la materia en descomposición depende de las características del suelo, la calidad de los restos vegetales y de las condiciones climáticas (Serrada 1990), lo que puede verse reflejado incluso a pequeña escala como ocurre en el estudio IV.

En el estudio IV se observó que en las dehesas pastadas el suelo superficial es más rico en nutrientes bajo los árboles (con arbustos y sin ellos), intermedio bajo los arbustos dispersos y los montones de restos de poda y más pobre en los pastizales. El suelo bajo los árboles recibe nutrientes de muchas fuentes: de los excrementos del ganado y de pájaros, del flujo de agua interceptada que baja por el tronco del árbol ("stemflow"), del goteo de agua desde la superficie de las hojas al suelo ("throughfall"), de la hojarasca (Escudero *et al.* 1985, Vetaas 1992, Gallardo 2003, Gea-Izquierdo *et al.* 2010) y de la hierba en descomposición. Esto permite que el contenido de nutrientes en el suelo bajo los árboles sea muy elevado a pesar del secuestro de nutrientes por parte de las herbáceas, cuya producción primaria es a menudo tan elevada como en los pastizales (Rivest *et al*. 2013). En las dehesas pastadas la mayor parte de la hojarasca es desplazada por el viento hasta los arbustos y montones de restos de poda donde es retenida, aportando nutrientes a estos microhábitats a través de su descomposición. Como las hojas de roble son más difíciles de descomponer que la hierba (Begon *et al*. 2006) y la producción primaria en estos microhábitats es por lo general más baja (no hay herbáceas), los nutrientes se acumulan en el suelo superficial. En cambio, en los pastizales, el aporte de nutrientes al suelo proviene principalmente de las heces del ganado y de la hierba, que son más fáciles de descomponer que la hojarasca. Además, la descomposición en los pastizales se ve acelerada por los cambios más bruscos de humedad (Vetaas 1992, Köchy y Wilson 1997), mientras que en el resto de microhábitats estos cambios son amortiguados gracias a la protección de los árboles y/o la capa de hojarasca (Blanco Castro *et al*. 1997, Sayer 2005). Esto hace que en los pastizales los nutrientes regresen al suelo más rápidamente, pero la alta producción primaria recaptura esos nutrientes, dando lugar a un contenido bajo de nutrientes en el suelo.

1.2. Vegetación

Las perturbaciones antrópicas estudiadas afectaron tanto a la estructura de la vegetación como a la composición de especies de plantas. En el estudio I la cobertura vegetal disminuyó drásticamente tras el incendio, pero se recuperó rápidamente en el segundo y tercer años después del fuego, alcanzando valores incluso mayores que en las zonas no quemadas. Aunque las especies leñosas rebrotaron con rapidez, como es habitual en estos bosques (Luis y Tárrega 1993, Calvo *et al*. 1999), la momentánea disminución de la competencia permitió la proliferación de las herbáceas anuales, que germinaron desde el banco de semillas, probablemente estimuladas por el fuego (Keeley *et al*. 2005). El resultado fue una mayor cobertura y riqueza de especies herbáceas anuales en la zona quemada que en la control durante el segundo y tercer años tras el incendio, en concordancia con otros estudios (Trabaud y Lepart 1980, Casal *et al*. 1990, Bond y van Wilgen 1996, Calvo *et al*. 2002a).

En el estudio II, el ganado en las dehesas pastadas limitó la expansión de los arbustos, favoreciendo la proliferación de las herbáceas anuales y también de las perennes.

Sin embargo, la riqueza total de especies no difirió entre las dehesas abandonadas y las pastadas, ni a escala de punto de muestreo (riqueza alfa) ni de parcela (riqueza gamma), lo que coincide con los resultados de otros autores (Peco *et al*. 2005, 2006, Öckinger *et al*. 2006), a pesar de que el pastoreo extensivo suele favorecer la diversidad vegetal (Naveh y Whittaker 1979, Puerto *et al*. 1990, Montalvo *et al*. 1993, Bakker y Berendse 1999, Shackleton 2000, Poschlod *et al*. 2005, Acosta *et al*. 2006, Guretzky *et al*. 2007). Esta discrepancia de resultados puede deberse a que quizás los mecanismos de interacción entre las plantas y el ganado estén más desarrollados en los pastizales subhúmedos que en los semiáridos (Milchunas *et al*. 1998). Dentro de las dehesas pastadas, la variabilidad espacial de la vegetación (estimada por la riqueza beta) fue baja, probablemente porque el ganado dispersa las semillas de forma homogénea a través de sus heces (Peco *et al*. 2006). La riqueza beta, en cambio, fue mayor en las dehesas desbrozadas que en las pastadas, lo que puede deberse a diferentes mecanismos de regeneración de la vegetación, como ocurre en zonas donde el matorral se ha cortado experimentalmente (Calvo *et al*. 2002b).

Sí se encontraron diferencias entre las distintas formas de vida de las plantas, siendo mayor la riqueza y cobertura de herbáceas anuales en las dehesas pastadas que en las no pastadas, lo que coincide con otros estudios (McIntyre *et al*. 1995, Diaz *et al*. 2007, Guretzky *et al*. 2007, Tárrega *et al*. 2007), aunque discrepa con los resultados de Peco *et al*. (2005), que encontraron una riqueza de herbáceas anuales similar en dehesas pastadas y abandonadas. La riqueza de plantas leñosas y herbáceas perennes no difirió entre los tres tipos de dehesas, aunque la cobertura de leñosas sí fue mucho mayor en las dehesas abandonadas debido a la invasión de arbustos propia de la sucesión secundaria (Bakker y Berendse 1999, Gómez-Limón y de Lucio Fernández 1999, Peco *et al*. 2005, Poschlod *et al*. 2005; Öckinger *et al*. 2006, Maccherini *et al*. 2007). En las dehesas desbrozadas la cobertura de leñosas fue mayor (aunque no significativamente) que en las pastadas, gracias a la elevada capacidad de rebrote de los arbustos tras la corta (Calvo *et al*. 2002a, Maccherini *et al*. 2007).

Las dehesas pastadas y abandonadas también difirieron en composición de especies, coincidiendo con los resultados de otros autores (Peco *et al*. 2005, 2006, Öckinger *et al*. 2006). Las dehesas desbrozadas compartieron un 77% de especies con las dehesas abandonadas, probablemente debido al rápido rebrote de los arbustos tras el desbroce (Calvo *et al*. 2002a). Se podría esperar que la composición de la vegetación de las dehesas desbrozadas se asemejase más a las pastadas debido a que las condiciones de luz son similares entre ellas; sin embargo, las dehesas pastadas compartieron el mismo porcentaje de especies con las desbrozadas que con las abandonadas, sólo un 56%. Esto puede deberse a la escasez del banco de semillas de las dehesas desbrozadas, ya que las semillas de las herbáceas típicas de dehesas pastadas probablemente hayan muerto tras 20 años de abandono. De manera que es posible que el desbroce mecanizado no baste para restaurar las dehesas abandonadas (Maccherini *et al*. 2007) y que se requiera del restablecimiento del pastoreo extensivo para recuperar las características propias de la vegetación de las dehesas pastadas.

1.3. Carábidos y estafilínidos

Los cambios en la estructura de la vegetación debidos a las perturbaciones antrópicas tienen un fuerte efecto sobre la composición de los artrópodos del suelo, ya que alteran los recursos y las condiciones ambientales de los que estos dependen. Los carábidos son especialmente sensibles a las condiciones abióticas (Thiele 1977), entre las que destaca la cobertura del estrato arbóreo (Taboada *et al*. 2006b) y la abundancia de hojarasca en el suelo (Koivula *et al*. 1999); aunque también pueden verse influidos por la composición de la comunidad de plantas, ya que varias especies de carábidos incluyen semillas en su dieta o son exclusivamente granívoras (Honek *et al*. 2003). La composición de la fauna de estafilínidos depende en gran medida de las características de la capa de hojarasca, un medio que alberga una alta diversidad de especies (Bohac 1999, Thayer 2005, Mckenna *et al*. 2015), y de la presencia de otros recursos como son los excrementos (Skidmore 1991) o las setas (Newton 1984) sobre los que viven las especies coprófilas y micófilas respectivamente. La cobertura vegetal y sobre todo la hojarasca regulan el microclima cerca del suelo y generan condiciones ambientales favorables para los dos grupos de coleópteros, con menores fluctuaciones térmicas y una humedad elevada (Sayer 2005). Además, la hojarasca proporciona microhábitat y recursos para las presas de estos coleópteros, que son en su mayoría depredadores. El abandono de las prácticas tradicionales de gestión origina un aumento de la cobertura vegetal (Tárrega *et al*. 2007), mientras que las perturbaciones antrópicas la reducen, lo que afecta a la abundancia, la riqueza y la composición de especies de la fauna de coleópteros del suelo.

En el estudio I el incendio forestal consumió la mayor parte de la hojarasca y de la vegetación del sotobosque, causando efectos desiguales sobre los carábidos y los estafilínidos. Durante el primer año, la abundancia y la composición de especies de la fauna de carábidos no difirieron entre transectos quemados y control, quizás debido a la supervivencia de los carábidos al fuego o a la rápida recolonización de la zona incendiada desde las zonas no quemadas. Durante el segundo y tercer años, las comunidades de carábidos se fueron haciendo más diferentes entre transectos quemados y control, y aumentaron en abundancia y riqueza de especies. Esto se debió en parte a la afluencia de especies de zonas abiertas como las del género *Harpalus* en la zona quemada, que pudieron verse favorecidas por las condiciones más cálidas y secas después del incendio (Thiele 1977, Gongalsky *et al*. 2006) y por el aumento de la cobertura de las herbáceas anuales, que producen semillas de las que se alimentan (Honek *et al*. 2003). Por su parte, los estafilínidos no difirieron en abundancia o riqueza de especies entre la zona quemada y la zona control, pero sí en composición de especies. El incendio redujo la cobertura de hojarasca y pudo afectar negativamente a los hongos (Ahlgren 1974), perjudicando a las especies fitodetritícolas y micófilas, mientras que favoreció a las especies adaptadas a cazar activamente en zonas abiertas, como *Ocypus olens* y *Othius punctulatus*, y a las especies coprófilas como *Aleochara bipustulata*. Durante el segundo y tercer años, la recuperación de la cubierta vegetal y el aumento de la capa de hojarasca en la zona quemada devolvieron algunas de las características originales al medio, por lo que la composición de la fauna de estafilínidos se fue asemejando a la de la zona control.

En el estudio III los tres tipos de dehesas (pastadas, abandonadas y desbrozadas) presentaron distintas condiciones ambientales y recursos para la fauna de carábidos y estafilínidos. En las dehesas pastadas, la proliferación de las herbáceas anuales favoreció a los carábidos granívoros como los del género *Harpalus*, y la abundancia de heces de oveja a los estafilínidos coprófilos como *Anotylus inustus* y *Aleochara bipustulata*. Así, las dehesas pastadas fueron las más ricas en especies exclusivas (y en diversidad y riqueza total para los carábidos) y su composición de especies difirió de la de las dehesas abandonadas y desbrozadas. La composición de especies de los dos grupos de coleópteros en las dehesas abandonadas fue muy distinta, asemejándose más a la de los bosques circundantes (García-Tejero *et al*. datos no publicados; ver Taboada *et al*. 2006a). En estas dehesas, la diversidad de estafilínidos fue mayor que en las pastadas, tal vez por la mayor cobertura de hojarasca, un medio en el que los estafilínidos han evolucionado, diversificándose notablemente (Thayer 2005, Mckenna *et al*. 2015). Por su parte, en las dehesas desbrozadas se acumularon los restos de los arbustos cortados, lo que pudo representar un importante recurso para los artrópodos detritívoros como colémbolos y dípteros, favoreciendo a los depredadores oportunistas (Halaj y Wise 2002) como los carábidos *Carabus amplipennis*, *Nebria salina* y *Steropus globosus* o los estafilínidos *Liogluta longiuscula* y *Ocypus olens*. Aunque la abundancia de carábidos fue mayor en las dehesas desbrozadas, la riqueza y la diversidad de especies fueron menores que en las pastadas y abandonadas, pudiendo indicar que el desbroce mecanizado tiene efectos negativos sobre la diversidad de carábidos, como ocurre con las aves (Camprodon y Brotons 2006). Sin embargo, desde el punto de vista cualitativo (considerando sólo la presencia/ausencia de especies), las comunidades de carábidos y estafilínidos en las dehesas desbrozadas se parecieron más a las de las pastadas que a las de las abandonadas, indicando que, para estos insectos, el desbroce mecanizado puede ser un primer paso hacia la restauración de las comunidades características de las dehesas pastadas.

En el estudio IV se observó que algunos de los factores que afectan a la composición de especies de carábidos y estafilínidos a nivel de parcela, también lo hacen a una escala más pequeña, a nivel de microhábitat. Así, la composición de la fauna de carábidos fue muy diferente en los pastizales, donde las condiciones más cálidas y la presencia de herbáceas anuales favorecieron a especies granívoras (Thiele 1977, Saska 2008).

De manera similar, la composición de la fauna de estafilínidos difirió entre pastizales y árboles y el resto de microhábitats (arbustos dispersos, arbustos bajo árbol y montones de restos de poda): en los primeros abundan las heces de oveja que favorecen a las especies coprófilas, mientras que los últimos albergan especies adaptadas a la hojarasca. La acumulación de hojarasca en los arbustos y montones de restos de poda favoreció a la fauna de carábidos y estafilínidos de distintas maneras. Por un lado, los arbustos dispersos albergaron especies más grandes que cazan activamente en los pastizales, pero que requieren de piedras o vegetación espesa para protegerse (Coiffait 1974, Bohac 1999, Morris 2000, Brose 2003). En estos arbustos, la riqueza de especies de carábidos fue mayor que en los demás microhábitats (a excepción de los pastizales), lo que los hace destacar como estructuras clave (*sensu* Tews *et al*. 2004) para estos coleópteros. En los arbustos bajo árbol, la abundancia y la biomasa de carábidos fueron el doble que en los demás microhábitats, quizás porque en este microhábitat la combinación de hojarasca y sombra del árbol proporcionan un microclima más suave, pudiendo favorecer tanto a los carábidos como a sus presas (Koivula *et al*. 1999, Sayer 2005). La biomasa de estafilínidos también fue mayor en los arbustos bajo árbol, donde abundaron las especies de tamaño intermedio, si bien la composición de especies de estafilínidos fue muy similar en los tres microhábitats que retienen hojarasca. Por último, los montones de restos de poda presentaron características intermedias entre los arbustos dispersos y aquéllos bajo árbol, pudiendo contribuir a aumentar la superficie de hábitat óptimo para las especies de coleópteros adaptadas a la hojarasca.

2. Consideraciones para la conservación y gestión

Las perturbaciones antrópicas estudiadas (incendio forestal de superficie en un bosque maduro, y pastoreo, abandono de los usos del suelo y desbroce mecanizado tras el abandono en sistemas adehesados) tuvieron diferentes efectos sobre el ecosistema. Mientras que el fuego y el pastoreo contribuyeron a aumentar la diversidad de plantas y coleópteros, el abandono y el desbroce mecanizado afectaron negativamente a la diversidad. Los incendios de poca intensidad pueden ayudar a mantener la heterogeneidad espacial típica de la gestión tradicional a la que los ecosistemas de *Quercus pyrenaica* están adaptados (Tárrega *et al*. 2007, Hjältén *et al*. 2010). El incendio supone un cambio drástico en la estructura de la vegetación, lo que afecta al microclima y, con ello, a la fauna de carábidos y estafilínidos, y, además, reduce la competencia durante un breve periodo de tiempo, permitiendo que prolifere una diversa comunidad de plantas anuales y de carábidos granívoros que se alimentan de sus semillas. La rápida recuperación de la vegetación perenne gracias a su capacidad de rebrote tras el fuego hace que la composición de especies, particularmente la de plantas y estafilínidos, se asemeje notablemente a la del bosque control en tan solo dos años después del incendio. Se puede decir, por tanto, que un incendio de estas características, de superficie, poco extenso, de baja intensidad y de primavera, tiene efectos temporales de poca duración sobre el ecosistema, entre los que se incluyen cambios positivos como un aumento puntual de la diversidad de especies de plantas y de carábidos. Además, a una escala mayor, la presencia de zonas quemadas y sin quemar podría contribuir a aumentar la biodiversidad a nivel de paisaje, al mantener un mosaico de etapas sucesionales. Estas razones refuerzan la hipótesis de que un régimen apropiado de incendios puede tener efectos neutros e incluso positivos sobre la biodiversidad en ecosistemas adaptados a esta perturbación (Pausas 2012). Además, el fuego puede utilizarse de manera controlada como una herramienta de gestión para reducir el combustible del sotobosque y evitar incendios mayores (Baeza 2004). Estos aspectos deben considerarse dentro de una perspectiva muy concreta y es la de unos ecosistemas fuertemente influenciados por el hombre durante siglos, en los que el abandono de las prácticas tradicionales de gestión en las últimas décadas ha supuesto la proliferación del sotobosque y el consecuente aumento del riesgo de incendios más extensos y severos (San-Miguel-Ayanz *et al*. 2012, Hernández 2015).

El abandono de los usos del suelo, en cambio, conlleva la invasión de arbustos en la dehesa, resultando en un menor número de especies exclusivas, tanto de plantas como de carábidos y estafilínidos en las dehesas abandonadas que en las pastadas. Además, el abandono aumenta la homogeneidad a nivel de paisaje, ya que las condiciones ambientales y, con ellas, las comunidades de coleópteros pasan a asemejarse a las de los boques circundantes (García-Tejero *et al*. datos no publicados). La diversidad de coleópteros respondió al abandono de forma diferente para cada grupo: la diversidad de carábidos disminuyó, pero la de estafilínidos aumentó respecto a la de las dehesas pastadas. Los pastizales de las dehesas pastadas carecen de hojarasca porque la desplaza el viento, mientras que en las dehesas abandonadas ésta es retenida por los arbustos y por una vegetación herbácea más densa, lo que puede explicar la mayor diversidad de estafilínidos, dado que la hojarasca es un medio en el que habitan multitud de especies (Thayer 2005, Mckenna *et al*. 2015). Si en el estudio III se hubieran incluido los tres microhábitats que retienen hojarasca, posiblemente la diversidad de estafilínidos de las dehesas pastadas hubiera sido mayor, como se extrae de los resultados obtenidos en el estudio IV.

Esto remarca una vez más la importancia de los arbustos en las dehesas. Los resultados obtenidos indican que una carga ganadera moderada, que permita la presencia de pequeños arbustos dispersos y arbustos bajo algunos árboles, podría ser más beneficiosa que una explotación más intensiva que cause la homogenización del medio. Por otra parte, hay que destacar que el abandono de las dehesas puede resultar interesante para otros fines como la regeneración del arbolado (Plieninger *et al*. 2003, Canteiro *et al.* 2011), pero no para preservar a largo plazo el funcionamiento y la provisión de servicios de estos ecosistemas (Moreno *et al.* 2013), y puede que sea necesario mantener un mosaico de dehesas pastadas y abandonadas a nivel de paisaje para asegurar su viabilidad a largo plazo (Moreno y Pulido 2008, Ramírez y Díaz 2008).

Después de un periodo de abandono, las dehesas pueden restaurarse para recuperar su estructura original, siendo un primer paso el desbroce mecanizado del matorral. Sin embargo, los efectos inmediatos del desbroce suponen una disminución de la riqueza de plantas y de la riqueza y diversidad de carábidos. Además, los resultados obtenidos indican que el desbroce no es una práctica de gestión eficiente por sí sola para conseguir una composición de especies similar a la de las dehesas pastadas, aunque para carábidos y estafilínidos puede suponer un buen comienzo, ya que, desde un punto de vista cualitativo, sus comunidades empiezan a parecerse más a las de las dehesas pastadas. Por otro lado, desbrozar el matorral puede ser una práctica aconsejable para disminuir el riesgo de incendios al reducir el combustible disponible para el fuego, lo que puede completarse también a través del pastoreo (Baeza 2004). En cualquier caso, a la hora de llevar a cabo el desbroce mecanizado sería recomendable dejar sin cortar una cierta cantidad de arbustos dispersos para favorecer a la fauna local, por los motivos expuestos más arriba, y como ya recomiendan algunos manuales de gestión (Jiménez Fernández *et al*. 2006, Fernández de Córdoba Sanz y Montoya Oliver 2007). El desbroce debería complementarse con la introducción de una carga ganadera adecuada que limite la expansión del matorral, y que podría dispersar las semillas de las especies herbáceas desde las dehesas pastadas (Peco *et al*. 2006), ayudando a recuperar las condiciones previas al abandono. Si estas técnicas de gestión no se aplican tras el desbroce, el rápido rebrote de los arbustos, cuyas raíces sobreviven a la corta, conduciría a condiciones similares a las de las dehesas abandonadas en un breve periodo de tiempo (Calvo *et al*. 2002a).

Por otro lado, las dehesas pastadas destacaron por su riqueza de especies exclusivas y por la presencia de grupos funcionales particulares, además de por su heterogeneidad a pequeña escala, la cual potencia la diversidad de coleópteros. El pastoreo supone una perturbación intermedia mantenida a lo largo del tiempo, que favorece a la diversidad de especies (Huston 1994, Martins da Silva *et al*. 2008, Bergmeier *et al*. 2010). Además, el ganado limita la expansión de los arbustos y beneficia a las herbáceas anuales y perennes al dispersar sus semillas con las heces (Peco *et al*. 2006), que también contribuyen a fertilizar el suelo y mantener el pasto. A su vez, las semillas de las herbáceas favorecen a las especies de carábidos granívoros y los excrementos a las especies de estafilínidos coprófilos, resultando en un alto número de especies exclusivas de estos tres grupos taxonómicos en los pastizales de las dehesas pastadas.

Pero, para los coleópteros, la dehesa pastada es estructuralmente aún más compleja, ya que constituye un mosaico de microhábitats en el que cada uno aporta diferentes recursos y condiciones ambientales, permitiendo la presencia de distintas comunidades de especies dentro de la misma dehesa y aumentando con ello la riqueza de especies a pequeña escala (ver Moreno *et al.* en prensa) . Además, algunos microhábitats actúan como estructuras clave (*sensu* Tews *et al*. 2004) tanto para los coleópteros como para otros animales, como puede ser el caso de los arbustos dispersos. Los arbustos dispersos albergaron carábidos y estafilínidos depredadores de mayor tamaño, especies que cazan en espacios abiertos como el pastizal, pero requieren de pequeñas estructuras de mayor complejidad donde refugiarse. Los arbustos también han demostrado ser importantes para mariposas (Dover *et al*. 1997), reptiles (Martín y López 2002, Godinho *et al*. 2011), micromamíferos (Castién y Gosálbez 2001, Mariné *et al*. 2001) y aves (Hartel *et al*. 2014). En las dehesas pastadas, los arbustos bajo árbol destacaron por tener una abundancia y una biomasa de carábidos dos veces mayor que el resto de microhábitats, lo que puede beneficiar a niveles tróficos superiores, favoreciendo la conservación de la vida silvestre (Vickery *et al.* 2001, Woodcock *et al.* 2009), de gran importancia en las dehesas (Bugalho *et al*. 2011).

En las dehesas pastadas, los árboles aislados fueron importantes para los estafilínidos, que mostraron una composición de especies particular bajo su copa, más similar a la de los pastizales que a la del resto de microhábitats. Los árboles dispersos son también estructuras clave para aves y murciélagos (DeMars *et al*. 2010, Fischer *et al*. 2010) y la poda en trasmocho, tan común en las dehesas, promueve la creación de oquedades en el tronco, lo que favorece a las aves que anidan en cavidades preexistentes (Robles *et al*. 2011) y a los insectos saproxílicos (Sebek *et al*. 2013). Además, los montones de restos que surgen de la poda contribuyen a aumentar la superficie de microhábitat disponible para los coleópteros que viven en la hojarasca, aunque es posible que su aportación a la conservación de la fauna de artrópodos sea relativa (Kirby 1992). Todos estos resultados enfatizan el alto valor de conservación que tienen las dehesas y otros pastos arbolados y la importancia de mantener la gestión tradicional para preservarlos (Bergmeier *et al*. 2010, Bugalho *et al*. 2011, Plieninger *et al*. 2015).

CONCLUSIONES

Los resultados de la tesis confirman la utilidad de los carábidos y los estafilínidos para evaluar los cambios producidos por las perturbaciones antrópicas. Estos cambios influyen en los recursos y condiciones ambientales del ecosistema, produciendo respuestas cuantificables en las comunidades de plantas y coleópteros, y confirmando a estos últimos como buenos bioindicadores de las alteraciones del hábitat (Bohac 1999, Rainio y Niemelä 2003, Taboada Palomares 2007). Los dos grupos de coleópteros estudiados respondieron principalmente a los cambios en la estructura de la vegetación, particularmente a la cobertura y profundidad de la capa de hojarasca y a la cobertura del estrato arbóreo. Ambos factores modifican las condiciones microclimáticas, que determinan en gran medida la composición de especies de carábidos y estafilínidos y de otros artrópodos del suelo (ver Thiele 1977, Sayer 2005). El análisis de la importancia de la heterogeneidad de microhábitats en las dehesas pastadas demostró que los coleópteros responden a cambios en estas condiciones ambientales incluso a escalas muy pequeñas. Aunque no se estudió su efecto de manera directa, los carábidos y los estafilínidos también se vieron afectados por la presencia de herbáceas anuales y las heces del ganado, que suponen nuevos recursos para estos dos grupos de coleópteros. Un aumento de la cobertura de herbáceas anuales uno y dos años después del incendio y la considerable cobertura de las mismas en las dehesas pastadas permitió la presencia de carábidos granívoros. De la misma manera, los excrementos de oveja en pastizales y bajo los árboles en las dehesas pastadas atrajeron a estafilínidos coprófilos.

Cada perturbación antrópica tiene efectos diferentes sobre el ecosistema, y actúa a distintas escalas espaciales y temporales. Así, el fuego y el desbroce mecanizado reducen drásticamente la biomasa del sotobosque y devuelven nutrientes al suelo a partir de los restos vegetales, pero los cambios que producen en la estructura de la vegetación duran poco tiempo debido al avance del proceso de sucesión secundaria. El abandono de los usos del suelo es precisamente el resultado de esta sucesión, con la consiguiente invasión de matorral, mientras que el pastoreo detiene este proceso y supone una perturbación intermedia que favorece la diversidad y permite una alta heterogeneidad ambiental dentro de las dehesas.

Los cambios que producen el fuego y el desbroce mecanizado son a corto plazo y similares en algunos aspectos. El fuego redujo temporalmente la competencia y permitió que proliferasen algunos grupos funcionales que se ven desplazados en el bosque maduro, como las herbáceas anuales, los carábidos granívoros y algunos estafilínidos que cazan activamente en zonas abiertas. Estos cambios son de poca duración y dos años después del incendio la estructura de la vegetación y la composición de las comunidades de plantas y estafilínidos ya se aproximaban a las de las zonas no quemadas. El desbroce mecanizado también favoreció en parte a las herbáceas anuales, y, aunque produjo un aumento en la abundancia de carábidos y estafilínidos, su diversidad disminuyó con respecto a la de las dehesas abandonadas. Aunque la composición de especies fue diferente entre dehesas desbrozadas y pastadas para plantas y carábidos, desde un punto de vista cualitativo (considerando sólo la presencia o ausencia de las especies), el desbroce permitió que ambas comunidades se asemejaran más a las de las dehesas pastadas. Por lo tanto, desbrozar el matorral puede ser un primer paso para la restauración de las dehesas abandonadas, aunque resulta insuficiente si no se complementa con el mantenimiento de las prácticas tradicionales de gestión, en concreto el pastoreo extensivo.

En las dehesas abandonadas, la proliferación de los arbustos no implicó una disminución de la riqueza de especies de plantas, pero sí de la abundancia y la diversidad de carábidos con respecto a las dehesas pastadas, y una composición diferente de especies de plantas y estafilínidos. Además, las dehesas pastadas albergaron numerosas especies exclusivas de plantas y coleópteros, incluyendo grupos funcionales escasos en otras dehesas como los carábidos granívoros y los estafilínidos coprófilos. Sólo la diversidad de estafilínidos resultó mayor en las dehesas abandonadas, probablemente debido a la acumulación de hojarasca en estas dehesas, que es retenida por los arbustos y una vegetación herbácea más densa. Sin embargo, en términos generales, se podría considerar que el abandono supone una disminución del valor de conservación de las dehesas, ya que contribuye a que la composición de especies de coleópteros se parezca más a la de los bosques circundantes, disminuyendo la diversidad a escala de paisaje. Estos son algunos de los motivos para promover la conservación de las dehesas pastadas mediante el mantenimiento de la gestión tradicional, aunque permitir el abandono cada cierto tiempo puede ser necesario para asegurar la regeneración del arbolado y su persistencia a largo plazo (Moreno y Pulido 2008, Ramírez y Díaz 2008).

Los microhábitats principales de las dehesas, los pastizales y los árboles aislados, son el resultado de la gestión tradicional mantenida durante siglos mediante pastoreo, poda y desbroce manual. Sin embargo, la disminución del uso de las dehesas en las últimas décadas ha permitido la proliferación de microhábitats que resultarían más escasos con cargas ganaderas mayores y con un mantenimiento más exhaustivo. Es el caso de los arbustos, tanto dispersos como bajo árbol, y de los montones de restos de poda, que acumulan la hojarasca arrastrada por el viento, impidiendo que este recurso se pierda para el ecosistema, y aportando nutrientes para los grupos de artrópodos detritívoros, que pueden servir de presas para la fauna de carábidos y estafilínidos. Los resultados obtenidos mostraron que la diversidad de microhábitats permite que, dentro de la misma dehesa, se encuentren especies de zonas abiertas y especies que habitan en la hojarasca, destacando particularmente los estafilínidos a este respecto. Además, los arbustos sirvieron de refugio para depredadores de mayor tamaño que cazan activamente, tanto carábidos como estafilínidos, confirmándose como estructuras clave dentro de la dehesa para estas especies, como probablemente también lo son para algunos de sus depredadores (reptiles, micromamíferos), lo que remarcaría su valor para preservar la elevada biodiversidad de las dehesas. Los arbustos bajo árbol también fueron importantes para los coleópteros y destacaron por la abundancia y la elevada biomasa de carábidos, subrayando el papel de las estructuras clave, resultado de una gestión tradicional de intensidad moderada (Diacon-Bolli *et al*. 2012), para el mantenimiento de la biodiversidad en los pastos arbolados (Hartel *et al*. 2014).

A lo largo de la tesis se defienden los beneficios de la gestión tradicional para promover la biodiversidad en ecosistemas de *Quercus pyrenaica*. Sin embargo, esta recomendación debe tomarse dentro de un contexto específico, que son las masas de melojar donde las intervenciones humanas han tenido lugar durante siglos y que se muestran resilientes a las mismas. Además, el uso humano debe ser moderado, puesto que ha sido la presión excesiva y prolongada la que ha conducido a la degradación en la que se encuentran actualmente muchas de las masas forestales de melojo (Blanco Castro *et al*. 1997, Consejería de Fomento y Medio Ambiente 2002). En las masas forestales maduras y bien conservadas, la gestión silvícola debería estar orientada a la preservación de las características del bosque natural a fin de mejorar las estructura del bosque y favorecer a los especialistas forestales, desde los carábidos (Taboada

Palomares 2007) al urogallo cantábrico (González *et al*. 2012). De este modo, los beneficios del fuego pueden ser discutibles, ya que trasladan al ecosistema a fases tempranas de la sucesión secundaria, alejándolo de su fase clímax, si bien los cambios pueden durar poco en el tiempo, sobre todo si el incendio es superficial y poco intenso. Por otra parte, las ventajas de la gestión tradicional para la conservación de las dehesas pastadas están considerablemente respaldadas por la numerosa bibliografía aparecida en las dos últimas décadas. Esta tesis confirma este argumento desde una perspectiva diferente, tomando como organismos modelo de estudio a carábidos y estafilínidos, y respalda la idea de que un uso antrópico moderado puede potenciar aún más la heterogeneidad espacial a pequeña escala y la biodiversidad en las dehesas y en los pastos arbolados en general.

AGRADECIMIENTOS

A todos los que habéis contribuido a hacer esta tesis posible y en especial a mis directores, Ángela Taboada, Reyes Tárrega y José María Salgado.

A la Junta de Castilla y León por concederme una ayuda para la formación de personal investigador y a mis directores un proyecto de investigación (Ref. LE008A06) con los que pudimos sufragar estos estudios.

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COMMUNITY ECOLOGY 14(1): 110-120, 2013
1585-8553/$20.00 © Akadémiai Kiadó, Budapest
DOI: 10.1556/ComEc.14.2013.1.12

Differential responses of ecosystem components to a low-intensity fire in a Mediterranean forest: a three-year case study

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Keywords: Carabids, Plant community, *Quercus pyrenaica* forest, Staphylinids, Topsoil, Wildfire.

Abstract: Mediterranean forests are especially prone to fire, a periodic disturbance that affects all the ecosystem components in different ways. Gathering knowledge on the particular responses and rate of recovery of multiple ecosystem components following a wildfire is crucial to reliably evaluate its consequences on biodiversity. Using eight sampling transects, we studied the changes in four ecosystem components (topsoil, plants, carabids, and staphylinids) during three years after a spring wildfire in a *Quercus pyrenaica* forest; and compared them with the surrounding unburnt forest (hereafter control). We found great variety of responses to fire suggesting each component may deal with this recurring disturbance via different adaptations, and that the time spent to recover to pre-disturbance conditions depends on the group of focus. Topsoil characteristics were highly variable and minor differences were found between burnt and control transects. Plant community was considerably affected by fire but rapidly recovered exceeding the control forest in species richness and cover, partly due to proliferation of annual herbs. However, plant species composition differed between burnt and control forests during the whole study period. Carabid beetles were more abundant and richer in species in the burnt forest, thanks to the arrival of seed predators favoured by post-fire drier and warmer conditions. Staphylinid beetle composition differed between control and burnt transects during the whole period, although their abundance was strongly variable. Distinct post-fire plant, carabid and staphylinid species composition suggests scattered low-intensity wildfires in this region may help to maintain habitat heterogeneity benefiting biodiversity at the landscape scale.

Abbreviations: B–Burnt transect; C–Control transect; GLMM–Generalised linear mixed model; PCA–Principal components analysis; PERMANOVA–Permutational multivariate analysis of variance; RDA–Redundancy analysis.

Introduction

The Mediterranean climate is characterised by a drought period of at least two months during the summer season (Blondel and Aronson 1999). These warm and dry conditions, together with fuel accumulation, make Mediterranean ecosystems extremely prone to fire, a recurring disturbance that has shaped these landscapes for centuries (Trabaud 1987, Naveh 1994). Frequent fires have especially affected the areas covered by the Pyrenean oak, *Quercus pyrenaica*, an ecosystem almost restricted to the Iberian Peninsula (Costa et al. 1998) which may form mature forests but that is usually reduced to an immature and dense stage due to strong and repeated human activities (i.e., fire, clear-cutting, thinning, and livestock grazing) (Luis et al. 2000). These disturbances create an oak mosaic landscape with a haphazard distribution of patches subjected to different historical events that should be taken into account when investigating the responses of this ecosystem to perturbation. In *Q. pyrenaica* forests, several studies have been conducted on the vegetation response (Tárrega and Luis 1989, Calvo et al. 1991, 1999, Luis and Tárrega 1993) and on the soil changes (Marcos et al. 1995, Tárrega et al. 1996) after fire. However, there hardly are studies on insect responses to fire (García-Villanueva et al. 1998) and none that considers all these ecosystem components together.

Wildfires have been found to affect the components of the ecosystem in different ways. At the topsoil layer, ashes tend to increase pH values and the amount of available nutrients (Debano et al. 1977, Marcos et al. 1995, Antunes et al. 2009), especially during the first months after fire. Besides, soil organic matter content can be either increased or diminished, depending on fire intensity (Luis et al. 2000). Soil microbiology may also be affected by fire, in terms of biomass, diversity and activity (Mataix-Solera et al. 2009). In some cases, strong transformations suffered after fire impede proper soil functioning, whereas in others, only the aboveground parts of plants are affected, fertilizing the soil and changing the trophic position of some elements sequestered by the vegetation (Cerdá and Mataix-Solera 2009). In any case, the changes and the speed of recovery depend to a great extent on the characteristics of the fire and on the previous conditions of each specific ecosystem (Marcos et al. 1995, Tárrega et al. 1996, Certini 2005) and may be very variable due to the multiple factors that take part in wildfires (Cerdá and Mataix-Solera 2009).

Changes in the topsoil features after fire may further affect plant communities that usually exhibit high resilience and recover by autosuccession (Hanes 1971) (i.e., the species present after fire are the same ones that already occupied the area as they are adapted to survive or regenerate fast) (Keeley 1986, Trabaud 1987, Luis et al. 2000). Although direct succession is not the only trend in the Mediterranean Basin (Rodrigo et al. 2004, Pausas et al. 2008), it is the case in *Q. pyrenaica* forests, where the majority of woody species resprout after fire (Tárrega and Luis 1989, Calvo et al. 1991, Luis and Tárrega 1993, Tárrega et al. 1996, Álvarez et al. 2009). Woody resprouters are the first to start the vegetation recovery as they do not require rain as seeders do (Trabaud 1987, Buhk et al. 2007). However, meanwhile resprouters spread out, annual and perennial herbs increase in richness and abundance, reaching a maximum one year after fire (Luis and Tárrega 1993, Calvo et al. 1999).

Insects may be affected either by the direct effects of fire (i.e., heat and oxygen depletion) or indirectly through changes in soil characteristics and vegetation structure (Wikars and Schimmel 2001). Carabid (Coleoptera: Carabidae) and Staphylinid (Coleoptera: Staphylinidae) beetles have been commonly studied as environmental indicators due to their sensitivity to changes in vegetation structure, climate and microclimate (Bohac 1999, Rainio and Niemelä 2003). The majority of carabid beetles are generalist predators, but many others complement their diet with seeds or are specialised granivores (Honek et al. 2003, and references therein). In the same way, although some staphylinid beetles feed on fungi or pollen, the majority are also predators (Bohac 1999) and many are adapted to ephemeral microhabitats such as carrion, dung, rotting plants and fungi, where they mainly feed on fly larvae and other small arthropods (Muona and Rutanen 1994). In general, the response of carabids and staphylinids to fire mainly includes changes in species composition and richness (Holliday 1991, Ghandi et al. 2001, Hjältén et al. 2010, Samu et al. 2010). Despite carabid and staphylinid beetle response to fire has been extensively studied in boreal forests (Holliday 1991, Gandhi et al. 2001, Buddle et al. 2006, Gongalsky et al. 2006, Hjältén et al. 2010), little is known in Mediterranean ecosystems (Pryke and Samways 2012), particularly for staphylinid beetles (García-Villanueva et al. 1998). Moreover, to our knowledge this is the first time that the effects of fire on staphylinid beetles are studied at the species level in a Mediterranean ecosystem.

In this study we intended to compare the responses of four ecosystem components (namely topsoil properties, plant community, and carabid and staphylinid beetle assemblages) to a wildfire in a *Q. pyrenaica* forest during the first three years of post-fire recovery, with reference to the surrounding unburnt forest. We expected all the ecosystem components to have a high adaptation and resilience to fire since it is a recurrent disturbance in this ecosystem. Although all the ecosystem components were predicted to rapidly return to pre-fire conditions, we hypothesised that the speed and dynamics of recovery would differ between them according to their particular characteristics.

Materials and methods

Study area

The study was conducted in the *Q. pyrenaica* oak mosaic landscape located in León province, Spain (42° 50’ N, 5° 10’ W), at an altitude between 1110 and 1230 m a.s.l. on siliceous soils. Mean annual temperature is 9.8 °C (mean of the coldest month: 2.2 °C; mean of the warmest month: 18.2 °C). Mean annual precipitation is 1009 mm and a dry period, characteristic of the Mediterranean climate, occurs in July and August.

A wildfire took place in May 2006 burning a patch of 13 ha in a 55 ha mature oak forest (mean tree height = 7 m, mean tree perimeter = 34 cm). Fire destroyed the understorey but most of the aboveground part of trees survived although their canopy was sharply decreased. Since forest fires are unpredictable and scarce in the region, this study was conducted on a single burnt patch and its surroundings as it is usual in this kind of research (e.g., Holliday 1991, Ukmar et al. 2007, Fattorini 2010, Samu et al. 2010, Elia et al. 2012). One month after the fire, four transects 50 m long and at least 75 m apart were placed in the burnt patch (B1, B2, B3, and B4; Fig. 1). Four unburnt transects (C1, C2, C3, and C4; hereafter control transects) of the same length were located in the surroundings, two at each side of the burnt patch (Fig. 1) in order to retrieve the likely spatial variability caused by past management practices. Transects followed the direction of the slope (ca. 15%) and were spatially close in order to reduce the heterogeneity of habitat characteristics and to highlight variability due to year. Aspect was southern in B1, B2 and B4, eastern in B3, south-eastern in C1and C2, and south-western in C3 and C4 (see Fig. 1).

Sampling methods

For topsoil analyses, we took the first five centimetres of soil from five evenly spaced samples along each transect. Samples were homogenised to get a uniform sample for each transect, which was air-dried and passed through a 2 mm mesh sieve for later analysis. Topsoil pH, organic matter content (O.M.), total nitrogen (N), C/N ratio and available phosphorus (P), calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and sodium (Na^+) were determined for each sample, following the official methods of topsoil analysis (M.A.P.A. 1994). Vegetation and beetles were sampled at three equidistant sampling points, 25 m apart, along transects. At each point, cover of every plant species was visually estimated in three 1 m^2 quadrats, arranged in a regular triangle and spaced out a metre from each other. Plant species follow the nomenclature in Flora Europaea (see Appendix 1). To study the effect of habitat structure on beetle species composition, the percentage cover of bare soil, litter, lower (<0.5 m height),

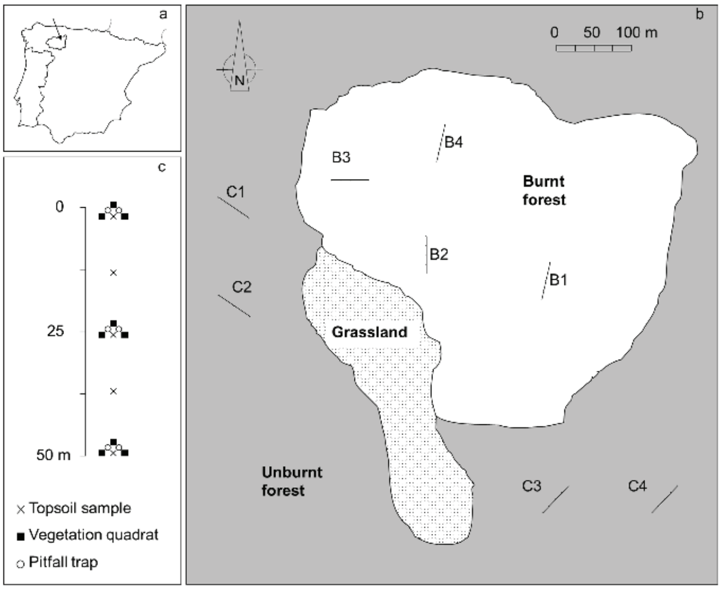

Figure 1. Details on the sampling design: (a) location of the study area; (b) location of burnt (B1, B2, B3, and B4) and control (C1, C2, C3, and C4) transects; and (c) layout of the eight 50 m transects used to sample topsoil, vegetation and carabid and staphylinid beetles.

medium (0.5-2 m) and upper (>2 m) vegetation layers were visually estimated, and litter depth was measured at each sampling quadrat. For collecting beetles, we used plastic pitfall traps (depth 86 mm, diameter 60 mm) covered by 10 cm × 10 cm roofs and partly filled with 25% propylene glycol. Two pitfall traps (0.5 - 2 m apart) were placed at each sampling point (48 traps in total) and emptied on a 20-day basis. Beetles were identified using standard keys, and we adopted the nomenclature in current species catalogues (listed in Appendix 1). All carabids and the great majority of staphylinids (99.5%) were identified to species level; those which could not be assigned to any species (14 individuals) were excluded from the study.

Sampling was carried out from 2006 to 2008: topsoil samples were collected in September, vegetation samples in July and beetles were captured from June to October. Trap loss was very low, accounting only 2.8% of the total trapping days. Pitfall catches reflect beetle activity-density (Thiele 1977, Thomas et al. 2006) that will be referred hereafter as abundance or number of individuals. To work with the data, vegetation cover estimates were averaged and beetle capture was pooled for each transect and sampling year; this yielded four replicates for each treatment (burnt, control) and sampling year (2006, 2007, and 2008) for topsoil, vegetation, carabids, and staphylinids.

Data analysis

To analyse the differences between levels of factor treatment (burnt and control) and factor year (2006, 2007, and 2008) and their interaction for the response variables, generalised linear mixed models (GLMMs) were performed using the following error distributions: Gaussian for topsoil variables, Poisson for vegetation and beetle species richness, quasi-Poisson for percentage cover of vegetation as a whole and for the different plant life forms (i.e., annual herbs, perennial herbs, and woody species), and negative binomial for beetle abundances. Treatment and year were modelled as fixed factors and transect identity as a random factor. The log number of trapping days was included as an offset term in the beetle abundance models to account for trap losses in the field.

Multivariate ordination methods were used to study multiple variables at a time. Principal components analysis (PCA) was used for topsoil variables and plant and beetle species composition. Redundancy analysis (RDA) was used to relate beetle species composition with habitat structure variables. Appropriate transformations were applied prior to PCA and RDA analyses. Topsoil variables were scaled to unit variance in order to give the same weight to all of them. Vegetation cover and beetle abundance were Hellinger-transformed to reduce the influence of extreme values and the effect of the double-absences in the data matrix (Legendre and Gallagher 2001). Applying Hellinger transformation makes PCA and RDA to preserve Hellinger distances (instead of the usual Euclidean distances) which are ecologically meaningful and appropriate for species composition data (Legendre and Gallagher 2001). Although all species were used in the multivariate analyses, only the most characteristic ones are represented in the ordination graphs for better clarity. Explanatory variables included in the RDA were chosen using step-wise forward selection. Variables were selected one by one when significant ($p<0.05$) according to their contribution to the model (i.e., the variables which increased most the R^2 of the model were first selected). Significance was tested at each step using 10000 permutations.

In order to look for compositional differences between treatments, permutational multivariate analyses of variance (PERMANOVA) were performed. This method, equivalent to a classic multivariate analysis of variance (MANOVA), allows the use of any dissimilarity measure and is suitable for count data when the number of species exceeds the number of sites (Anderson 2001). Monte Carlo asymptotic p values were used to assess differences, as suggested by Anderson (2005) when the number of replicates is low. PERMANOVA analyses were performed separately for each year. We used the same dissimilarity measures preserved in the ordination methods, namely Euclidean distances for topsoil and Hellinger distances for vegetation and beetles. Distances were transformed to ranks prior to the analysis to make the method more robust (Anderson 2005) and 10000 permutations were used for the tests.

Indicator value analysis (Dufrêne and Legendre 1997) was used on vegetation, carabid and staphylinid data to detect the species characteristic of burnt forest for each sampling year (2006, 2007, and 2008) and of control forest as a whole. Monte Carlo permutation tests with 1000 permutations were used to assess statistical significance. Results are reported in the Appendix 2 and only those species which significantly responded to the indicator value analysis are cited in the PCA results and discussion.

Statistical analyses were carried out with R statistical software (R Development Core Team 2012) using the 'MASS' (glmmPQL function), 'vegan' and 'LabDSV' packages, and with PERMANOVA (Anderson 2005).

Results

Topsoil features

Fire effects on the topsoil characteristics were not marked (Tables 1 and 2). Mean pH values decreased significantly the third year in the burnt transects. Organic matter content increased with time in both treatments, more markedly in control than in burnt transects, rendering a significant interaction term. P consistently increased with time in both treatments. Finally, N was maximum the second year in burnt transects and the third year in the control ones, while K^+ decreased over time in burnt transects and it increased in the control ones, giving significant interaction terms between factors treatment and year (Tables 1 and 2).

The first two axes of the PCA represented 58.3% of the total variance and did not clearly separate burnt from control transects (Fig. 2a). The temporal trend was more obvious for control transects, with the third year samples linked to the highest values in organic matter content, N, Ca^{2+}, K^+, and Na^+, and the first year samples related to their lowest values. Generally, consecutive sampling years of the same transect clustered apart in the graph, except for C4 transect, which accounted for the highest Mg^{2+} values. Finally, B2 transect stood alone in the figure and was linked to the highest values in pH and P. PERMANOVA results agreed with the observed PCA pattern since multivariate differences between treatments were only found in 2006 (Table 3).

Plant community

A total of 84 species were found, 62 in the burnt and 69 in the control transects. In general, only annual herb richness and cover and perennial herb richness were significantly different between burnt and control transects (Table 2, Fig. 3a, b). However, time and its interaction with treatment had a big effect on all plant life forms richness and cover, rendering significant results for all of them. In general, richness and cover were lowest in burnt transects during the first year. However, shortly afterwards, they strongly increased, even outnumbering the results from control transects where plant

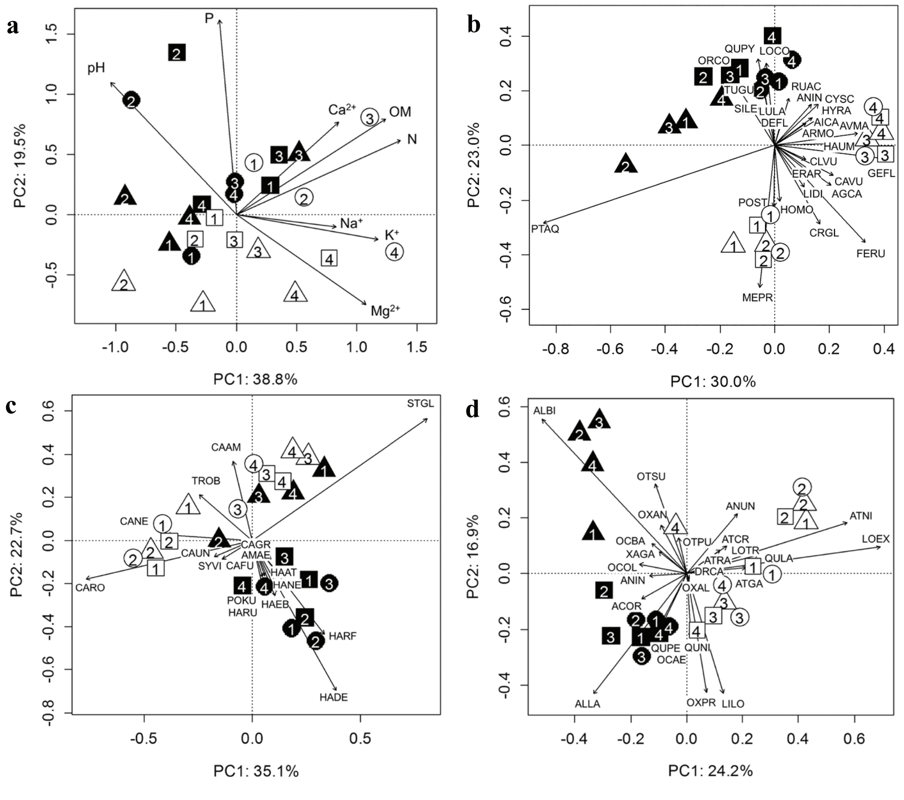

Figure 2. PCA graphs for (**a**) topsoil variables and (**b**) vegetation, (**c**) carabid, and (**d**) staphylinid species composition. Treatment and year are indicated by symbol colour and shape, respectively: black symbols (burnt) and white symbols (control); triangles (2006), squares (2007), and circles (2008). Transect number is indicated inside each symbol. Variance represented by each axis is specified in the axis legend. For vegetation, carabid and staphylinid plots, only the most frequent, abundant or representative species are shown with their names abbreviated by four letters (see Appendices 3, 4 and 5 for species correspondences).

Table 1. Mean and standard deviation (in parentheses) values (four replicates) of topsoil variables in the burnt (B) and control (C) transects.

	B-06	C-06	B-07	C-07	B-08	C-08
pH	5.82 (0.32)	5.36 (0.18)	5.82 (0.40)	5.52 (0.22)	5.49 (0.26)	5.26 (0.21)
O.M. (%)	5.64 (1.58)	5.62 (1.10)	6.93 (0.62)	5.99 (0.70)	6.27 (1.28)	8.73 (2.40)
Total N (%)	0.21 (0.04)	0.20 (0.05)	0.25 (0.05)	0.20 (0.05)	0.22 (0.04)	0.26 (0.05)
C/N	15.70 (1.57)	17.01 (2.00)	16.17 (1.78)	17.49 (2.17)	16.96 (1.53)	19.34 (2.85)
Ca^{2+} (cmol/kg)	4.10 (1.03)	4.26 (0.91)	4.51 (1.86)	4.58 (0.88)	3.47 (0.33)	5.10 (0.73)
Mg^{2+} (cmol/kg)	1.04 (0.33)	1.70 (1.28)	0.93 (0.17)	1.51 (1.10)	0.85 (0.85)	1.59 (0.97)
K^{+} (cmol/kg)	0.54 (0.13)	0.47 (0.09)	0.47 (0.10)	0.49 (0.08)	0.46 (0.04)	0.62 (0.02)
Na^{+} (cmol/kg)	0.02 (0.01)	0.02 (0.01)	0.05 (0.02)	0.06 (0.02)	0.02 (0.01)	0.06 (0.06)
P (mg/kg)	5.13 (1.01)	0.79 (0.34)	7.10 (2.76)	3.50 (0.97)	8.80 (5.46)	6.99 (1.82)

Table 2. Generalised linear mixed model (GLMM) results (*F* test and *p* value) contrasting treatment, sampling year and their interaction term for the topsoil properties, total plant and life-form (woody, perennial and annual herb) species richness and percentage cover, and total carabid and staphylinid beetle species richness and overall abundance. Error distributions used in the models: Gaussian for topsoil properties, Poisson for plant and beetle species richness, quasi-Poisson for plant cover and negative binomial error distribution for beetle abundance. p values smaller than 0.05 are in bold face. Standard deviations (SDs) of the random effects (plot and residual) are also given. O.M. = organic matter content.

	Fixed effects						Random effects	
	Treatment		Year		T x Y		Plot	Residual
	F	*p*	*F*	*p*	*F*	*p*	SD	SD
pH	3.5	0.110	10.9	**0.002**	1.8	0.210	0.207	0.113
O.M. (%)	0.4	0.538	5.5	**0.020**	4.8	**0.029**	0.735	0.981
Total N (%)	0.0	0.838	3.3	0.074	4.8	**0.030**	0.030	0.027
C/N	2.3	0.184	2.8	0.102	0.3	0.744	1.108	1.368
Ca^{2+} (cmol/kg)	1.4	0.277	0.3	0.739	1.7	0.217	0.429	0.814
Mg^{2+} (cmol/kg)	1.3	0.291	2.3	0.145	0.5	0.645	0.687	0.141
K^{+} (cmol/kg)	0.9	0.382	1.1	0.363	4.1	**0.043**	0.032	0.066
Na^{+} (cmol/kg)	2.9	0.140	3.2	0.076	1.9	0.190	0.000	0.022
P (mg/kg)	5.6	0.056	8.9	**0.004**	0.6	0.583	1.179	1.989
Total plant species richness	0.0	0.922	38.7	**< 0.001**	47.4	**< 0.001**	0.126	0.490
Woody species richness	0.1	0.749	9.1	**0.004**	10.1	**0.003**	0.226	0.288
Perennial herb richness	18.7	**<0.001**	15.0	**< 0.001**	14.9	**< 0.001**	0.059	0.512
Annual herb richness	7.5	**0.034**	13.8	**< 0.001**	25.5	**< 0.001**	0.367	0.505
Total plant cover (%)	0.3	0.605	20.2	**< 0.001**	50.0	**< 0.001**	0.074	1.473
Woody species cover (%)	0.0	0.923	15.2	**< 0.001**	18.6	**< 0.001**	0.257	1.477
Perennial herb cover (%)	0.0	0.958	13.4	**< 0.001**	33.9	**< 0.001**	0.209	1.233
Annual herb cover (%)	10.0	**0.019**	2.8	0.100	6.8	**0.011**	0.207	1.049
Carabid species richness	22.8	**0.003**	1.8	0.207	3.0	0.088	0.156	0.414
Carabid abundance	20.3	**0.004**	4.9	**0.028**	11.7	**0.002**	0.183	1.281
Staphylinid species richness	1.1	0.329	7.5	**0.008**	2.0	0.175	0.202	0.550
Staphylinid abundance	3.2	0.125	8.7	**0.005**	0.1	0.922	0.460	1.218

richness and cover hardly changed through time (Fig. 3a, b). While perennial and woody plant richness and cover steadily increased through time, reaching their peak on the third year, annual plant richness and cover reached their maxima on the second year and decreased after that.

The first two axes of the PCA graph (Fig. 2b) represented 53.0% of the total variance and depicted burnt transects clustering apart from control ones which formed two groups (C1 with C2, and C3 with C4) and hardly changed over time; on the other hand, burnt transects varied over time to a greater extent. In control transects, perennial herb species abounded, such as *Agrostis capillaris*, *Cruciata glabra, Festuca* gr. *rubra* or *Potentilla sterilis*; a small number of annual herbs such as *Melampyrum pratense* were abundant too (Appendices 2 and 3). The burnt transects hosted very few species in the first year (Fig. 2b) but several annual herbs, such as *Andryala integrifolia, Ornithopus compressus, Silene* sp. or *Tuberaria guttata*, perennial herbs such as *Lotus corniculatus*

Table 3. PERMANOVA results for topsoil (Euclidean distances), vegetation, carabids and staphylinids (Hellinger distances). Analyses were conducted separately for each year. *F* statistic and *p* values are given. *p* values smaller than 0.05 are in bold face.

	Topsoil	Vegetation	Carabids	Staphylinids
2006				
F	16.62	13.53	1.07	24.86
p	**0.005**	**0.012**	0.367	**0.004**
2007				
F	3.45	18.13	5.51	5.99
p	0.061	**0.006**	**0.033**	**0.026**
2008				
F	1.14	5.82	12.40	17.83
p	0.349	**0.028**	**0.009**	**0.004**

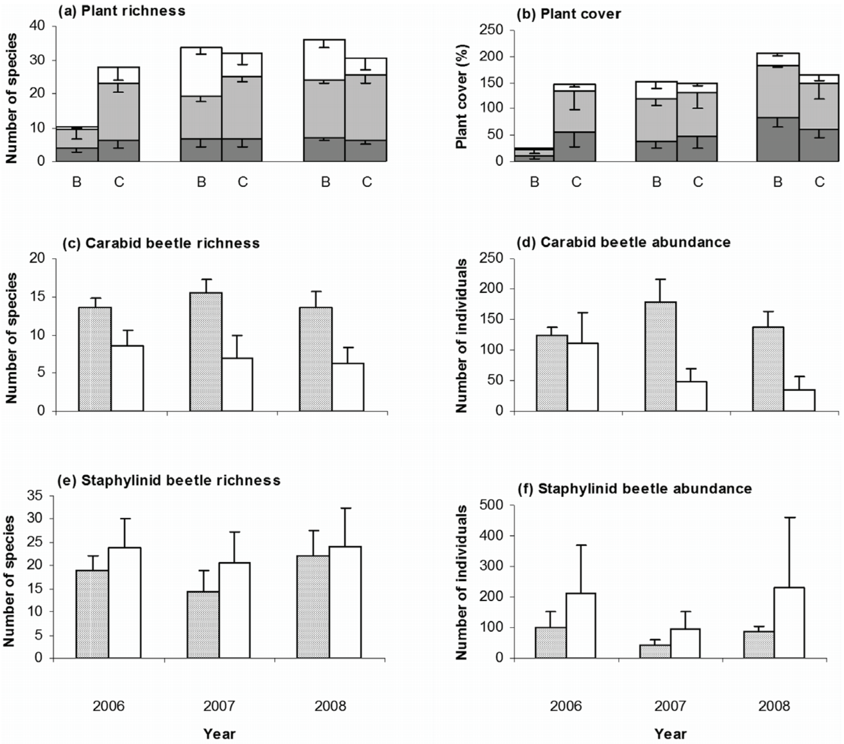

Figure 3. Mean values of plant cover and richness and carabid and staphylinid abundance and richness in burnt (B, dotted bars) and control (C, plain bars) treatments during the three sampling years (2006, 2007, and 2008). Plants were split into woody (dark grey background), perennial herbs (light grey background), and annual herbs (white background) according to their life form. Error bars indicate standard deviation from the mean.

and woody species such as *Q. pyrenaica* (small resprouts in the understorey), became typical of this treatment in the following years. In accordance with the PCA, PERMANOVA found that plant community was significantly different between treatments for all years (Table 3).

Carabid beetle assemblage

A total of 42 carabid species (2532 individuals) were collected, 39 present in the burnt transects and 24 in the control ones. Species richness and abundance were significantly higher in burnt than in control transects during the whole study period (Table 2, Fig. 3c, d). Moreover, carabid abundance significantly changed through time, but the response differed between treatments: abundance peaked in burnt transects during the second year while in control transects it decreased all along the study period, rendering a significant interaction term between factors treatment and year in the GLMM.

The first two axes of the PCA graph (Fig. 2c) represented 57.8% of the total variance and depicted control transects clustering in two groups (C1 with C2, and C3 with C4) and differing little through time. Burnt transects were more variable through time, overlapping C3 and C4 the first year and differing from control transects in the following years. The high relative abundance of *Steropus globosus*, which represented more than half of the total capture in the first year for the burnt, C3 and C4 transects, could account for this pattern in the PCA graph (Fig. 2c). The change of carabid assemblages in burnt transects through time could be due to species which were absent the first year, but proliferated in burnt transects the second and third years, namely *Amara aenea, Calathus fuscipes, Poecilus kugelanni* and the majority of *Harpalus* species (Fig. 2c; Appendices 2 and 4). This agrees with PERMANOVA results (Table 3) where burnt and con-

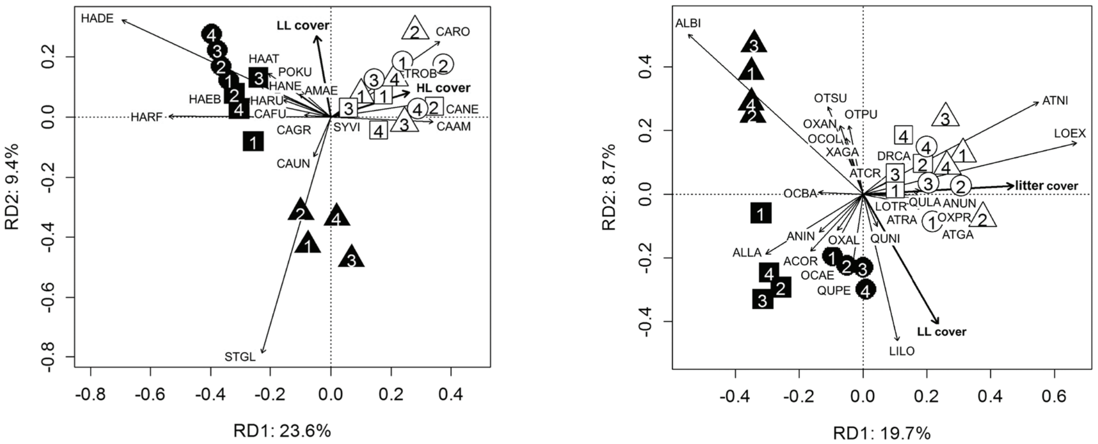

Figure 4. RDA graphs for (**a**) carabid and (**b**) staphylinid species composition in relation to habitat structure variables. Treatment and year are indicated by symbol colour and shape, respectively: black symbols (burnt), and white symbols (control); triangles (2006), squares (2007), and circles (2008). Transect number is indicated inside each symbol. LL = lower vegetation layer. UL = upper vegetation layer. Variance explained by each axis is specified in the axis legend. Only the most frequent, abundant or representative species are indicated with their names abbreviated by four letters (see Appendices 4 and 5, for species correspondences).

trol assemblages were not different in the first sampling year, but they significantly differed in the second and third years.

RDA found that upper and lower vegetation layers were the main habitat structure variables which explained carabid species composition (Fig. 4a). This retrieved only two constrained axes which explained 33.0% of the total variance in the dataset. The upper vegetation layer in control transects was positively associated with *Calathus rotundicollis*, *Carabus amplipennis*, *C. nemoralis* and *Trechus obtusus*. In the burnt forest, the cover of the upper vegetation layer remained low during the whole study period favouring *Steropus globosus* the first year and *Harpalus* species the second and third years as the lower vegetation layer increased.

Staphylinid beetle assemblage

In overall, 99 species were collected (3073 identified individuals), 71 in the burnt transects and 70 in the control ones. No significant differences were found either in species richness or overall abundance for factor treatment. Species richness and overall abundance varied significantly through time, being lowest in the second year and increasing again the third year both for control and burnt transects (Fig. 3e, f; Table 2).

The first two axes of the PCA graph represented 41.1% of the total variance and showed that staphylinid assemblages were very variable through time, especially in the burnt transects, and different between treatments during the study period (Fig. 2d). The differences in the assemblages between burnt and control transects could be due to some species which were hardly ever shared by both treatments; examples of this are *Acrotona orbata*, *Aleochara bipustulata* or *Quedius persimilis* which occurred in the burnt transects and *Atheta gagatina*, *A. nigritula* or *Lordithon exoletus* which were found in the control ones (Appendices 2 and 5), especially in C1 and C2. Burnt transects seemed to slightly approach C3 and C4 transects as time passed by, while C1 and especially C2 transects remained quite apart (Fig. 2d). According to PERMANOVA burnt and control assemblages were significantly different throughout the whole sampling period (Table 3).

RDA found that litter cover and the lower vegetation layer were the main habitat structure variables that explained staphylinid beetle composition (Fig. 4b). This retrieved only two constrained axes which explained 28.4% of the total variance in the dataset. Litter cover in the control transects was positively associated to *Atheta nigritula* and *Lordithon exoletus*. Small values of the lower vegetation layer in the burnt transects were positively related to predator species such as *Ocypus olens*, *Othius punctulatus* or *O. subuliformis* and to the coprophilous species *Aleochara bipustulata* which proliferated the first year.

Discussion

In general, differences were observed between control and burnt transects for all the ecosystem components except for topsoil. However, the temporal pattern of these differences depended on the ecosystem component considered. Greatest differences in plant community composition between burnt and control transects were found in the first year and decreased through time. The carabid composition showed no differences between treatments the first year, but became different in the second and third years. Finally, the staphylinid composition differed between control and burnt transects during the whole study.

In the *Q. pyrenaica* woodlands of northwest Spain, wildfires usually spread as surface fires which mainly affect the understorey and do not greatly modify the topsoil features (Luis et al. 2000). In our study area, the fire totally destroyed the understorey and just slightly affected the topsoil, something usual in low-intensity fires such as those occurring in spring. Loss of organic matter is usually a good indicator of fire intensity (Certini 2005), so in agreement to what Úbeda et al. (2009) reported for slightly burnt areas, we found no significant differences in organic matter content four months after fire. Moreover, an increase in organic matter content was found in the burnt transects the following years, probably due to the incorporation of partially burnt residues to the mineral soil (Johnson and Curtis 2001). The lack of significant changes in pH, cations or total N agrees with the results of previous studies on oak forest wildfires (Marcos et al. 1995, Ferran et al. 2005) and with low-temperature warming laboratory experiments (Prieto-Fernández et al. 2004, Marcos et al. 2007). We only found a significant increase in available P that may be due to the deposition of P-rich ashes (Romanya et al. 1994, Sánchez et al. 1994, Antunes et al. 2009) and to the smaller P losses by run-off and washing compared to cations. Besides, in the burnt transects, there was a continuous increase of P in time, which was also observed in heathlands two years after fire (Marcos 1997) and in garrigues during the first five years post-fire (Trabaud 1983).

The reported fast recovery of the vegetation after fire agrees with prior studies on *Q. pyrenaica* ecosystems (Tárrega and Luis 1989, Calvo et al. 1991, 1999, Luis and Tárrega 1993, Álvarez et al. 2009). Recovery occurs by autosuccession, woody and perennial herb resprouters being the first ones to emerge after fire. Also resprouts of *Q. pyrenaica* appeared in the first sampling period post-fire. Indeed, the species has been classified as "resprouting dependent" by Reyes and Casal (2008), due to its high level of resprouting stimulation after fire. *Q. pyrenaica* rapidly increased in cover, in such a manner that in two years mean woody plant cover in the understorey was higher in burnt than in control transects. In this ecosystem, great woody plant cover in the understorey usually happens as a consequence of fire and other disturbances (Tárrega et al. 2006).

One year after the fire, we observed an increase in annual herb richness and cover, which lasted till the end of the study, a usual pattern in Mediterranean ecosystems after fire and other disturbances (Trabaud and Lepart 1980, Casal et al. 1990, Bond and van Wilgen 1996, Calvo et al. 2002). Keeley et al. (2005) indicated that the initial increase in diversity after fire may be influenced by life-history specialisation since fire triggers the germination of the species which persisted in the area as a dormant seed bank. In our study area, however, the increased overall plant species richness of the burnt transects during the second and third years after fire was not significantly greater than the control ones.

Carabid beetle richness and abundance were higher in burnt than in control transects, especially during the second and third years after fire. This has been observed by other authors (Gongalsky et al. 2006, Hjältén et al. 2010, Samu et al. 2010) and may be due to an increase in beetle movement related to the new habitat and resource conditions created by fire. The first year, the small values of the lower vegetation layer in burnt transects likely implied a reduction in the environmental resistance and an increase in temperature at the surface level which may positively affect beetle catchability (Thomas et al. 2006) and thus explain the higher carabid abundance in burnt transects (Muona and Rutanen 1994, Gongalsky et al. 2006, Hjältén et al. 2010). Moreover, a reduction in prey availability in burnt transects may have also triggered an increase in carabid activity as beetles would need to cover longer distances to find food (Guillemain et al. 1997), thus increasing their catchability.

According to PERMANOVA, carabid assemblages did not differ between burnt and control treatments during the first year. This may be caused by high beetle survival after fire or by fast recolonisation of the burnt transects from the nearby unburnt forest, thus keeping the assemblages similar in species composition. The differences between burnt and control assemblages the second and third years coincide with the arrival of some new species favoured by suitable post-fire conditions resulting from the reduction in the upper vegetation layer and the increase in the lower vegetation layer in burnt transects during these years (see Taboada et al. 2006 and references therein). This might be the case of several open habitat carabids such as *Harpalus* species which have been reported to come to recently burnt sites (Holliday 1991, Gongalsky et al. 2006, Samu et al. 2010) where they probably prefer the warmer and more xeric conditions (Thiele 1977, Gongalsky et al. 2006). These beetles actively feed on seeds (Honek et al. 2003) which may be plentiful in the burnt transects following the proliferation of annual herbs the first year after fire.

Staphylinid beetles are supposed to properly survive wildfires thanks to their high mobility and to their ability to hide into crevices (Paquin and Coderre 1997, Wikars and Schimmel 2001). Therefore, the difference in staphylinid assemblages between burnt and control transects may not be explained by the direct effect of fire and may rather reflect a change in the microhabitat conditions. Fire sharply reduced the upper vegetation layer and destroyed an important amount of the litter layer, where the majority of staphylinid beetles are usually found (Bohac 1999) and may have also negatively affected mushrooms (Ahlgren 1974), a medium inhabited by many staphylinids such as *Lordithon* spp., *Atheta gagatina*, *A. nigritula* and *A. ravilla* (Newton 1984).

Very few staphylinids were more abundantly captured in burnt than in control transects (see Hjältén et al. 2010). The likely reduction in environmental resistance may have enhanced the captures of predators such as *Ocypus olens*, *Othius punctulatus* and *O. subuliformis* and even *Aleochara bipustulata*, a coprophilous species (Koch 1989), probably favoured by higher ease to find excrements in the less-vegetated and litter-covered burnt transects. However, some of the observed patterns (i.e., the decrease in mycophilous and the increase in coprophilous species in the burnt transects) contradict what Muona and Rutanen (1994) observed in boreal forests. Since fire intensity and weather conditions greatly differ between boreal and Mediterranean forests, differences in the ecosystem responses to fire disturbance are likely to occur. For example, while fungi are favoured by fire in boreal forests, fire intensity in Mediterranean forests may cause them to decline (Dahlberg 2002), thus negatively affecting mycophilous species.

Finally, the clearest trend in the ecosystem responses to fire was temporal (i.e., the four burnt transects sampled the same year were highly similar and differed from the other two years) for all the components except topsoil. Unexpectedly, topsoil showed a clearer temporal trend in control than in burnt transects, with an increase in organic matter and nutrients towards the third sampling year. The temporal trend in the topsoil features of the burnt transects was ambiguous, since the effects of fire on nutrient cycles (Certini 2005) may lead to a much more erratic response. Dissimilarity in topsoil properties among burnt transects may have resulted from varying temperature patterns occurred during the wildfire (Gimeno-García et al. 2004), which may have contributed to different soil nutrient dynamics and, thus, to the following distinct post-fire response of each transect. For plant, carabid and staphylinid species composition, the trend was rather spatial in control transects since they clustered into two separate groups (i.e., C1 and C2 on one side, and C3 and C4 on the other), despite belonging to the same oak forest. The fact that control transects were much more variable in species composition than expected for the three taxa (see Pryke and Samways 2012) may be due to the uneven and haphazard management (e.g., grazing, burning, thinning, etc.) of oak forests in the area (see Tárrega et al. 2006).

Conclusions

The wildfire had different effects on the ecosystem components studied. While topsoil features hardly differed between control and burnt transects, plant community was greatly affected by fire, although it almost recovered to pre-fire conditions during the following years, mainly due to resprouting of woody species. During the second and third years, annual herbs proliferated thanks to reduced competition, producing a good yield of seeds which may have fed the carabid seed predators that colonised the warm and dry burnt transects during that period, therefore increasing overall carabid richness and abundance. Staphylinid beetles were mostly negatively affected by fire during the first two years, maybe due to a decrease in the number or quality of the microhabitats they require to feed and reproduce, but their assemblages approached those of the control transects during the third sampling year. For carabids and staphylinids, control transects were spatially more different than the burnt ones as the possible pre-existing differences between burnt transects could have been overcome due to the homogenising effect of fire. All these patterns underline the fact that spring fires in Mediterranean oak forests may help to maintain the spatial heterogeneity typical of traditional management practices to which the ecosystem components are adapted (see Hjältén et al. 2010). In this sense, vegetation rapidly recovered by autosuccession, carabids increased their abundance and species richness and, together with staphylinids, they developed different assemblages from those of the unburnt surrounding forest thus enhancing biodiversity at the landscape scale.

Acknowledgements: This paper is part of a research project supported by the Junta de Castilla y León (Ref. LE008A06). S. García-Tejero was financed by the Junta de Castilla y León. A. Taboada is funded by Ministerio de Educación, Spain (postdoctoral fellowship EX2009-0989).

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Received September 11, 2012
Revised January 18, March 18, 2013
Accepted April 29, 2013

Appendices

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Community Ecology - Electronic Appendix

Differential responses of ecosystem components to a low-intensity fire in a Mediterranean forest: A 3-year case study

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Appendix 1. Reference list of the standard keys used for carabid and staphylinid beetle identification, and the species catalogues adopted for plant, carabid and staphylinid nomenclature

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Appendix 1 (*Continued*)

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Appendix 2. Vegetation, carabid and staphylinid species distinguished by the Indicator Value analysis as characteristic from the burnt (years: 2006, 2007, and 2008) and control forest. Only significant indicator species ($p<0.05$) are shown together with their indicator value. Plant life form categories are indicated after the species name (A: annual herbs, P: perennial herbs, and W: woody species)

Burnt 2006		**Burnt 2007**		**Burnt 2008**		**Control**	
Vegetation							
		Scleranthus annuus A	75.0	*Aira caryophyllea* A	75.2	*Festuca* gr. *rubra* P	88.2
		Arnoseris minima A	73.5	*Lolium perenne* P	72.1	*Cruciata glabra* P	86.4
		Teesdalia nudicaulis A	72.4	*Rumex* gr. *acetosella* P	71.1	*Luzula forsteri* P	70.8
		Tuberaria guttata A	68.9	*Andryala integrifolia* A	69.7	*Calluna vulgaris* W	61.4
		Ornithopus compressus A	68.6	*Hieracium* gr. *pilosella* P	63.2	*Genista florida* W	59.5
		Silene sp. A	64.7	*Hypochoeris radicata* P	58.1	*Potentilla sterilis* P	58.3
		Logfia minima A	57.7	*Genista micrantha* W	56.9	*Halimium umbellatum* W	50.0
		Jasione montana A	52.3	*Viola riviniana* P	49.6	*Agrostis capillaris* P	48.7
				Quercus pyrenaica (resprouts) W	47.0		
				Erica arborea W	43.1		
Carabids							
Amara equestris	75.0	*Harpalus ebeninus*	83.2	*Amara aenea*	96.8		
		Harpalus neglectus	75.0	*Harpalus rubripes*	80.4		
		Calathus fuscipes	61.8	*Harpalus attenuatus*	69.4		
				Harpalus decipiens	62.7		
				Harpalus rufipalpis	59.0		
				Poecilus kugelanni	57.7		
Staphylinids							
Aleochara bipustulata	93.1			*Quedius persimilis*	83.0	*Lordithon exoletus*	98.7
Mycetoporus mulsanti	75.0			*Liogluta longiuscula*	57.9	*Atheta nigritula*	95.7
Othius subuliformis	69.9			*Acrotona orbata*	53.9	*Atheta gagatina*	75.9
Oxypoda annularis	60.6					*Drusilla canaliculata*	58.7
Othius punctulatus	56.3						

Appendix 3. Mean percentage cover and standard deviation (in parentheses) value (four replicates) of annual, perennial herbs and woody plant species in the burnt (B) and control (C) plots in the three study years (2006, 2007, and 2008). Name abbreviations are indicated for those species represented in the PCA graph

		B-06	C-06	B-07	C-07	B-08	C-08
ANNUAL HERBS							
Aira caryophyllea	AICA	0.0 (0.0)	2.6 (3.0)	0.4 (0.7)	0.7 (1.4)	4.9 (4.4)	0.5 (1.0)
Aira praecox		0.0 (0.0)	0.0 (0.0)	0.9 (1.4)	0.0 (0.0)	0.1 (0.3)	0.0 (0.0)
Andryala integrifolia	ANIN	0.0 (0.0)	0.7 (0.9)	0.9 (0.9)	1.6 (2.0)	4.5 (3.1)	0.9 (1.3)
Arnoseris minima		0.0 (0.0)	0.0 (0.0)	4.5 (1.7)	0.1 (0.2)	1.6 (1.1)	0.1 (0.3)
Campanula rapunculus		0.0 (0.0)	1.0 (1.4)	0.0 (0.0)	0.9 (1.1)	0.0 (0.0)	0.8 (1.2)
Cerastium glomeratum		0.0 (0.0)	0.0 (0.0)	0.5 (0.6)	0.3 (0.6)	0.3 (0.3)	0.1 (0.3)
Crucianella angustifolia		0.0 (0.0)	0.8 (1.2)	1.2 (1.1)	1.3 (1.5)	2.2 (1.7)	1.3 (1.7)
Daucus carota		0.0 (0.0)	0.2 (0.5)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	0.2 (0.1)
Filago vulgaris		0.0 (0.0)	0.0 (0.0)	0.6 (0.9)	0.0 (0.0)	0.7 (1.0)	0.0 (0.0)
Galium aparine		0.0 (0.0)	0.6 (0.8)	2.2 (1.2)	0.6 (0.4)	1.9 (0.8)	0.3 (0.3)
Herniaria glabra		0.0 (0.0)	0.0 (0.0)	0.2 (0.3)	0.0 (0.0)	0.2 (0.3)	0.0 (0.0)
Jasione montana		0.0 (0.0)	0.1 (0.2)	0.6 (0.4)	0.2 (0.3)	0.4 (0.4)	0.0 (0.0)
Logfia minima		0.0 (0.0)	0.0 (0.1)	2.1 (2.4)	0.2 (0.4)	1.4 (0.6)	0.1 (0.2)
Melampyrum pratense	MEPR	0.0 (0.0)	7.9 (10.8)	0.0 (0.0)	10.3 (12.7)	0.1 (0.3)	9.3 (12.2)
Myosotis discolor		0.0 (0.0)	0.0 (0.0)	0.4 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Ornithopus compressus	ORCO	0.2 (0.2)	0.0 (0.0)	8.4 (3.4)	0.1 (0.2)	3.6 (2.1)	0.0 (0.0)
Petrorhagia prolifera		0.0 (0.0)	0.0 (0.0)	0.6 (0.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Scleranthus annuus		0.0 (0.0)	0.0 (0.0)	1.4 (1.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Senecio vulgaris		0.0 (0.0)	0.0 (0.0)	0.2 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Silene sp.	SILE	0.0 (0.0)	0.0 (0.0)	6.9 (9.2)	0.0 (0.0)	1.1 (2.2)	0.0 (0.0)
Teesdalia nudicaulis		0.0 (0.0)	0.2 (0.4)	1.2 (1.5)	0.3 (0.6)	0.3 (0.5)	0.0 (0.0)
Trifolium arvense		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.3)	0.0 (0.0)	0.0 (0.0)
Trifolium campestre		0.0 (0.0)	0.0 (0.1)	0.8 (0.9)	0.2 (0.3)	1.1 (1.3)	0.1 (0.1)
Tuberaria guttata	TUGU	0.0 (0.0)	0.0 (0.0)	4.9 (5.3)	0.0 (0.0)	2.2 (2.6)	0.0 (0.0)
Vicia sativa subsp. *nigra*		0.0 (0.0)	0.4 (0.3)	2.2 (2.7)	1.3 (0.9)	0.8 (0.7)	1.2 (1.5)
PERENNIAL HERBS							
Achillea millefolium		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.5)	0.0 (0.0)	0.1 (0.2)
Agrostis capillaris	AGCA	0.0 (0.1)	5.1 (5.3)	1.4 (1.3)	7.7 (2.4)	5.6 (4.3)	7.3 (4.3)
Arenaria montana	ARMO	0.0 (0.0)	5.5 (2.2)	14.4 (2.6)	5.5 (2.6)	14.4 (4.4)	7.1 (2.2)
Avenula marginata subsp. *sulcata*	AVMA	0.1 (0.1)	9.6 (6.6)	8.1 (5.0)	11.8 (7.8)	10.4 (5.1)	7.8 (2.3)
Carex gr. *muricata*		0.8 (0.8)	2.3 (2.1)	0.8 (0.9)	1.7 (0.6)	0.7 (1.1)	1.9 (2.1)
Clinopodium vulgare	CLVU	0.0 (0.0)	3.8 (3.2)	2.8 (2.4)	3.8 (2.5)	4.5 (1.9)	3.3 (2.2)
Cruciata glabra	CRGL	0.0 (0.0)	3.7 (2.5)	0.1 (0.2)	7.1 (3.6)	0.8 (1.0)	4.9 (2.7)
Dactylis glomerata		0.0 (0.0)	0.2 (0.3)	0.0 (0.0)	0.4 (0.7)	0.0 (0.0)	0.0 (0.0)
Deschampsia flexuosa	DEFL	0.0 (0.0)	2.0 (2.6)	4.6 (3.9)	0.4 (0.7)	2.4 (3.6)	1.0 (2.0)
Festuca gr. *rubra*	FERU	0.0 (0.1)	10.3 (2.3)	0.0 (0.0)	9.3 (4.7)	1.5 (0.5)	15.0 (5.4)
Galium rotundifolium		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.6 (1.1)	1.4 (2.8)
Geum sylvaticum		0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	1.1 (2.1)	0.0 (0.0)	0.3 (0.6)
Helichrysum stoechas		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.1)
Helleborus foetidus		0.0 (0.0)	0.2 (0.3)	0.0 (0.0)	0.1 (0.2)	0.0 (0.0)	0.4 (0.9)
Hieracium castellanum		0.1 (0.2)	0.3 (0.6)	0.4 (0.9)	0.4 (0.9)	0.4 (0.5)	0.4 (0.8)
Hieracium murorum		0.0 (0.1)	0.6 (1.2)	0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.9 (1.1)
Hieracium gr. *pilosella*		0.0 (0.0)	0.2 (0.3)	0.2 (0.3)	0.5 (0.8)	0.8 (0.7)	0.3 (0.3)
Holcus mollis	HOMO	0.0 (0.1)	3.6 (4.7)	1.0 (0.9)	5.4 (6.3)	0.3 (0.6)	3.6 (5.2)
Hyacinthoides non-scripta		0.0 (0.0)	0.2 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Hypericum perforatum		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.1 (2.1)	0.0 (0.0)

Appendix 3. (*Continued*)

		B-06	C-06	B-07	C-07	B-08	C-08
PERENNIAL HERBS							
Hypochoeris radicata	HYRA	0.0 (0.0)	1.5 (1.7)	1.3 (1.8)	1.3 (2.0)	4.1 (2.9)	2.0 (2.0)
Linaria triornithophora		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.3)
Lolium perenne		0.0 (0.0)	0.0 (0.0)	1.6 (1.7)	0.0 (0.0)	4.1 (3.4)	0.0 (0.0)
Lotus corniculatus	LOCO	0.1 (0.1)	0.2 (0.2)	9.5 (3.5)	1.0 (0.7)	12.5 (4.4)	0.8 (0.2)
Luzula forsteri		0.0 (0.0)	4.7 (1.0)	0.7 (1.3)	4.8 (0.4)	1.3 (1.2)	4.6 (2.8)
Luzula lactea	LULA	1.3 (2.5)	0.4 (0.5)	5.0 (10.0)	0.0 (0.0)	1.5 (3.1)	0.6 (0.5)
Orchis sp.		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.3)	0.1 (0.2)	0.8 (1.1)
Phleum pratense		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.2)
Physospermum cornubiense		0.0 (0.0)	0.1 (0.1)	0.2 (0.3)	0.1 (0.2)	0.0 (0.0)	0.0 (0.0)
Plantago holosteum		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.6)	0.4 (0.8)	0.1 (0.2)
Plantago lanceolata		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.3)	0.0 (0.0)	0.0 (0.0)
Polygala microphylla		0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.0 (0.0)	0.1 (0.3)	0.1 (0.1)
Potentilla sp.		0.0 (0.0)	0.1 (0.2)	0.0 (0.0)	0.0 (0.1)	0.0 (0.0)	0.0 (0.0)
Potentilla sterilis	POST	0.0 (0.0)	2.2 (4.1)	0.0 (0.0)	1.8 (2.4)	0.0 (0.0)	2.2 (3.4)
Pteridium aquilinum	PTAQ	9.9 (10.3)	19.9 (24.0)	25.1 (18.7)	15.2 (18.5)	20.4 (12.6)	15.8 (18.0)
Rumex gr. *acetosella*	RUAC	0.0 (0.0)	0.4 (0.9)	2.3 (2.8)	0.6 (0.8)	7.9 (4.7)	1.7 (2.7)
Sanguisorba minor		0.0 (0.0)	0.0 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Sedum forsteranum		0.0 (0.0)	0.3 (0.4)	0.0 (0.0)	0.6 (0.9)	0.0 (0.0)	0.2 (0.4)
Silene nutans		0.1 (0.2)	0.1 (0.2)	0.0 (0.0)	0.1 (0.2)	0.0 (0.0)	0.3 (0.6)
Stellaria holostea		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.4 (0.5)	0.0 (0.0)	1.0 (1.2)
Trifolium pratense		0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.3 (0.6)
Veronica officinalis		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.6)
Viola riviniana		0.3 (0.3)	0.3 (0.2)	1.7 (0.4)	0.4 (0.3)	2.5 (1.1)	1.2 (0.4)
WOODY SPECIES							
Calluna vulgaris	CAVU	0.0 (0.0)	2.0 (1.3)	0.0 (0.0)	3.2 (1.1)	1.5 (1.6)	4.2 (1.2)
Crataegus monogyna		0.0 (0.0)	0.0 (0.0)	0.1 (0.3)	0.2 (0.3)	0.3 (0.6)	0.0 (0.0)
Cytisus scoparius	CYSC	0.7 (1.0)	5.6 (5.2)	5.5 (3.8)	7.2 (7.0)	12.5 (11.9)	7.6 (7.5)
Erica arborea	ERAR	1.0 (0.5)	13.8 (3.7)	4.2 (3.2)	9.8 (9.4)	13.5 (5.6)	14.0 (6.6)
Erica australis subsp. *aragonensis*		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.4 (2.8)	0.0 (0.0)
Genista florida subsp. *polygaliphylla*	GEFL	0.0 (0.0)	10.4 (7.1)	0.9 (0.4)	7.3 (7.6)	2.6 (3.8)	8.3 (6.4)
Genista micrantha		0.0 (0.0)	0.0 (0.0)	1.3 (1.1)	0.0 (0.0)	4.1 (4.4)	0.0 (0.0)
Halimium alyssoides		0.1 (0.1)	0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Halimium umbellatum	HAUM	0.0 (0.0)	2.5 (2.9)	0.0 (0.0)	1.9 (2.1)	0.0 (0.0)	2.2 (2.6)
Lavandula stoechas		0.0 (0.0)	0.2 (0.4)	0.0 (0.0)	0.1 (0.2)	0.0 (0.0)	0.0 (0.0)
Lithodora diffusa	LIDI	0.0 (0.1)	3.3 (4.6)	0.3 (0.3)	2.9 (3.1)	0.9 (1.0)	3.8 (4.5)
Quercus pyrenaica (resprouts)	QUPY	9.2 (7.8)	17.3 (11.9)	23.5 (9.8)	15.5 (4.9)	44.7 (9.7)	20.3 (9.9)
Rosa sp.		0.2 (0.3)	0.0 (0.0)	0.6 (0.8)	0.0 (0.0)	1.0 (1.1)	0.1 (0.2)
Thymus mastichina		0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Thymus serpyllum		0.0 (0.0)	0.0 (0.0)	0.3 (0.6)	0.1 (0.2)	0.0 (0.0)	0.0 (0.0)

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Appendix 4. Mean abundance and standard deviation (in parentheses) value (four replicates) of carabid beetle species captured in the burnt (B) and control (C) plots in the three study years (2006, 2007, and 2008). Name abbreviations are indicated for those species represented in the PCA and RDA graphs

		B-06	C-06	B-07	C-07	B-08	C-08
Amara (*Amara*) *aenea* (De Geer, 1774)	AMAE	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	2.5 (1.3)	0.0 (0.0)
Amara (*Bradytus*) *crenata* Dejean, 1828		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Amara (*Percosia*) *equestris* (Duftschmid, 1812)		1.0 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Amara (*Amara*) *eurynota* (Panzer, 1796)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Amara (*Amara*) *ovata* (Fabricius, 1792)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Badister (*Badister*) *meridionalis* Puel, 1925		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Brachinus (*Brachinoaptinus*) *bellicosus* Dufour, 1820		0.3 (0.5)	0.3 (0.5)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Calathus (*Neocalathus*) *asturiensis* Vuillefroy, 1866		0.5 (0.6)	0.0 (0.0)	0.5 (0.6)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Calathus (*Calathus*) *fuscipes* (Goeze, 1777)	CAFU	0.3 (0.5)	0.5 (1.0)	3.5 (4.4)	0.0 (0.0)	1.8 (1.7)	0.0 (0.0)
Calathus (*Neocalathus*) *granatensis* Vuillefroy, 1866	CAGR	0.5 (1.0)	0.3 (0.5)	1.3 (1.5)	0.0 (0.0)	1.0 (1.2)	0.0 (0.0)
Calathus (*Neocalathus*) *rotundicollis* Dejean, 1828	CARO	21.5 (23.3)	31.5 (34.6)	31.3 (21.3)	18.8 (19.4)	7.5 (7.3)	15.0 (16.9)
Calathus (*Calathus*) *uniseriatus* Vuillefroy, 1866	CAUN	4.5 (3.7)	6.8 (12.2)	6.5 (5.2)	1.3 (2.5)	1.0 (2.0)	0.3 (0.5)
Carabus (*Oreocarabus*) *amplipennis* Lapouge, 1924	CAAM	5.3 (6.6)	22.5 (15.0)	1.0 (0.8)	5.0 (5.9)	1.5 (1.3)	1.3 (1.0)
Carabus (*Chrysocarabus*) *lineatus* Dejean, 1826		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Carabus (*Mesocarabus*) *macrocephalus* Dejean, 1826		0.5 (1.0)	0.5 (0.6)	1.0 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Carabus (*Archicarabus*) *nemoralis* Müller, 1764	CANE	2.3 (1.9)	10.0 (11.5)	0.5 (1.0)	2.5 (2.9)	0.0 (0.0)	1.8 (2.4)
Cicindela (*Cicindela*) *campestris* Linnaeus, 1758		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Dinodes (*Dinodes*) *dives* (Dejean, 1826)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Harpalus (*Harpalus*) *attenuatus* Stephens, 1828	HAAT	0.0 (0.0)	0.0 (0.0)	2.8 (5.5)	0.0 (0.0)	6.3 (7.9)	0.0 (0.0)
Harpalus (*Harpalus*) *decipiens* Dejean, 1829	HADE	0.0 (0.0)	0.0 (0.0)	20.5 (17.3)	0.0 (0.0)	34.5 (19.9)	0.0 (0.0)
Harpalus (*Harpalus*) *dimidiatus* (Rossi, 1790)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Harpalus (*Harpalus*) *ebeninus* Heyden, 1870	HAEB	0.3 (0.5)	0.0 (0.0)	15.3 (10.7)	0.3 (0.5)	2.8 (3.8)	0.0 (0.0)
Harpalus (*Harpalus*) *neglectus* Audinet-Serville, 1821	HANE	0.0 (0.0)	0.0 (0.0)	13.5 (10.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Harpalus (*Harpalus*) *rubripes* (Duftschmid, 1812)	HARU	0.3 (0.5)	0.0 (0.0)	1.3 (0.5)	0.3 (0.5)	6.5 (3.9)	0.0 (0.0)
Harpalus (*Harpalus*) *rufipalpis* Sturm, 1818	HARF	3.0 (0.8)	0.0 (0.0)	12.3 (5.7)	1.3 (2.5)	22.5 (11.0)	0.0 (0.0)
Harpalus (*Harpalus*) *sulphuripes* German, 1824		0.0 (0.0)	0.0 (0.0)	0.8 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Leistus (*Pogonophorus*) *spinibarbis* (Fabricius, 1775)		1.0 (1.4)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.3 (0.5)	0.0 (0.0)
Masoreus wetterhallii (Gyllenhal, 1813)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Microlestes gallicus Holdhaus, 1912		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Nebria (*Nebria*) *salina* Fairmaire & Laboulbène, 1856		0.3 (0.5)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Nothiophilus biguttatus (Fabricius, 1779)		0.8 (1.5)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)	0.5 (0.6)

Appendix 4. (*Continued*)

		B-06	C-06	B-07	C-07	B-08	C-08
Ophonus (*Metophonus*) *brevicollis* (Audinet-Serville, 1821)		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Orthomus (*Orthomus*) *hispanicus* (Dejean, 1828)		1.3 (2.5)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Panagaeus cruxmajor (Linnaeus, 1758)		0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	0.8 (1.0)	0.0 (0.0)	0.8 (1.0)
Poecilus (*Macropoecilus*) *kugelanni* (Panzer, 1797)	POKU	0.8 (1.0)	0.3 (0.5)	2.5 (3.1)	0.5 (0.6)	5.0 (3.7)	0.5 (1.0)
Porotachys bisulcatus (Nicolaï, 1822)		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Pseudomasoreus canigoulensis (Fairmaire & Laboulbène, 1854)		0.0 (0.0)	1.0 (0.8)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.3 (0.5)
Pseudoophonus (*Pseudoophonus*) *rufipes* (DeGeer, 1774)		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Steropus (*Sterocorax*) *globosus* (Fabricius, 1792)	STGL	68.8 (33.7)	33.5 (29.9)	59.0 (40.0)	12.8 (14.6)	25.5 (12.6)	2.0 (1.8)
Synuchus vivalis (Illiger, 1798)	SYVI	2.5 (2.1)	1.5 (3.0)	0.8 (1.0)	0.3 (0.5)	2.0 (2.4)	1.0 (1.2)
Trechus (*Trechus*) *cuniculorum* Méquignon, 1921		2.5 (5.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Trechus (*Trechus*) *obtusus* Erichson, 1837	TROB	4.0 (3.5)	1.8 (2.2)	1.8 (2.4)	3.5 (2.4)	15.8 (24.7)	11.8 (9.8)

Appendix 5. Mean abundance and standard deviation (in parentheses) value (four replicates) of staphylinid beetle species captured in the burnt (B) and control (C) plots in the three study years (2006, 2007, and 2008). Name abbreviations are indicated for those species represented in the PCA and RDA graphs

		B-06	C-06	B-07	C-07	B-08	C-08
Acrolocha sulcula (Stephens, 1834)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Acrotona orbata (Erichson, 1837)	ACOR	0.8 (1.0)	0.0 (0.0)	0.8 (0.5)	0.0 (0.0)	1.8 (1.0)	0.0 (0.0)
Aleochara (*Coprochara*) *bipustulata* (Linnaeus, 1761)	ALBI	38.3 (31.1)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	2.0 (2.4)	1.0 (0.8)
Aleochara (*Dyschara*) *inconspicua* Aubé, 1850		0.3 (0.5)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)	0.3 (0.5)
Aleochara (*Xenochara*) *laevigata* Gyllenhal, 1810		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Aleochara (*Aleochara*) *laticornis* Kraatz, 1856	ALLA	6.0 (2.6)	9.8 (2.6)	14.3 (12.4)	6.5 (8.6)	9.0 (4.8)	8.3 (9.4)
Aleochara sp. A		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Aleochara (*Heterochara*) sp. A		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Aleochara (*Xenochara*) *sparsa* Heer, 1839		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Alevonota gracilenta (Erichson, 1839)		0.3 (0.5)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	0.5 (1.0)	0.0 (0.0)
Alevonota rufotestacea (Kraatz, 1856)		0.0 (0.0)	0.0 (0.0)	0.5 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Anotylus inustus (Gravenhorst, 1806)	ANIN	0.5 (0.6)	0.0 (0.0)	4.5 (9.0)	0.0 (0.0)	0.3 (0.5)	0.8 (0.5)
Anotylus sculpturatus (Gravenhorst, 1806)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Anthobium (*Anthobium*) *unicolor* (Marsham, 1862)	ANUN	6.0 (5.4)	27.3 (27.6)	1.0 (1.4)	10.8 (17.5)	5.0 (3.4)	15.0 (24.3)
Astenus (*Eurysunius*) *callaecianus* Coiffait, 1971		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Astrapaeus ulmi (Rossi, 1790)		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Atheta (*Atheta*) *castanoptera* (Mannerheim, 1830)		0.0 (0.0)	0.3 (0.5)	0.3 (0.5)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Atheta (*Atheta*) *crassicornis* (Fabricius, 1792)	ATCR	0.3 (0.5)	1.0 (1.4)	0.0 (0.0)	1.8 (2.4)	0.0 (0.0)	7.0 (12.7)
Atheta (*Dimetrota*) *europaea* Likovský, 1984		0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	1.0 (1.2)	0.0 (0.0)	0.5 (1.0)
Atheta (*Atheta*) *gagatina* (Baudi, 1848)	ATGA	0.3 (0.5)	11.0 (18.7)	0.5 (0.6)	2.8 (2.9)	0.5 (1.0)	4.3 (2.6)
Atheta (*Philhygra*) *luridipennis* Mannerheim, 1830		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Atheta (*Atheta*) *nigritula* (Gravenhorst, 1802)	ATNI	1.3 (1.3)	58.8 (74.8)	0.0 (0.0)	4.5 (2.9)	0.3 (0.5)	35.8 (38.4)
Atheta (*Atheta*) *oblita* (Erichson, 1839)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Atheta (*Atheta*) *ravilla* Erichson, 1839	ATRA	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	4.3 (4.3)
Atheta (*Earota*) *reyi* (Kiessenwetter, 1850)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Atheta (*Alaobia*) *scapularis* (C.R. Sahlberg, 1831)		0.3 (0.5)	0.3 (0.5)	0.5 (1.0)	0.8 (1.0)	0.5 (1.0)	0.3 (0.5)
Atheta sp. A		0.5 (0.6)	0.5 (0.6)	0.3 (0.5)	0.0 (0.0)	2.0 (2.8)	0.3 (0.5)
Atheta (*Alaobia*) *trinotata* (Kraatz, 1856)		0.5 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Autalia longicornis (Scheerpeltz, 1947)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.5 (1.0)
Bolitobius castaneus (Stephens, 1832)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Bryaxis sp. A		0.8 (1.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)

Appendix 5. (*Continued*)

		B-06	C-06	B-07	C-07	B-08	C-08
Callicerus rigidicornis (Erichson, 1839)		0.3 (0.5)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	1.0 (1.4)
Drusilla canaliculata (Fabricius, 1787)	DRCA	0.3 (0.5)	2.5 (1.7)	0.0 (0.0)	0.8 (1.0)	0.0 (0.0)	2.3 (3.3)
Gauropterus fulgidus (Fabricius, 1787)		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Hadrognathus cantabricus Scheerpeltz, 1933		0.0 (0.0)	0.5 (1.0)	0.0 (0.0)	0.5 (1.0)	0.0 (0.0)	0.3 (0.5)
Liogluta alpestris (Heer, 1839)		0.5 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Liogluta longiuscula (Gravenhorst, 1802)	LILO	0.0 (0.0)	3.3 (4.6)	2.3 (1.9)	5.3 (3.3)	14.0 (6.1)	15.3 (8.0)
Lomechusa pubicollis Brisout de Barneville, 1860		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Lordithon (*Lordithon*) *exoletus* (Erichson, 1839)	LOEX	0.0 (0.0)	41.0 (41.8)	0.0 (0.0)	11.3 (9.4)	0.5 (1.0)	59.3 (89.3)
Lordithon (*Bobitobus*) *lunulatus* (Linnaeus, 1760)		0.0 (0.0)	0.8 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (2.0)
Lordithon (*Lordithon*) *trinotatus* (Erichson, 1839)	LOTR	0.0 (0.0)	0.8 (1.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	19.5 (39.0)
Metopsia clypeata (P. Müller, 1821)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)
Micropeplus staphylinoides (Marsham, 1802)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	1.0 (2.0)	0.3 (0.5)	1.5 (1.9)
Mycetoporus baudueri Mulsant & Rey, 1875		0.0 (0.0)	0.8 (1.5)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Mycetoporus lepidus (Gravenhorst, 1806)		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Mycetoporus mulsanti Ganglbauer, 1895		0.8 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Mycetoporus niger Fairmaire & Laboulbène, 1856		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Mycetopurs rufescens (Stephens, 1832)		0.0 (0.0)	1.0 (1.4)	0.0 (0.0)	0.8 (0.5)	0.0 (0.0)	0.0 (0.0)
Myrmoecia sp. A		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	3.0 (6.0)
Ocalea badia Erichson, 1839	OCBA	3.5 (5.0)	0.3 (0.5)	0.5 (0.6)	1.8 (2.9)	1.5 (1.7)	2.0 (4.0)
Ocypus (*Pseudocypus*) *aeneocephalus* (DeGeer, 1774)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Ocypus (*Pseudocypus*) *aethiops* (Waltl, 1835)	OCAE	6.3 (4.0)	11.8 (4.5)	5.8 (2.2)	14.3 (8.6)	12.5 (8.8)	6.3 (3.0)
Ocypus (*Psudocypus*) *fulvipennis* Erichson, 1840		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)
Ocypus (*Ocypus*) *olens* (O. Müller, 1764)	OCOL	5.8 (7.6)	10.5 (14.4)	2.0 (2.7)	2.8 (4.3)	1.0 (1.4)	1.0 (1.4)
Ocypus (*Ocypus*) *ophtalmicus* (Scopoli, 1763)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Ocypus (*Pseudocypus*) *picipennis* (Fabricius, 1793)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Olophrum piceum (Gyllenhal, 1810)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	1.0 (2.0)	0.0 (0.0)	0.8 (1.5)
Omalium ferrugineum Kraatz, 1857		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Omalium nigriceps Kiesenwetter, 1850		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.5 (1.0)
Omalium rugatum Mulsant & Rey, 1880		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Othius punctulatus (Goeze, 1777)	OTPU	3.0 (0.8)	1.5 (1.3)	0.3 (0.5)	1.3 (1.0)	0.3 (0.5)	2.8 (1.7)
Othius subuliformis Stephens, 1832	OTSU	9.5 (8.2)	1.5 (1.7)	0.0 (0.0)	1.0 (1.2)	2.3 (3.9)	3.0 (2.6)
Othius laeviusculus Stephens, 1832		1.5 (1.7)	0.0 (0.0)	0.5 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Appendix 5. (*Continued*)

		B-06	C-06	B-07	C-07	B-08	C-08
Oxypoda (*Mycetodrepa*) *alternans* (Gravenhorst, 1802)	OXAL	0.5 (0.6)	1.5 (1.7)	2.0 (1.8)	5.5 (7.1)	1.3 (1.9)	2.0 (4.0)
Oxypoda (*Bessopora*) *annularis* (Mannerheim, 1839)	OXAN	3.5 (3.3)	0.3 (0.5)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	1.8 (2.4)
Oxypoda (*Bessopora*) *ferruginea* Erichson, 1840		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.0 (4.0)	0.0 (0.0)
Oxypoda (*Podoxya*) *induta* Mulsant & Rey, 1861		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Oxypoda (*Baeoglena*) *praecox* Erichson, 1839	OXPR	2.3 (3.9)	2.5 (4.4)	0.5 (0.6)	6.5 (4.0)	11.8 (7.9)	19.8 (12.6)
Oxypoda sp. A		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Oxypoda (*Baeoglena*) sp. A		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Oxypoda (*Mycetodrepa*) sp. A		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Oxypoda (*Sphenoma*) sp. A		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.5 (0.6)	0.5 (1.0)	1.0 (1.4)
Oxypoda (*Sphenoma*) sp. B		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Oxypoda (*Sphenoma*) *togata* Erichson, 1839		2.5 (3.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Oxypoda (*Podoxya*) *umbrata* (Gyllenhal, 1810)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)
Parabolitobius inclinans (Gravenhorst, 1806)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.3 (0.5)
Philonthus (*Philonthus*) *nitidicollis* (Lacordaire, 1835)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (1.5)	0.0 (0.0)
Phyllodrepa (*Dropephylla*) *palpalis* Luze, 1906		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Placusa (*Placusa*) *pumilio* (Gravenhorst, 1802)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Platydracus (*Platydracus*) *meridionalis* (Rosenhauer, 1847)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Proteinus brachypterus (Fabricius, 1792)		0.0 (0.0)	0.8 (1.0)	0.0 (0.0)	0.3 (0.5)	0.5 (0.6)	0.3 (0.5)
Quedius (*Microsaurus*) *abietum* Kiesenwetter, 1858		0.0 (0.0)	0.3 (0.5)	0.3 (0.5)	0.5 (1.0)	0.8 (1.0)	0.0 (0.0)
Quedius (*Microsaurus*) *curtipennis* Bernhauer, 1908		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (1.5)	0.0 (0.0)	0.0 (0.0)
Quedius (*Raphirus*) *latinus* Gridelli, 1938	QULA	0.3 (0.5)	14.3 (17.9)	0.8 (1.0)	7.5 (9.7)	0.5 (1.0)	3.0 (4.8)
Quedius (*Raphirus*) *nigriceps* Kraatz, 1857	QUNI	0.0 (0.0)	0.5 (1.0)	0.5 (0.6)	2.0 (2.3)	1.5 (1.3)	1.3 (1.0)
Quedius (*Raphirus*) *persimilis* Mulsant & Rey, 1876	QUPE	0.0 (0.0)	0.3 (0.5)	0.5 (0.6)	0.0 (0.0)	3.3 (1.3)	0.3 (0.5)
Quedius (*Raphirus*) *picipes* (Mannerheim, 1830)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Quedius (*Raphirus*) *pineti* Brisout, 1866		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.8 (1.0)	0.0 (0.0)	0.3 (0.5)
Quedius (*Raphirus*) *semiobscurus* (Marsham, 1802)		0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)
Sepedophilus nigripennis (Stephens, 1832)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Stenus (*Hemistenus*) *elegans* Rosenhauer, 1856		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Stenus (*Hemistenus*) *impressus* Germar, 1824		0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)
Tachyporus (*Tachyporus*) *hypnorum* (Fabricius, 1775)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (1.0)	0.0 (0.0)
Tasgius (*Rayacheila*) *morsitans* (Rossi, 1790)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)

Appendix 5. (*Continued*)

		B-06	C-06	B-07	C-07	B-08	C-08
Xantholinus (*Polyodontophallus*) *elegans* (Olivier, 1795)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
Xantholinus (*Xantholinus*) *gallicus* Coiffait, 1956	XAGA	1.5 (0.6)	1.0 (1.2)	0.0 (0.0)	0.3 (0.5)	1.5 (1.7)	1.0 (2.0)
Xantholinus (*Xantholinus*) *linearis* (Olivier, 1795)		0.0 (0.0)	0.3 (0.5)	0.5 (1.0)	0.3 (0.5)	1.3 (1.5)	1.0 (0.8)
Zyras (*Pella*) *humeralis* (Gravenhorst, 1802)		0.0 (0.0)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Zyras (*Glossacantha*) *lugens* (Gravenhorst, 1802)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)

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Forest Ecology and Management 257 (2009) 731–738

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Abandonment and management in Spanish dehesa systems: Effects on soil features and plant species richness and composition

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ARTICLE INFO

Article history:
Received 15 July 2008
Received in revised form 4 October 2008
Accepted 6 October 2008

Keywords:
Land use change
Management
Oak dehesa
Quercus pyrenaica
Species richness
Topsoil
Understory composition

ABSTRACT

Quercus pyrenaica dehesas have been traditionally used as communal extensive grazing systems in the León province (NW Spain). In this region, recent abandonment of rural areas and the subsequent gradual decrease in livestock load have led to the invasion of shrubs in the understory, increasing the risk of fires. Indeed, even if there is no need of creating new pasturelands for livestock breeding, the remaining landowners keep on burning to clear these montane patches. Alternatively, the regional administration encourages shrub cutting as a better way of managing these areas and preserving the pasturelands. Our aim was to determine the effects of the dehesa abandonment and shrub cutting on plant species richness (annual herbs, perennial herbs and woody plants) and species composition, as well as on topsoil properties. For that, we compared three types of dehesas with different management regimes: (1) grazed dehesas (used at the present), (2) abandoned dehesas (more than 20 years without grazing) and (3) dehesas where shrub cutting was applied after abandonment (i.e. cleared dehesas). We selected three replicates or stands per dehesa type. The highest organic matter content (O.M.), total nitrogen (N) and available phosphorus (P) were found in cleared dehesas, while the lowest values corresponded to the grazed ones. Abandoned dehesas were characterized by the highest values for available calcium (Ca^{2+}). No significant differences were detected regarding the vegetation richness values (S alpha, gamma or beta), although higher mean values of S alpha and gamma were found in grazed dehesas, and lower values in the cleared ones. Concerning the vegetation life forms, grazed dehesas held significantly greater species richness and cover of annual herbs, while abandoned dehesas had significantly higher woody species cover. Both grazed and abandoned dehesas harboured plant species (38 and 13 species, respectively), which were exclusively found in one dehesa type. Contrary to that, cleared dehesas scarcely had "exclusive" species. To conclude, our results indicated that shrub cutting alone (not followed by livestock grazing) may cause loss of plant species richness, suggesting that it is not the most appropriate management method to restore vegetation, except for reducing the risk of fire.

1. Introduction

Dehesas are the most extended agroforestry systems in Europe (Eichhorn et al., 2006) and have been considered as an example of sustainable management (Gómez-Gutiérrez and Pérez-Fernández, 1996), although this has been discussed by other authors that indicate failures in oak regeneration (Plieninger, 2007). The dehesa systems are the result of a traditional form of management of the Mediterranean forests, in which native trees (*Quercus ilex*, *Q. suber*, *Q. pyrenaica*, *Juniperus* spp., etc.) are spaced out or inserted in a continuum of grasslands (Gómez-Limón and de Lucio Fernández, 1999). The maintenance of isolated trees has important effects on soil fertility and grass production in areas with oligotrophic soils and summer dry period (González Bernáldez et al., 1969; Escudero, 1985; Joffre and Rambal, 1993; Joffre et al., 1999; Gallardo, 2003; Moreno et al., 2007). Indeed, the Mediterranean dehesas can simultaneously support livestock, forestry and agricultural production without irreversible endangering the ecosystem functioning (Linares, 2007). Moreover, they show an interesting balance between resource exploitation and the conservation of biodiversity (González Bernáldez, 1981; Díaz et al., 1997; Montero et al., 2000; Plieninger and Willbrand, 2001).

The areas where extensive livestock grazing has been developed for thousands of years, as in the Mediterranean Basin, usually harbour great plant species richness (Naveh and Whittaker, 1979; Puerto et al., 1990; González Bernáldez, 1991; De Miguel and Gómez Sal, 2002). Modifying the type of use and management of these pasturelands can lead to important changes in the vegetation

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0378-1127/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2008.10.004

diversity and species composition (Pineda et al., 1981; Díez et al., 1991; Montalvo et al., 1993; Gómez-Limón and de Lucio Fernández, 1999; Poschlod et al., 2005). In Spain, as well as in most of Europe, the economic development and policies of the last decades have determined the progressive underutilization or abandonment of vast rural areas. Consequently, in these areas there has been a considerable increase in the woody biomass load and, thus, in the risk of fires, also potentially resulting in changes in plant species composition and soil conditions (Gómez-Limón and de Lucio Fernández, 1999; Luis-Calabuig et al., 2000; Peco et al., 2005, 2006).

In the study region (NE of the León province, NW Spain), the dehesa systems are located in naturally developing *Q. pyrenaica* (deciduous oak) forested areas. Although these dehesa ecosystems have several characteristics in common with the typical dehesa systems of SW Spain (mainly dominated by *Q. ilex*, evergreen oak), such as the coexistence of the traditional exploitation of resources and the conservation of biodiversity (see Taboada et al., 2006), there are also other features that differentiate them. Firstly, although both types of dehesas belong to the Mediterranean climate, the summer dry period is less marked in the dehesa systems of León province. Secondly, the northern dehesas are used as communal pasturelands, in contrast to the typical privately owned dehesas of W and SW (Rodríguez, 2001). It is very difficult to establish the livestock load of the dehesas in our region, which is moreover usually highly variable. Nowadays, some of these dehesa ecosystems are still being used, but others have been abandoned since the 70s and 80s and are thus characterized by a strongly developed shrubby understory. Recently in the study area, the regional administration (Junta de Castilla y León) has initiated management practices in the abandoned dehesas, specifically shrub cutting, in order to reduce the risk of fires and to preserve the pasturelands. This type of management of abandoned grasslands was previously applied as the usual method for restoring vegetation in other European countries (Poschlod et al., 2005). However, not just the abandonment, but also the subsequent management activities developed in the abandoned areas would strongly affect plant community diversity and composition (Bakker, 1989; Bakker and Berendse, 1999; Poschlod et al., 2005; Öckinger et al., 2006).

In this study, we intended to determine the effects of the abandonment and the subsequent management practices developed in *Q. pyrenaica* dehesa ecosystems, on the understory plant species diversity and composition, as well as on the topsoil properties. For that, we compared three types of dehesa systems with different management regimes (Fig. 1): (1) grazed dehesas, where the extensive traditional grazing system is maintained, (2) abandoned dehesas and (3) dehesas where shrub cutting was applied after abandonment in order to reduce the understory biomass load (cleared dehesas). We considered plant species richness at both small (sampling unit of 1 m^2) and stand scales, also analysing the spatial heterogeneity based on their comparison.

2. Materials and methods

We studied three types of oak (*Q. pyrenaica*) dehesa systems with different management regimes (Fig. 1): (1) grazed dehesas at the present ("G"), (2) abandoned dehesas ("A") (more than 20 years without grazing) and (3) cleared dehesas ("C") (where shrub cutting was applied only once, 1–2 years before the study was done, part of the slash being apparent on the ground by the time of sampling, see Fig. 1); and three replicates, stands or sites of each type (nine independent dehesas in total, the three sites of each management type were not clustered together). These dehesa ecosystems were the result of a traditional livestock (generally, sheep and goats, but sometimes cows too) management method in which the forest has been cleared, leaving a low density of trees that have been pruned to favour crown development at the expense of height growth. In the study stands, tree density is approximately 100 trees/ha, tree height is around 10–12 m and trunk perimeter (1 m above ground level) about 1–1.5 m. To minimise variability, geographically close dehesas were selected

Fig. 1. The three types of dehesa ecosystems studied, defined by the different management practices applied. G = grazed dehesas; A = abandoned dehesas; C = cleared dehesas.

Table 1
Mean and standard error (S.E.) (three replicates in all cases) values of the analysed soil variables. Results from ANOVA are included (*F*-test and *p*-value). Different letters within a row indicate significant differences ($p < 0.05$ or $p < 0.1$ by the Scheffe test, bold face) between the three dehesa types.

	Cleared		Abandoned		Grazed		ANOVA results	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	*F*-test	*p* value
pH	5.17a	0.08	5.46a	0.31	5.00a	0.10	1.45	0.305
O.M. (%)	8.35a	0.86	7.05ab	0.66	4.91b	0.91	4.49	**0.064**
N (%)	0.26a	0.02	0.21ab	0.02	0.17b	0.02	7.95	**0.021**
C/N	18.53a	1.08	19.36a	0.53	16.67a	1.66	1.35	0.328
Ca^{2+} (cmol kg^{-1})	2.20ab	0.18	2.62a	0.31	1.69b	0.06	5.16	**0.043**
Mg^{2+} (cmol kg^{-1})	0.70a	0.05	0.60a	0.13	0.44a	0.09	1.85	0.237
K^{+} (cmol kg^{-1})	0.29a	0.03	0.36a	0.10	0.38a	0.02	0.63	0.566
Na^{+} (cmol kg^{-1})	0.03a	0.01	0.03a	0.01	0.02a	0.01	0.70	0.533
P (mg kg^{-1})	4.16a	0.39	1.90b	0.64	<1b		9.00	**0.039**

(León province, NW Spain, 42°37′–42°46′N, 4°56′–5°05′W) at 975–1130 m of altitude and flat or less than 10% slope. Climate was sub-humid Mediterranean type (mean annual temperature 10.9 °C, mean annual precipitation 927 mm, dry period in July and August, according to Ministerio de Agricultura, 1980) and the type of soil was humic cambisol (Forteza et al., 1987).

Since the objective was not to characterize the dehesa ecosystems exhaustively but to compare them, a similar surface was studied, located in the centre of each stand, using a systematic sampling method. Two perpendicular transects of about 40 m were established in each stand and a quadrat of 1 m^2 was used as sampling unit. Fifteen quadrats were studied in each stand (seven in each transect and one in the centre), the first one randomly placed. All the species present in each quadrat were recorded, quantifying their abundance as a cover percentage (visually estimated always by the same researchers, so that the bias, if it exists, is similar in all the stands). Cover values higher than 100% were due to species superposition.

Topsoil sampling was carried out in the same transects. Five sub-samples, approximately 8 m apart, were taken from the first 5 cm of soil in each stand, and were homogenised to obtain a uniform sample of the characteristics of the stand as a whole. Soil samples were air-dried and passed through a 2-mm mesh sieve for later analysis. Soil pH, organic matter (O.M.) content, total nitrogen (N), C/N ratio and available phosphorous (P), calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and sodium (Na^+) were determined in each sample, following the official methods of soil analysis (M.A.P.A., 1994).

Plant species richness (S, number of species) was measured both at a small scale (per quadrat or m^2), alpha diversity or microcosmic diversity (Whittaker, 1972; Magurran, 1989, 2004), and at the stand scale, gamma diversity or macrocosmic diversity. S alpha was calculated as the mean number of species found per quadrat in each stand; S gamma as the total species number found in each stand (from the joint consideration of the samples carried out in the 15 quadrats). By using the comparison of both types of diversity, beta diversity or spatial heterogeneity was calculated by the Whittaker formula (in Magurran, 1989): S beta = (S gamma/S alpha) − 1.

One-way analysis of variance (ANOVA) was used to determine whether there were significant differences between dehesa types in terms of soil variables, cover values of annual, perennial herbaceous and woody species, and species richness (S alpha, S gamma and S beta). In all cases three replicates were considered. The Scheffe test was applied for *post hoc* comparisons when the ANOVA was significant ($p \leq 0.05$). Sample normality was checked beforehand using the Kolmogorov–Smirnov test and homogeneity of variances with the Cochran test.

For the joint comparison of the topsoil variables, a principal components analysis (PCA) was carried out, using the Statistica 6.0 program. Understory plant species composition was compared by a detrended correspondence analysis (DCA) with the software Community Analysis Package III (CAP3). Species appearing in only one stand were not considered in this analysis, so only 79 species were included.

3. Results

We found no statistically significant differences in topsoil pH (mean values of 5–5.5) between the three types of dehesa ecosystems (Table 1). Neither have we observed significant differences regarding the values of available Mg^{2+}, K^+ and Na^+, and the C/N ratio. However, organic matter content and total N were significantly higher in cleared than in grazed dehesas, with intermediate values corresponding to the abandoned ones. Also the available P was significantly higher in managed dehesas compared to the other two dehesa types. On the contrary, the greatest level of available Ca^{2+} was found in the abandoned dehesas and the lowest in the grazed ones. The joint comparison of all soil variables by a PCA (70% of variance explained by the first two axes) showed the clustering of grazed dehesas, with negative values for both axes. They were characterized by higher K^+ values and lower values of the other nutrients, organic matter and total N (Table 2, and Fig. 2). The three replicates of the cleared dehesas were also quite similar to each other, associated to higher values of available P, organic matter and total N; while the abandoned dehesa stands were more different to one another and did not clustered together.

Concerning the understory vegetation, at the sampling unit scale the highest mean alpha diversity (S alpha) was found in grazed dehesas (16.4 species/m^2) and the lowest in cleared dehesas (8.5), with an intermediate value in case of the abandoned ones (12.4), although these differences were not statistically significant (Fig. 3). At the stand scale, the results for gamma diversity (S gamma) showed a similar trend, with no significant differences either. Nevertheless, an opposite trend was observed for the spatial heterogeneity or pattern diversity (estimated by S

Table 2
Factor loadings of the soil variables for the first two axes of the principal components analysis.

	Axis I	Axis II
pH	−0.32	0.86
O.M.	0.93	0.19
N	0.90	0.21
Ca	0.18	0.83
Mg	0.20	0.87
K	−0.56	−0.02
Na	0.66	−0.21
P	0.64	0.53

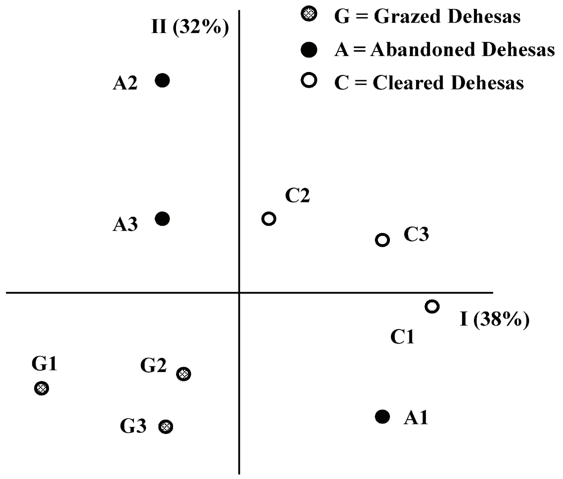

Fig. 2. Location of the dehesa stands in the plane defined by the first two axes of the principal components analysis (explained variance: axis 1 = 38%, axis II = 32%).

beta), with the highest significant value in cleared dehesas and the lowest in the grazed ones. On the other hand, the global species richness in the study area (i.e. the total number of species recorded in the nine dehesa stands) was 116 species. Comparing the total number of species recorded in the three stands of each dehesa type, the grazed dehesas sampled the highest number of species (86), of which 38 were "exclusive" (i.e. species either characteristic or not of this dehesa community, but that did not occur in the other two types of dehesa ecosystems in this study). The abandoned dehesas had 71 species and 13 "exclusive" ones. And the lowest number of species was recorded in the cleared dehesas (57 species), with only 2 "exclusive" ones. Besides, we found that only 30% of the species were shared by the three types of dehesa ecosystems. The abandoned and cleared dehesas were the most similar to each other, with 77% of the species in common, while the grazed dehesas shared 56% of the species with either the abandoned or cleared ones.

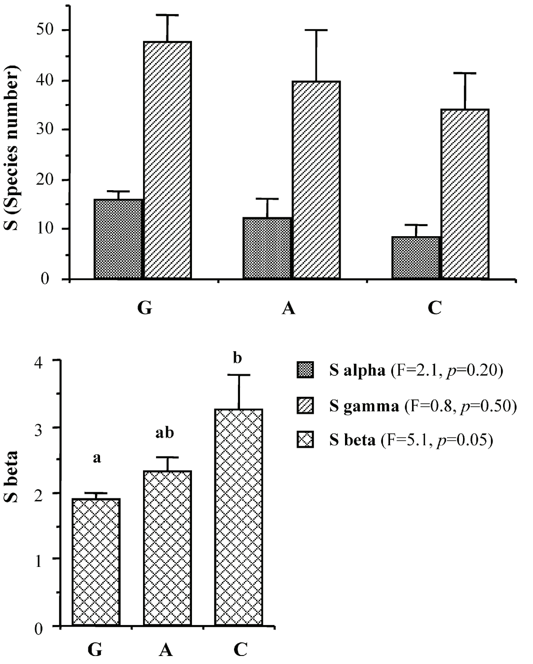

Fig. 3. Mean and standard error diversity values, measured as S alpha (species number/m^2), S gamma (species number/stand) and S beta. Results of ANOVA are also included (when $p < 0.05$, different letters indicate significant differences by the Scheffe test). G = grazed dehesas; A = abandoned dehesas; C = cleared dehesas.

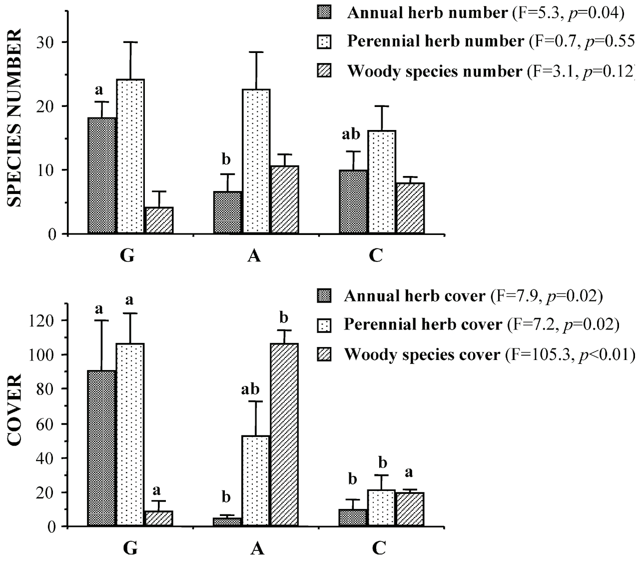

Fig. 4. Mean and standard error number of species and cover values of annual, perennial herbs and woody species in the studied dehesas. Results of ANOVA are also included (when $p < 0.05$, different letters indicate significant differences by the Scheffe test). G = grazed dehesas; A = abandoned dehesas; C = cleared dehesas.

The greatest differences regarding the species richness of the different life forms were observed for the number of annual herbaceous species, which was significantly higher in grazed dehesas and lower in the abandoned ones (Fig. 4). Opposite results were found for woody species richness, although differences were not statistically significant. The number of perennial herbaceous species was not significantly different in the three types of dehesa ecosystems studied. Differences between dehesa types were accentuated from a quantitative point of view, when analysing the percentage cover values of the different vegetation life forms. The mean percentage cover of annual herbs was higher than 90% in the grazed dehesas and lower than 10% in the other two dehesa types (Fig. 4), statistically significantly so. Perennial herb cover was significantly higher in grazed dehesas than in cleared ones, with intermediate values in the abandoned dehesas. The mean cover of woody species was higher than 100% in the abandoned dehesas, with significant differences in relation to the cleared (mean cover of 20%) and grazed ones (less than 10%). The total plant species cover was significantly lower ($F = 17.1$, $p = 0.003$) in the cleared dehesas (mean cover of 50%, although highly variable among the three replicates, see Table 3) than in the abandoned (165%) and grazed ones (higher than 200%).

Regarding plant species composition (Table 3), only two species occurred in the nine dehesa stands: the graminoid *Agrostis capillaris* and resprouts of *Q. pyrenaica* (less than 1 m height). Other frequent species recorded from most of the stands, although with different cover values, were *Aira caryophyllea*, *Teesdalia nudicaulis*, *Arenaria montana*, *Avenula marginata* subsp. *sulcata*, *Festuca* gr. *rubra*, *Hieracium* gr. *pilosella*, *Lotus corniculatus*, *Luzula forsteri* and *Calluna vulgaris*. The results of the DCA (87% of variance explained by the two first axes) showed that the three abandoned dehesa stands were the more similar to one another, related to high values of woody species cover, such as *C. vulgaris*, *Erica arborea*, *E. autralis* and *E. cinerea*, and to the presence of scarce "exclusive"

Table 3
The most frequent, abundant or representative annual, perennial herbs and woody species in the studied stands. Total understory cover (sum of all the species cover) is also included (values higher than 100% are due to species superposition). (C = cleared dehesas, A = abandoned dehesas, G = grazed dehesas). Species name abbreviations are also indicated for their inclusion in the DCA.

		C1	C2	C3	A1	A2	A3	G1	G2	G3
Annual herbaceous species										
Aira caryophyllea	AICA	4.6	0.0	0.9	0.0	4.3	1.3	15.0	8.0	27.5
Aira praecox	AIPR	0.3	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Cerastium glomeratum	CEGL	0.7	0.0	0.0	0.0	0.7	0.0	8.9	0.0	5.0
Cynosurus echinatus	CYEC	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.0	11.0
Filago lutescens	FILU	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.1	1.0
Jasione montana	JAMO	1.8	0.1	0.5	0.0	0.0	0.0	1.0	0.0	5.7
Ornithopus compressus	ORCO	1.5	0.8	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Petrorhagia prolifera	PEPR	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.4	5.1
Teesdalia nudicaulis	TENU	0.3	0.1	2.6	0.5	0.1	0.0	1.1	0.0	3.0
Trifolium campestre	TRCA	0.1	0.0	0.0	0.0	0.0	0.2	10.0	10.1	3.3
Tuberaria guttata	TUGU	0.3	0.0	0.1	0.0	0.1	0.0	19.0	1.0	30.5
Vulpia bromoides	VUBR	0.0	0.0	0.0	0.0	0.0	0.0	23.5	3.2	22.5
Perennial herbaceous species										
Agrostis capillaris	AGCA	1.4	1.2	4.1	1.2	5.0	6.5	24.7	24.9	31.0
Arenaria montana	ARMO	3.1	2.2	4.5	6.5	2.3	0.7	0.7	2.7	0.0
Avenula marginata subsp. *sulcata*	AVMA	4.4	0.3	0.7	1.8	8.7	15.2	0.0	7.5	0.0
Bellis perennis	BEPE	0.0	0.0	0.0	0.0	0.0	0.0	14.1	0.0	1.3
Carex gr. *muricata*	CAMU	0.5	0.4	3.3	1.3	5.3	1.6	3.3	18.5	0.0
Festuca gr. *rubra*	FERU	4.2	0.0	2.7	0.5	2.9	12.9	2.7	15.0	3.0
Hieracium castellana	HICA	3.5	0.0	0.0	0.1	1.5	0.5	15.3	0.0	4.2
Hieracium gr. *pilosella*	HIPI	1.1	0.0	0.6	0.0	10.5	2.6	12.7	11.3	6.5
Hippocrepis comosa	HICO	0.0	0.0	0.0	0.0	0.0	0.0	3.9	0.2	0.2
Lolium perenne	LOPE	1.9	0.0	0.0	0.0	0.3	0.0	1.2	0.0	0.0
Lotus corniculatus	LOCO	0.5	0.0	0.7	0.0	6.6	3.9	3.4	2.5	3.1
Luzula forsteri	LUFO	0.9	1.2	0.3	0.3	1.9	3.3	0.0	1.4	0.0
Plantago lanceolata	PLLA	0.0	0.0	0.2	0.0	0.5	1.1	7.0	2.7	2.9
Polygala microphylla	POMI	0.0	0.0	0.0	0.0	0.5	1.1	0.0	0.0	0.0
Prunella grandiflora	PRGR	0.0	0.0	0.0	0.0	1.4	2.5	0.0	0.0	0.0
Rumex gr. *acetosella*	RUAC	0.9	0.0	2.2	0.0	0.0	0.1	7.9	0.5	7.0
Trifolium pratense	TRPR	0.0	0.0	0.0	0.0	0.0	0.0	3.3	2.3	2.0
Woody species										
Calluna vulgaris	CAVU	4.6	1.9	3.7	40.0	36.7	43.3	0.0	6.7	0.0
Erica arborea	ERAR	1.9	0.0	0.9	15.0	13.0	9.7	0.0	0.0	0.0
Erica australis	ERAU	9.1	3.9	6.2	30.0	13.0	44.7	0.0	0.0	0.0
Erica cinerea	ERCI	0.0	0.0	0.2	0.0	27.7	1.3	0.0	0.0	0.0
Genista scorpius	GESC	0.0	0.3	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Halimium alyssoides	HAAL	0.0	10.1	8.9	0.0	0.0	3.3	0.0	0.0	0.0
Halimium umbellatum	HAUM	0.3	0.0	0.0	0.0	0.0	7.0	0.0	1.0	0.1
Quercus pyrenaica	QUPY	0.9	1.5	1.9	3.2	8.7	1.1	1.1	3.2	6.2
Total cover		72	26	56	109	205	181	231	186	218

species, such as *Prunella grandiflora* and *Polygala microphylla* (Fig. 5, and Table 3). Grazed dehesas were mainly characterized by the presence of annual herbaceous species, such as *Petrorhagia prolifera*, *Cynosurus echinatus*, *Tuberaria guttata* and *Vulpia bromoides*, but also perennial graminoids and other perennial herbs were present, such as *Bellis perennis*, *Hippocrepis comosa*, *Trifolium pratense*. Cleared dehesas were located in an intermediate position in the DCA diagram, due to the absence of "exclusive" species, except *Ornithopus compressus*.

4. Discussion

The results obtained for the comparison of topsoil features in the three types of dehesa ecosystems revealed that, to a certain degree, both abandonment and management by shrub cutting have influenced these properties. According to Moreno and Obrador (2007), the dehesa abandonment and the subsequent invasion by shrubs can improve soil fertility in the long term, due to an increase in organic N and exchangeable base cations. In our study, we observed a slight increase in all the variables that determine soil fertility in the abandoned dehesas compared to the grazed ones, although differences were not statistically significant. Indeed, the dehesa abandonment and the following invasion by shrubs lead to a progressive accumulation of organic matter in the soil, which would emphasize the differences between these two types of management (Moreno and Obrador, 2007). Furthermore, as the amount of N in the dehesa soil depends mostly on organic matter quality and quantity (Gallardo et al., 2000; Gallardo, 2003), shrub colonization also implies an increase in the total N content of the soil. Besides, we detected a significant increase in available Ca^{2+} in the abandoned dehesas that could be favoured by the presence of shrub species (Turrión et al., 2007) due to nutrient recycling via leaf litter and root turnover (Gallardo, 2003; Moreno et al., 2007). All these differences in topsoil properties were accentuated in case of the cleared dehesas, due to a significant increase in organic matter content, total N and available P. In fact, in the studied cleared dehesas, the residues originated by the shrub cutting were partly left on the ground and, in general, these remains contain tissues relatively rich in nutrients, causing a nutrient flush that starts 1 or 2 years after the cutting. The flush continues until the readily decomposed organic matter has been processed into more stable microbial biomass, or mineralized, or converted into relatively stable humus (Kimmims, 1987). Depending on the climatic conditions, soil properties and the quality of the

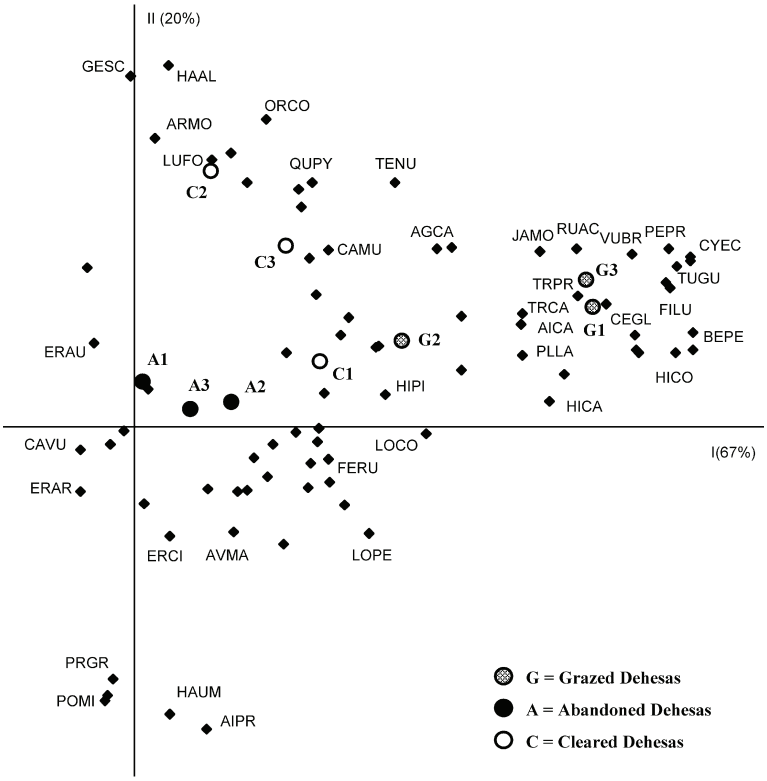

Fig. 5. Location of the dehesa stands and plant species in the plane defined by the first two axes of the detrended correspondence analysis (see Table 3 for species name abbreviations) (explained variance: axis 1 = 67%, axis II = 20%).

plant remains, the addition of these residues to the soil can have either positive or negative effects (Serrada, 1990). These effects have been extensively investigated from a forestry point of view in pine woodlands (Montero et al., 1999; Blanco et al., 2003), *Q. pyrenaica* oak forests (Cañellas et al., 1996) and chestnut (*Castanea sativa*) woodlands (Tokár, 1998). However, there is a lack of knowledge on the effects of shrub cutting on the soil characteristics. Consequently, according to our results, we can only conclude that shrub cutting appeared to favour soil fertility in the short term, provided that part of the plant residues were left on the ground. This effect was accentuated in the cleared dehesas because nutrient sequestration was minimum due to their scarce plant biomass compared to the other dehesa types.

Regarding plant species richness, the values observed in deciduous *Q. pyrenaica* dehesa seem to be lower than those found in evergreen typically Mediterranean dehesa (i.e. see Peco et al., 2006), but the sampling size is different in the different studies and species richness is very much dependent of sampling area (Magurran, 1989, 2004). Comparing the three types considered in this study, we found the highest richness value in grazed dehesas and the lowest in the cleared ones, either at small (per quadrat or m^2) or stand scales, although differences were not statistically significant. Many authors have found that the plant–herbivore interaction maintains or increases vegetation species diversity (Naveh and Whittaker, 1979; Puerto et al., 1990; Montalvo et al., 1993; Bakker and Berendse, 1999; Shackleton, 2000; Poschlod et al., 2005; Acosta et al., 2006; Guretzky et al., 2007), and that, on the contrary, grazing abandonment leads to a decrease in plant species richness. However, other authors have not detected differences in plant species richness between grazed and abandoned areas (Peco et al., 2005, 2006; Öckinger et al., 2006). These contradictory results can be related with the hypotehsis of Milchunas et al. (1998), who have suggested that feedback mechanisms between plants and herbivorous are more developed in subhumid grasslands than in semiarid ones. The lower spatial heterogeneity (estimated by S beta) that characterized the grazed dehesas has also been found in other studies, which attributed their homogeneous floristic composition to the role of livestock, acting as a seed disperser (Peco et al., 2006). Although we expected to find the greatest spatial heterogeneity in the abandoned dehesas, where the irregular distribution of shrub species probably determines differences in microclimate conditions, relevant to other plant species, the highest value corresponded to the cleared ones. Similarly, in experimentally cleared shrublands near the studied dehesas, the greatest spatial heterogeneity was observed in the first 2 years after prescribed cutting or burning, related to different mechanisms of plant species recovery (Calvo et al., 2002a).

In terms of the vegetation life forms, the greatest values for species richness and cover corresponded to annual herbs in the grazed dehesas, in accordance with other studies (McIntyre et al., 1995; Diaz et al., 2007; Guretzky et al., 2007; Tárrega et al., 2007). However, Peco et al. (2005) found similar values of relative cover of annuals vs. perennials in grazed and ungrazed zones. In our study, no significant differences were detected in the perennial species richness (either perennial herbs or woody species) in the three types of dehesa communities. In addition to the annual species richness, the main difference between the dehesa types corresponded to woody species cover, which was significantly higher in the abandoned dehesas, due to the expected consequences of secondary succession (Bakker and Berendse, 1999; Gómez-Limón and de Lucio Fernández, 1999; Peco et al., 2005; Poschlod et al., 2005; Öckinger et al., 2006; Maccherini et al., 2007). Besides, it is worth pointing out that woody species cover was higher (although not significantly so) in cleared dehesas than in the grazed ones even very soon (less than 2 years) after the shrub cutting treatment was applied. This difference in woody species cover was also observed by other authors (Maccherini et al., 2007), who attributed this result to the active vegetative resprouting of the dominant shrub species, also found in shrublands of the same study area (Calvo et al., 2002b). On the other hand, perennial herb cover was lower in the cleared dehesas, with regards to either the grazed or the abandoned ones.

Differences in the floristic composition of grazed and ungrazed areas have been found in previous studies, even when no differences in plant species richness after abandonment were detected (Peco et al., 2005, 2006; Öckinger et al., 2006). Several researchers have suggested that differences in species composition seemed to be more sensitive than diversity measures to detect the influence of management on the vegetation (Brosofske et al., 2001; Nagaike et al., 2003; Onaindía et al., 2004; Tárrega et al., 2006, 2007). In our study area, the complementarity of the floristic compositions of grazed and abandoned dehesas (i.e. the occurrence of different species in each dehesa type) determined greater plant diversity at the landscape scale. Waldhardt and Otte (2003) pointed out the importance of maintaining a mosaic of extensively used grassland stands of different ages to retain plant species and community diversity at the landscape level. This agrees with the general theory that stresses that the greatest diversity value is only achieved through the maintainance of different ecosystem successional stages, related to various types and intensities of use and management (Farina, 2000; Magurran, 2004). However, management by shrub cutting hardly increased the number of plant species, given that they only had two "exclusive" ones and shared 77% of the species with the abandoned dehesas. This may be partly because most of the shrub species in this area are capable of vegetative resprouting after cutting (Calvo et al., 2002b). Furthermore, we could expect higher similarity in species composition between cleared and grazed dehesas (i. e. due to a more similar light conditions in the ground layer) than between abandoned and grazed ones, but it was equivalent (56% of common species in both cases). This was probably due to the paucity of the soil seed bank of the cleared dehesas; most of seeds of typical species of grazed dehesas have dead and they cannot recolonize. In fact, more than 20 years have passed since the abandonment of the cleared dehesas, previously to the application of the shrub cutting treatment. Similar results have even been found in grassland areas considerable different from our dehesa systems. For instance, Maccherini et al. (2007) found that shrub cutting did not suffice to restore the community composition of semi-natural calcareous grasslands, because the restored grasslands did not reach a species composition similar to the reference grasslands. Öckinger et al. (2006) pointed out that for grassland management to be efficient, restoration actions should be carried out in sites at an early stage of the post-abandonment succession, where most management-dependent species are likely to be still present. Bakker and Berendse (1999) had already indicated that restoration of habitats after abandonment is difficult and often does not produce the species richness and composition associated with the original communities. This can be due to difficulties in species re-colonization as many plant species are not present in the soil seed bank and their dispersal is limited by landscape fragmentation. Thus, a suitable way of favouring the restoration of the cleared dehesas could possibly be the reintroduction of grazing activities, since livestock could act as disperser of seeds coming from another grazed dehesas (Malo and Suárez, 1995). In this way, Pykäla (2005) found that restarting grazing in abandoned pastures changed species assemblages towards that of the grazed pastures.

5. Final remarks

Therefore, from the results obtained in this study, we can conclude that, in the considered dehesa ecosystems, shrub cutting did not result in an effective management practice to recover a vegetation composition similar to that of the grazed dehesas, and even could cause the loss of plant species richness in the short term compared to the abandoned ones. Nevertheless, shrub cutting represents a suitable management method to reduce the risk of fire, through a decrease in the biomass load. The maintenance of this management practice would probably be favoured by incorporating an adequate livestock load, which could disperse plant seeds from another grazed dehesas. Indeed, the lower competition between herbs and woody species that characterizes the cleared dehesas, together with higher soil fertility (due to the permanence of shrub cutting remains on the ground and increased by livestock faeces) would probably favour the development of herbaceous species.

Acknowledgement

This paper is part of a research project supported by the Junta de Castilla y León (Ref. LE008A06).

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Biological Conservation 161 (2013) 58–66

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Land use changes and ground dwelling beetle conservation in extensive grazing dehesa systems of north-west Spain

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ARTICLE INFO

Article history:
Received 18 October 2012
Received in revised form 19 February 2013
Accepted 27 February 2013

Keywords:
Oak savannah-like forest
Traditional silvopastoral management
Land use abandonment
Shrub encroachment
Functional guild of species
Carabid and staphylinid assemblages

ABSTRACT

Traditional management practiced over centuries in Mediterranean cultural landscapes has led to singular agrosilvopastoral ecosystems such as dehesas. Recent abandonment of dehesa management has resulted in shrub encroachment, habitat homogenisation and increased fire risk. Mechanical shrub cutting to decrease biomass load creates novel cleared dehesas with yet unknown consequences for the ecosystem function. We investigated the effects of these land use changes on ground dwelling beetles (carabids and staphylinids) as model organisms by comparing traditionally grazed, long-time abandoned and newly cleared dehesas. Land use changes affected beetle species composition by altering habitat structure (e.g., litter layer) and the availability of feeding resources. Grazed dehesas held the highest number of exclusive species and particular functional guilds of carabid seed eaters and staphylinid coprophiles, utilizing food resources related to the presence of grazing livestock (annual herbs and coprophagous insects). Beetle assemblages of abandoned dehesas, resembling those known from surrounding human disturbed oak forests, exhibited the lowest abundance and greatly differed from beetle assemblages of grazed dehesas. Shrub clearance after dehesa abandonment benefited opportunistic beetle predators feeding on decomposers associated with cutting slash left on the ground. The habitat structure and beetle species composition of cleared dehesas slightly approached those of grazed dehesas, therefore suggesting shrub cutting as a first step towards restoration of abandoned dehesas. However, since livestock grazing is an essential driver of ground dwelling beetle composition, it should be promoted after shrub cutting in cleared dehesas to restore the characteristic assemblages, species interactions and ecosystem function of grazed dehesas.

1. Introduction

In the Mediterranean region, characterised by unique cultural landscapes and outstanding biodiversity, many species are strongly adapted to the recurrent disturbances caused by traditional management practiced through millennia (Blondel et al., 2010). Recent land use changes resulting in the abandonment of non-competitive Mediterranean traditional systems can then be detrimental for biodiversity and threaten the preservation of singular ecosystems (Blondel et al., 2010; Stoate et al., 2001) in which resource exploitation and nature conservation are achieved together (see Gómez-Limón and de Lucío Fernández, 1999). This is the case of the Spanish *dehesa* (and its Portuguese counterpart *montado*), a traditional agro-forestry system that simultaneously supports extensive livestock grazing, forestry and even agricultural production while maintaining high values of biodiversity, and that is strongly affected by the land use changes determined by national and EU agricultural policies (Gómez-Limón and de Lucío Fernández, 1999; Plieninger, 2006). The distinct habitat structure of the dehesa system, with mature trees scattered in a continuum of grasslands, depends entirely on traditional management practices and is created by the combination of tree thinning and pruning, shrub cutting and domestic livestock grazing. Dehesas also provide additional ecosystem services economically valuable such as beekeeping, game hunting, ecotourism and even carbon sequestration (Bugalho et al., 2011).

In north-west Spain, dehesas are scarce, mainly constituted by *Quercus pyrenaica* trees, and embedded in a mosaic of forests with different habitat structures shaped by a variety of human uses and disturbances (Tárrega et al., 2006, 2007). Contrary to the large dehesa systems of southern Spain that are privately owned, the small dehesas in north-west Spain function as public renting systems, typically shared by the livestock holders of neighbouring locations.

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0006-3207/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2013.02.017

Uniqueness of these dehesa systems is supported by their peculiar spatial arrangement (Taboada et al., 2006a; Tárrega et al., 2006) and great diversity in microhabitats (i.e., old-growth trees, pasture grassland, clusters of tree saplings, isolated shrubs, piles of pruning debris, etc.) which enhances biodiversity at the local and regional scales (Taboada et al., 2006a, 2011; Tárrega et al., 2006). In these dehesas, the maintenance of large mature trees, uncommon in the surrounding highly modified *Q. pyrenaica* landscape (Robles et al., 2011), is essential for the conservation of endangered species such as the Middle Spotted Woodpecker (Robles et al., 2007), as well as for the persistence of other adapted species like secondary cavity nesting birds (Robles et al., 2011). The singularity of these dehesa sites is reinforced by their cultural and historical values as being part of the traditional transhumance routes used for centuries to shepherd livestock between summer highland and winter lowland pasturelands.

During the last decades a progressive depopulation of the rural areas is threatening the conservation of dehesas (Gómez-Limón and de Lucío Fernández, 1999). The abandonment of dehesa management results in shrub encroachment which increases the risk of fire (Pinto-Correia and Mascarenhas, 1999), may decrease biodiversity (Bugalho et al., 2011) and may lead to habitat loss and reduction of the carrying capacity for livestock (Moreno and Pulido, 2009). To counteract these negative effects and preserve the pasturelands, shrub cutting with heavy machinery has been recently implemented in many places (Canteiro et al., 2011; Pinto-Correia and Mascarenhas, 1999). Mechanical shrub cutting may be detrimental to tree regeneration (Pinto-Correia and Mascarenhas, 1999) and may have negative effects on plant (Tárrega et al., 2009; but see Canteiro et al., 2011) and bird diversity (Camprodon and Brotons, 2006). In those dehesa systems of north-west Spain where grazing activities have become uneconomical, mechanical shrub cutting is a presently applied management practice whose effects on living organisms remain poorly known (Tárrega et al., 2009). As a consequence of the abandonment of traditional land uses and the implementation of new management activities, three types of dehesas currently exist in this region (Fig. 1): (1) traditionally managed dehesas where the extensive grazing system (generally, sheep and goats) is maintained, (2) long-time (more than 20 years) abandoned dehesas, and (3) cleared dehesas where mechanical shrub cutting is carried out by the regional administration to reduce the biomass load after grazing abandonment. The three dehesa management types differ in habitat structure, topsoil conditions and vegetation (Tárrega et al., 2009), which may in turn affect fauna diversity and composition.

Soil arthropods, and among them ground dwelling beetles such as carabids and staphylinids (Coleoptera: Carabidae, Staphylinidae), are particularly sensitive to land use changes (Bohac, 1999; Rainio and Niemelä, 2003). In temperate regions, these beetles are plentiful and diverse and greatly contribute to ecosystem functioning mainly by pest predation (Bohac, 1999; Lövei and Sunderland, 1996; Rainio and Niemelä, 2003) and seed consumption (Honek et al., 2003). The majority of carabids are generalist predators though some complement their diet with seeds or are specialised granivores (Honek et al., 2003 and references therein). Similarly, although some staphylinid beetles feed on fungi or pollen, the majority are also predators (Bohac, 1999), many being adapted to ephemeral microhabitats such as carrion, dung, rotting plants and fungi, where they principally feed on fly larvae and other small arthropods (Muona and Rutanen, 1994). Since carabids and staphylinids belong to high trophic levels of the soil food web (Halaj and Wise, 2002) they may reflect changes at lower trophic levels caused by shifts in the nutrient input, plant production, habitat structure and arthropod abundance and composition (Lövei and Sunderland, 1996; Thiele, 1977). Previous studies have demonstrated that the dehesa systems of north-west Spain greatly contribute to regional biodiversity as they hold distinct carabid assemblages different from those of adjacent *Q. pyrenaica* ecosystems (Taboada et al., 2006b) and pasturelands (i.e., grasslands not surrounded by a forest matrix; Taboada et al., 2011). Within these dehesa ecosystems, carabid assemblages also differ between the forested habitat and the pasture grassland (Taboada et al., 2006b) rendering high diversity values at the local scale. However, there are no studies on the staphylinid assemblages of these dehesa systems to date. Although several authors have studied the effects of dehesa grazing abandonment and shrub encroachment on ground dwelling arthropods (Azcárate and Peco, 2012; Barriga et al., 2010; Martins da Silva et al., 2008, 2009), to our knowledge,

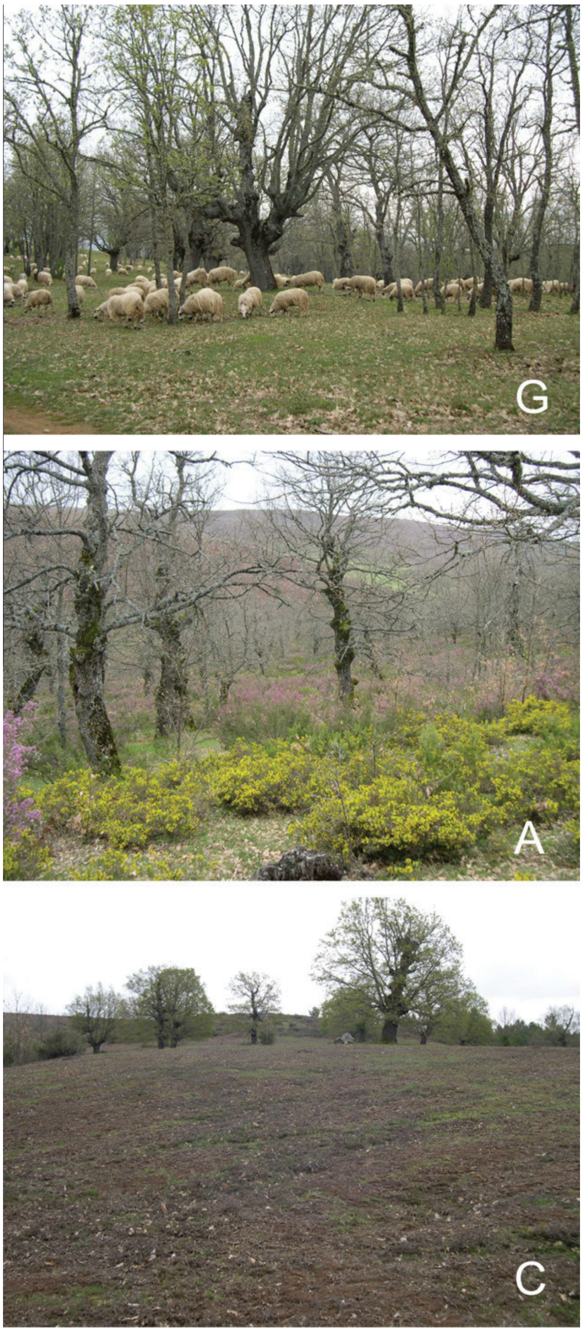

Fig. 1. The three types of dehesa systems, defined by the different management practices applied. G = grazed dehesas; A = abandoned dehesas; C = cleared dehesas.

Table 1
Habitat characteristics and arthropod abundance (mean ± SE) for each dehesa management type ($N = 3$).

	Management type		
	Grazed	Abandoned	Cleared
Topsoil characteristics			
Sand (%)	62.80 ± 2.50	66.67 ± 0.67	71.33 ± 6.57
Silt (%)	31.47 ± 1.64	28.67 ± 1.33	24.00 ± 6.11
Clay (%)	5.73 ± 1.19	4.67 ± 0.67	4.67 ± 0.67
pH	5.26 ± 0.19	5.46 ± 0.31	5.17 ± 0.08
OM (%)	6.19 ± 1.57	7.05 ± 0.66	8.35 ± 0.86
Total N (%)	0.26 ± 0.06	0.21 ± 0.02	0.26 ± 0.02
C/N	13.42 ± 1.03b	19.36 ± 0.53a	18.53 ± 1.08a
P (mg/kg)	5.54 ± 0.73a	1.90 ± 0.64b	4.16 ± 0.39a
Ca^{2+} (cmol/kg)	2.50 ± 0.08	2.62 ± 0.31	2.20 ± 0.17
Mg^{2+} (cmol/kg)	0.47 ± 0.06	0.36 ± 0.10	0.29 ± 0.03
K^{+} (cmol/kg)	0.46 ± 0.05	0.60 ± 0.13	0.70 ± 0.05
Na^{+} (cmol/kg)	0.02 ± 0.01	0.03 ± 0.01	0.03 ± 0.01
Habitat structure			
Bare soil cover (%)	4.30 ± 2.60b	10.56 ± 2.42b	23.56 ± 1.66a
Stones cover (%)	0.40 ± 0.28	0.29 ± 0.29	0.11 ± 0.11
Litter cover (%)	1.93 ± 1.41b	48.22 ± 10.67a	63.67 ± 5.34a
Litter depth (cm)	1.10 ± 0.55b	3.29 ± 0.39a	3.49 ± 0.45a
Herb cover (%)	95.95 ± 2.68a	77.78 ± 5.33b	24.58 ± 4.70c
Shrub cover (%)	0.00 ± 0.00b	27.11 ± 5.49a	0.00 ± 0.00b
Oak tree cover (%)	0.00 ± 0.00	2.00 ± 1.20	0.00 ± 0.00
Oak tree distance (m)	22.29 ± 4.19	13.56 ± 2.66	15.36 ± 0.44
Arthropod abundance (number of individuals)			
Formicidae	2341.33 ± 633.55a	681.00 ± 156.00b	705.00 ± 52.92b
Araneae	768.00 ± 131.61	701.00 ± 138.29	544.67 ± 94.22
Opilionida	1.00 ± 0.58b	133.00 ± 48.51a	85.67 ± 17.70a
Diptera	869.00 ± 69.57a	215.00 ± 24.06c	627.67 ± 94.73b
Collembola	37215.00 ± 11012.42a	3831.67 ± 451.04b	20731.67 ± 12760.57a

Different letters indicate significant differences ($p < 0.05$) between management types according to the GLMs.

no data exist on the effects of shrub clearance in dehesas following abandonment.

In this study we aim to assess the effects of recent land use changes on the ground dwelling beetle fauna of the dehesa systems of north-west Spain. Using carabids and staphylinids as the model organisms, we intend to determine how different management strategies affect their abundance, species richness, diversity and composition in three types of dehesa systems: (1) grazed, (2) abandoned, and (3) cleared dehesas. Moreover, we want to know if the effects of management on beetle assemblages can be explained by the changes caused on topsoil characteristics, habitat structure and arthropod abundance. Specifically, we hypothesised that (1) species richness and diversity would be highest in grazed dehesas, due to intermediate disturbance via grazing (see Perevolotsky and Seligman, 1998) and lowest in cleared dehesas due to habitat homogenisation; (2) grazed and cleared dehesas, with apparently alike habitat structures, would hold more similar beetle assemblages compared to the abandoned dehesas; and (3) differences in habitat structure would be the main factor affecting carabid and staphylinid species composition in the three dehesa management types. The study will provide new insights into the effectiveness of mechanical shrub cutting to restore the habitat structure of long-term abandoned dehesas and recover the ground dwelling beetle assemblages characteristic of traditionally grazed dehesas.

2. Materials and methods

2.1. Study area

Q. pyrenaica forests are almost restricted to the Iberian Peninsula (Blanco et al., 1997) and represent 6.5% (ca. 950 000 ha) of the forested area in Spain (Maldonado et al., 2001). Despite their conservation value (Directive 92/43/CEE), only 2.24% of this area is protected in Spain (Maldonado et al., 2001). In north-west Spain, these forests are located in the transition zone between typical Mediterranean forests (mainly *Q. ilex*) and temperate deciduous forests (e.g., *Fagus sylvatica*) (Blanco et al., 1997). Pyrenean oak forests have persisted thanks to their high adaptability to human exploitation and grazing pressures (see Pardo and Gil, 2005), which have shaped the landscape in a mosaic of forests with diverse understory and canopy structures (see Tárrega et al., 2006, 2007).

The study was conducted in a *Q. pyrenaica* mosaic landscape located at the lower slopes of the Cantabrian mountain range, north-west Spain (42°33'-42°46′N, 4°55′–5°08′W), at an altitude of 975–1130 m a.s.l. Climate is sub-humid Mediterranean type (mean annual temperature 10.9 °C, mean annual precipitation 927 mm, dry period in July and August) and the type of soil is humic cambisol. Dehesa systems with three different types of management were selected: (1) currently grazed dehesas ("*G*", size range of the studied dehesas = 5.2–27.6 ha), (2) abandoned dehesas ("*A*", 7.3–13.0 ha) (more than 20 years without grazing) and (3) cleared dehesas ("C", 5.9-8.1 ha) where mechanical shrub cutting took place 1–2 years before the study and part of the slash remained present at the sampling time. The surrounding habitat of the studied dehesas was mainly dominated by agricultural land and dense mature oak forests. Also, pine plantations were present in the proximity of the three dehesa systems. Three independent replicates (i.e., not clustered together and at least 1 km apart, Supplementary Fig. S1) of each management type were chosen. The study sites were flat or with less than 10% slope, tree density was approximately 100 trees/ha, tree height was around 10–12 m and trunk perimeter (at breast height) about 1–1.5 m. In abandoned dehesas, the dominant shrub species were *Calluna vulgaris* and *Erica australis* forming an extended shrub layer (ca. 30% cover) (Tárrega et al., 2009). In grazed dehesas, shrubs were scarce and scattered but well developed (height: 50–110 cm; width: 100–200 cm), while in cleared dehesas they consisted of small resprouts from the roots of cut shrubs. Further details on soil characteristics and habitat structure are found in Table 1.

2.2. Sampling method

Sampling focused on the main livestock grazing area of the grazed dehesas or at its former location previous to shrub encroachment in the abandoned and cleared dehesas. Additional microhabitats present in the dehesa other than the pasture grassland (i.e., trees, trees surrounded by saplings, isolated shrubs and piles of pruning debris) were left unsampled in this study (García-Tejero et al., unpublished). Five sampling points were located in each dehesa at least 25 m apart from each other and from site edges. Data on arthropods, habitat structure and topsoil variables were collected at each sampling point.

2.2.1. Arthropods

We used plastic pitfall traps (depth 86 mm, diameter 60 mm) covered by 10 × 10 cm roofs, partly filled with 25% propylene glycol and flush to the soil surface to collect the arthropods. Pitfall catches reflect arthropod activity-density (Thiele, 1977) that will be referred hereafter as abundance or number of individuals. Two pitfall traps, 50–200 cm apart, were placed at each sampling point (i.e., 10 traps per site, 90 traps in total). Arthropods were collected continuously from 1 June to 20 October 2007, emptying the traps every 3 weeks. Carabids and staphylinids were identified using standard keys, and were named according to current species catalogues (Supplementary Table S1). All carabids and most staphylinids (95.7%) were identified to species level; staphylinids which could not be assigned to any species (45 individuals) were only included in the analysis of overall abundance. Several arthropod groups which were considered to likely influence carabid and staphylinid species composition (Thiele, 1977) via potential competition (ants, spiders and harvestmen) or as prey items (Diptera and springtails) were sorted out and counted (see Table 1).

2.2.2. Habitat characteristics

Topsoil characteristics were analysed from the first five centimetres of soil at each sampling point. Samples were homogenised in a uniform sample for each site, which was air-dried and passed through a 2 mm mesh sieve for later analysis. Topsoil pH, organic matter content (O.M.), total nitrogen (N), C/N ratio and available phosphorus (P), calcium (Ca^{2+}), potassium (K^{+}), magnesium (Mg^{2+}) and sodium (Na^{+}) were determined for each sample, following the official methods of topsoil analysis.

Habitat structure was surveyed at each sampling point using three 1 m^2 quadrats arranged in a regular triangle and spaced out one metre (see Tárrega et al., 2009), at the vicinity of the pitfall traps to detect the main relations between beetle captures and habitat variables by ordination methods (see below; e.g., Taboada et al., 2006b). Percentage cover of bare soil, stones, litter, herb (<0.5 m height) and shrub (0.5–2 m) layers, and oak tree canopy above sampling point was visually estimated at each quadrat. Estimations were performed always by the same researcher, so that the bias, if it existed, was similar in all sampling points. Litter depth was also measured at quadrat level and included slash in cleared dehesas. Distance to the four nearest oak trees was measured at each sampling point. Details are shown in Table 1.

2.3. Data analysis

Prior to the analyses, arthropod catches were pooled for each dehesa site (i.e., the five sampling points) and for the whole trapping period. Similarly, average values for habitat structure variables were calculated for each site.

Generalised linear models (GLMs) were used to look for differences in overall beetle abundance and diversity between the three management types. Diversity was calculated as the exponential of Shannon entropy, advocated by Jost (2006) as a true diversity index. This gives the effective number of species, which is the amount of equally-common species that would be present in an equivalent community with the same entropy value (Jost, 2006). Abundance and diversity data were modelled using negative binomial and Gaussian error distributions, respectively. GLMs were also used to look for differences in habitat characteristics and arthropod abundance variables between management types (Table 1). Soil and habitat structure variables were modelled using Gaussian error distributions and arthropod abundances using negative binomial distributions.

Sample-based rarefaction was used to calculate the number of species present in each treatment relative to the number of individuals captured. This allows for comparison of species richness between treatments taking into account differences in beetle abundance. The 95% confidence intervals of the randomization curves were used to assess significant differences in species richness between treatments.

Patterns in species composition between sampling sites were investigated with principal components analysis (PCA). The analysis was carried out on the whole species datasets, but only species with more than five individuals are shown in the figures to improve visualization.

Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was performed to test for differences in species composition between management types. The analysis was performed on Hellinger distances and significance was assessed using Monte-Carlo p values (9999 permutations), appropriate when the number of replicates is low (Anderson, 2005).

Redundancy analysis (RDA) was used in a variation partitioning scheme to relate the species composition patterns with four different groups of explanatory variables (Table 1): management type, topsoil characteristics, habitat structure and arthropod abundances. Variation partitioning (Borcard et al., 1992) allows discriminating between the percentage of variation independently explained by each group of explanatory variables and by all their possible combinations. Prior to this analysis, the best explanatory variables in each group were chosen using step-wise forward selection. This procedure is the most commonly used in RDA, although the order of inclusion of variables might affect the subsequent variables included in the model, thus becoming a possible source of bias. Variables were selected one by one when significant ($p < 0.05$) according to their contribution to the model (i.e., the variables which increased most the R^2 of the model were first selected). Significance was tested at each step using 1000 permutations and the R^2 value of the global model was used as stopping criterion (i.e., the selection procedure stopped when the inclusion of a new variable increased the R^2 value over that of the model containing all the explanatory variables) (Blanchet et al., 2008).

Prior to their inclusion in PCA and RDA analyses, the number of individuals were Hellinger-transformed in order to reduce the influence of extreme values and the effect of the double-absences in the data matrix (Legendre and Gallagher, 2001). Management type, a categorical variable, was coded into a matrix of dummy binary variables to allow its inclusion in variation partitioning (see Borcard et al., 2011). The procedure for PCA, RDA, forward selection and variation partitioning follows Borcard et al. (2011).

Distinctness in species composition between and within management types was assessed using the Complementarity Index in Colwell and Coddington (1995). This is a qualitative measure of beta diversity (i.e., it takes into account only species presence-absence) mathematically defined in Koleff et al. (2003) as:

$$\beta_{cc} = 100 * \left(\frac{a+b}{a+b+c}\right)$$

where a is the number of species unique to the first site, b is the number of species unique to the second site and c is the number of species common to both sites. Complementarity values vary from 0% (identical species list) to 100% (no species shared).

Analyses were carried out with widely available free statistical programs, namely R statistical software (R Development Core Team, 2009), EstimateS (Colwell, 2006) and PERMANOVA (Anderson, 2005).

3. Results

3.1. Species abundance, diversity and richness

We collected 3632 individuals and 55 species of carabids and 1046 individuals and 86 species of staphylinids (Supplementary Tables S2 and S3). While the majority of the species were represented by few individuals, the four most abundant carabid species accounted for 79.3% of the total capture: *Steropus globosus* (1858 individuals, 51.2%), *Nebria salina* (581, 16.0%), *Calathus fuscipes* (257, 7.1%) and *Poecilus kugelanni* (182, 5.0%).The four most abundant staphylinid species represented 46.5% of the total capture: *Aleochara bipustulata* (198 individuals, 18.9%), *Oxypoda ferruginea* (109, 10.4%), *Ocypus olens* (95, 9.1%) and *Aleochara laticornis* (85, 8.1%).

Several species were exclusively collected in grazed (16 carabids and 26 staphylinids), abandoned (10 and 13) and cleared (3 and 19) dehesa management types. All exclusive species were represented by less than seven individuals, with the exception of the carabid *Harpalus distinguendus* (148 individuals) and the staphylinids *Philonthus cognatus* (13) and *Quedius semiaeneus* (31), only found in grazed dehesas.

Carabid overall abundance was significantly higher ($\chi^2 = 3.85$, $p = 0.02$) in cleared than in abandoned dehesas, grazed dehesas having an intermediate number of individuals (Fig. 2). Staphylinid overall abundance did not differ between management types ($\chi^2 = 0.36$, $p = 0.25$), but more individuals were caught in cleared than in abandoned dehesas, while in grazed dehesas the capture varied widely from site to site (Fig. 2).

Carabid diversity (i.e., effective number of species) significantly differed between management types ($F = 9.79$, $p = 0.01$), being higher in grazed than in cleared dehesas, with abandoned dehesas in an intermediate position (Fig. 2). Staphylinid diversity did not differ between management types ($F = 3.39$, $p = 0.10$), but grazed dehesas held lower effective number of species than abandoned ones, while diversity varied widely in cleared dehesas (Fig. 2).

Rarefied carabid species richness was significantly higher in abandoned and grazed than in cleared dehesas, according to 95% confidence intervals, but no differences were found for staphylinids (Fig. 2).

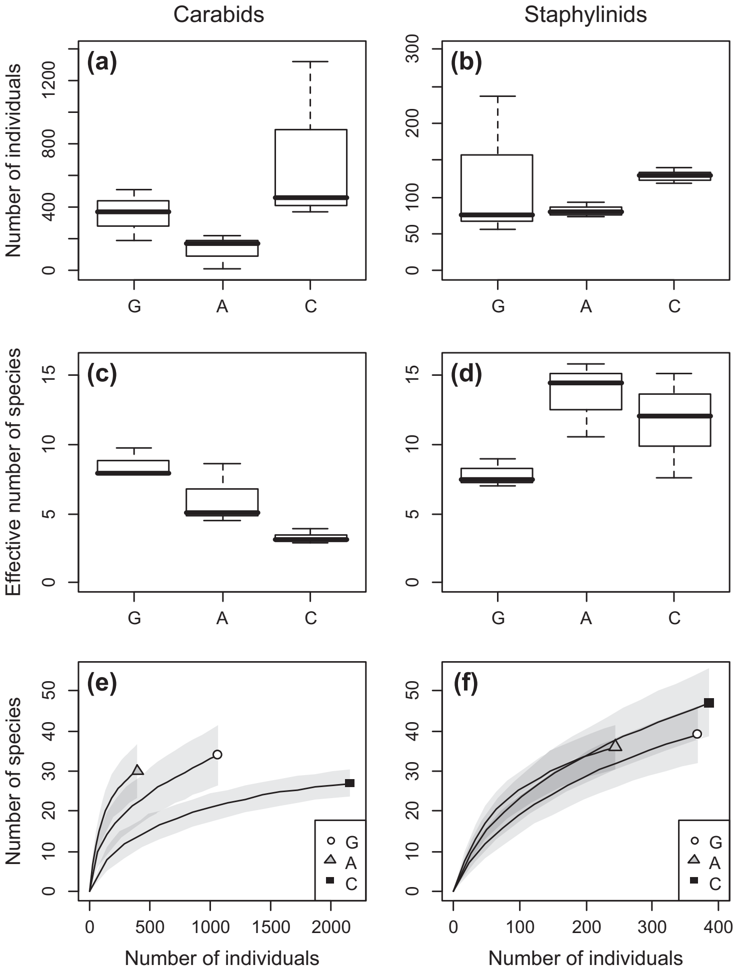

Fig. 2. Boxplots of the number of individuals, effective number of species (diversity) and rarefied number of species for carabid (a, c, and e) and staphylinid (b, d, and f) beetles at the three management types: G = grazed, A = abandoned, C = cleared dehesas. Boxplots show the median (black bold line), the first and third quartiles (lower and upper limits of the box) and the range (ends of the whiskers). Rarefaction curves (e and f) represent the number of species relative to the number of individuals for each management type. 95% confidence intervals for each curve are indicated in light grey shading.

3.2. Species assemblage composition

The PCA for carabids (Fig. 3a) shows that grazed dehesas contained beetle assemblages that were different from the cleared and abandoned dehesas, mainly as a result of some characteristic species such as *Amara aenea*, *C. fuscipes*, *Harpalus anxius* and *H. distinguendus* abundant in grazed sites, but uncommon under the other management types. Abandoned dehesas held quite different assemblages, two of the sites accounting for a high proportion of the *P. kugelanni* individuals collected and the other one with very low number of individuals, mainly represented by *Synuchus vivalis* and *Trechus obtusus*. The latter two species were also found in cleared dehesas, where *Carabus amplipennis*, *N. salina* and *S. globosus* dominated. PERMANOVA results backed up these patterns confirming that carabid species composition significantly differed among management types (global test, $F = 2.82$, $p = 0.02$), specifically between grazed and cleared dehesas (pairwise *post-hoc* test, $t = 2.73$, $p = 0.01$).

The PCA for staphylinids (Fig. 3b) showed that species composition was more different between grazed and abandoned dehesas, while cleared dehesas clustered in between and held assemblages similar to either grazed or abandoned dehesas. Grazed dehesas contained high proportion of the captures of *A. bipustulata*, *Anotylus inustus*, *O. ferruginea* and *Quedius semianeneus,* the first two species being also in common with one cleared dehesa site. The remaining two cleared dehesa sites held assemblages more similar to abandoned dehesas since they accounted for high proportion of *Liogluta longiuscula* and *O. olens* which, along with *A. laticornis* and *Oxypoda praecox*, were abundant in abandoned dehesas. The staphylinid species composition of one of the abandoned dehesas differed slightly from the rest, probably due to the high proportion of *Anthobium unicolor* and *Drusilla canaliculata* found there. The overall pattern was confirmed by PERMANOVA results that found significant differences in staphylinid composition among management types (global test, $F = 2.53$, $p = 0.03$), specifically between grazed and abandoned dehesas (pairwise *post-hoc* test, $t = 1.92$, $p = 0.04$).

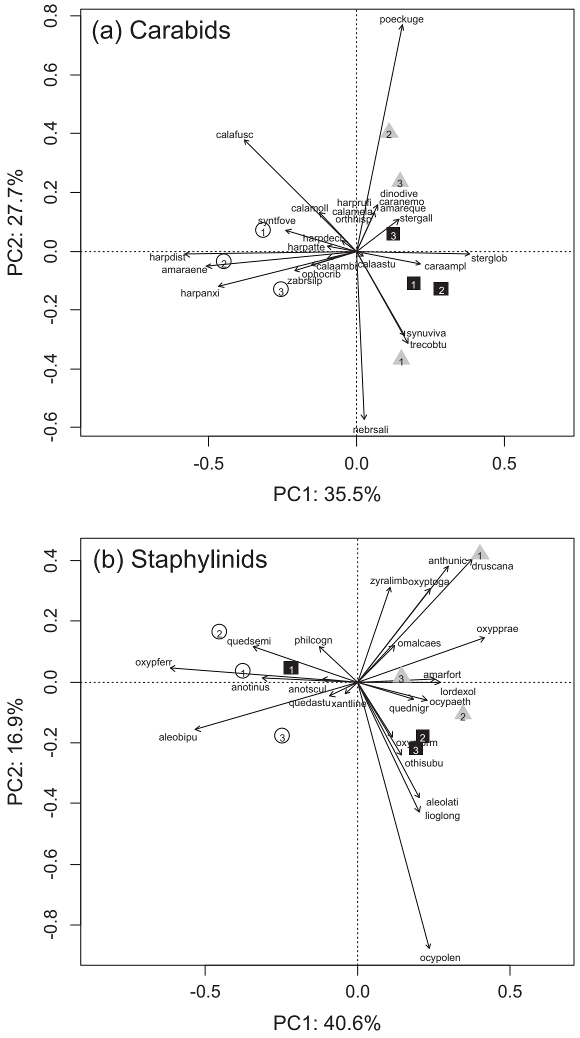

Fig. 3. Plot of the first two axes of PCA for (a) carabid and (b) staphylinid assemblages. Percentage of represented variance is indicated for each axis. Sites are depicted by symbols (○ = grazed, ▲ = abandoned, ■ = cleared dehesas). For clarity, only the species with more than five individuals are represented in the plot. Species names are formed by the first four letters of the genus and the first four letters of the species names (see Supplementary Tables S2 and S3 for correspondences).

Table 2
Mean (±SE) percentage of species that are complementary to sites within and between dehesa management types by using the complementarity index in Colwell and Coddington (1995).

	Management type		
	Grazed	Abandoned	Cleared
Carabids			
Grazed	54.8 (±4.6)	79.5 (±2.0)	72.0 (±4.1)
Abandoned		77.0 (±7.5)	71.7 (±4.0)
Cleared			63.9 (±10.5)
Staphylinids			
Grazed	71.6 (±4.8)	88.1 (±1.3)	81.8 (±1.9)
Abandoned		59.6 (±0.9)	70.2 (±1.8)
Cleared			64.7 (±4.6)

High complementarity values indicate low similarity between sites or management types.

Complementarity values for carabids and staphylinids were highest between grazed and abandoned dehesas, indicating a very different qualitative species composition between these management types (Table 2). The lowest complementarity values were found within grazed dehesas for carabids and within abandoned ones for staphylinids.

3.3. Response to environmental variables

For carabid species composition, 64% of the total variation was explained by the four groups of explanatory variables considered (Fig. 4a). Management type accounted for 30% of the variation, while habitat structure (specifically litter cover) and topsoil characteristics (C/N and Ca^{2+}) individually explained 10% and 9%, respectively, and 16% jointly. The only significant explanatory variable in the arthropod group was the abundance of ants that accounted for 7% of the total variation.

Variation partitioning for staphylinids showed that 41% of the total variation was explained by the four groups of explanatory variables (Fig. 4b). Habitat structure (litter depth and canopy cover above sampling point) individually explained 23% of the variation and 18% together with management and arthropods (number of Diptera). Although phosphorous was selected as significant explanatory variable in the RDA models, it only explained a low proportion of variation which was also accounted for by the other groups of variables.

4. Discussion

4.1. Management effects

Differences between dehesa management types were found in carabid and staphylinid species composition and overall

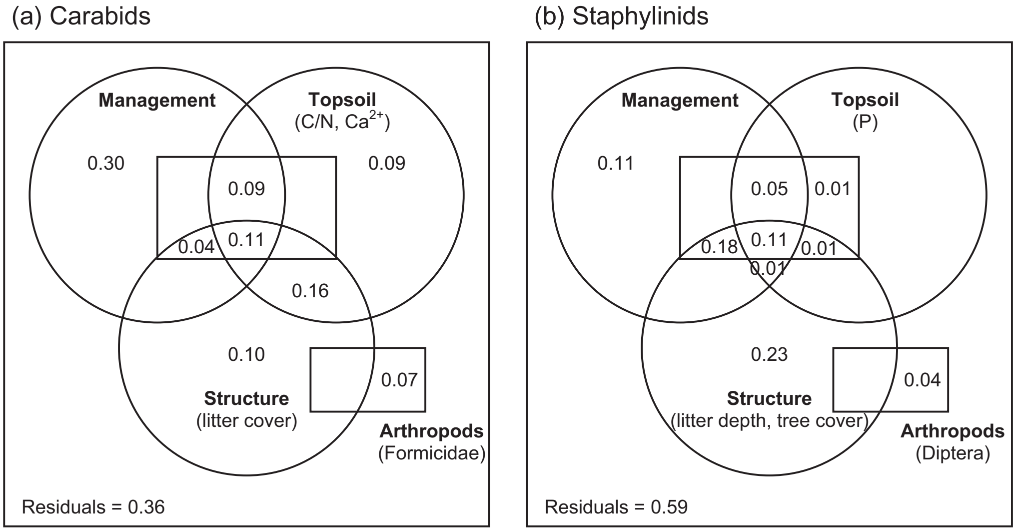

Fig. 4. Venn's diagrams representing the partition of variation of (a) carabid and (b) staphylinid beetle composition explained by four groups of variables: management, topsoil, habitat structure, and arthropod abundances. Each group of variables is represented by a circle, except arthropod abundances, indicated by two rectangles. Variables included in each group were selected using a step-wise forward procedure and are indicated between parentheses. The proportion of variation explained by each group or combination of groups is indicated. Missing values correspond to negative values of variation explained, which are not important in model interpretation (see Borcard et al., 1992).

abundance, and also in carabid diversity and species richness. Extensively grazed dehesas held the highest number of exclusive species and particular assemblages of ground dwelling beetles, underlying the relevance of traditional management in Mediterranean silvopastoral systems for conservation purposes. These results also highlight the importance of low intensity grazing for the protection of biodiversity and for the maintenance of the functional roles of these beetles in ecosystem processes and services (see Bugalho et al., 2011; Perevolotsky and Seligman, 1998; Watkinson and Ormerod, 2001). Many studies have evidenced that traditional management practices are crucial for the conservation of biodiversity in comparable cultural landscapes: beetles in calcareous grasslands in UK (Woodcock et al., 2005) and cork-oak woodlands in Portugal (Martins da Silva et al., 2009), true bugs in extensive meadows in Switzerland (Di Giulio et al., 2001), and plants (Peco et al., 2006), beetles (Taboada et al., 2011), spiders (Barriga et al., 2010), and lizards (Martín and López, 2002) in different kinds of Spanish dehesas. Consequently, the recent decline and loss of traditional management in these human-shaped ecosystems can have serious ecological impacts and negative conservation implications in the European context, particularly in southern Europe (Stoate et al., 2001).

Distinctness in ground dwelling beetle species composition was expected to be greatest for the abandoned dehesas, the most different management type in terms of habitat structure resulting from shrub encroachment, compared to grazed and cleared dehesas. Contrary to this prediction, our results confirm the uniqueness of the carabid and staphylinid assemblages inhabiting traditionally grazed dehesas, further reinforced by the existence of many exclusive species collected here (see Tárrega et al., 2009 for plants). From a qualitative point of view, the ground dwelling beetle species composition of cleared dehesas slightly approached that of grazed dehesas, by comparison to the abandoned ones. Yet, the carabid species composition of grazed dehesas differed from that of cleared ones, despite the apparent equivalence of the open habitat structure devoid of shrub cover, resulting from these two types of management. In the case of staphylinid beetles, the species composition of grazed dehesas was markedly distinguishable from the abandoned ones. For both groups of ground dwelling beetles, habitat structure was an important factor determining the species composition of their assemblages. However, while staphylinid beetle composition was mostly influenced by habitat structure variables such as litter depth and tree cover above sampling point, carabids were primarily affected by the type of management alone, followed by habitat structure (i.e., litter cover).

Outstandingly, the ground dwelling beetle assemblages of grazed dehesas were essentially constituted by functional guilds absent from the abandoned and cleared dehesas. These particular functional guilds consisted of seed eater species in the case of carabid beetles and coprophilous species in the case of staphylinids. The prevalence of these guilds of species might be explained by the presence of livestock in the grazed dehesas. Sheep contribute to disperse annual herbs by spreading the seeds contained in their faeces (Peco et al., 2006) and transporting the seeds adhered to their wool (Manzano and Malo, 2006), very likely increasing the availability of food resources for seed-eater species, such as the carabids *A. aenea*, *H. anxius* and *H. distinguendus*. The annual plant community that characterises the grazed dehesas has been reached after decades of traditional extensive management, at the same time as lost after abandonment and not completely restored after shrub clearing (Tárrega et al., 2009). Sheep faeces also provide suitable habitat for coprophagous insects upon which coprophilous species feed, such as the staphylinids *A. bipustulata* and *A. inustus*. Prey availability for coprophilous staphylinids directly depends on the amount of sheep droppings, which in turn is determined by the type of management developed in the dehesa (i.e., low intensity grazing). Our results suggest that the accidental livestock passage across cleared dehesas in route to neighbouring grazed dehesas might be responsible for the existence of shared coprophilous staphylinid species. This supports the idea that shrub clearance after management abandonment should be complemented by extensive livestock grazing in order to restore the functional guilds of species, ecological interactions and ecosystem services characteristic of traditional dehesa systems (Bugalho et al., 2011; Hobbs et al., 2009; Pinto-Correia and Mascarenhas, 1999; Tárrega et al., 2009).

Most ground dwelling beetle species had lower abundances in abandoned dehesas compared to the other management types.

Although the abandonment of traditional dehesa management and the subsequent shrub encroachment did not affect ground dwelling beetle diversity and species richness, abandonment has led to ground dwelling beetle assemblages resembling those of the surrounding oak forest matrix (García-Tejero et al., unpublished; see Taboada et al., 2006a), without enhancing diversity at the landscape scale. In many historical silvopastoral systems like the dehesas of north-west Spain, the abandonment of extensive livestock grazing activities is usually considered as detrimental for biodiversity (Azcárate and Peco, 2012; and references therein). Indeed, shrub encroachment causes habitat homogenisation reducing reptile (Godinho et al., 2011), bird (Pulido and Diaz, 1992) and mammal (Gonçalves et al., 2012) species diversity (but see Azcárate and Peco, 2012 for seed eater ants). From a ground dwelling beetle perspective, the novel dehesa ecosystem created by shrub cutting after the abandonment of traditional management represents a new environment completely transformed from the historic dehesa system (see Hobbs et al., 2009). Cleared dehesas contain large open sun-exposed areas covered by considerable amount of rotting slash left on the ground after shrub clearance, which may represent an abundant nutrient source and an essential microhabitat for decomposers like fly larvae and collembolans. These prey items may favour opportunistic predators (Halaj and Wise, 2002), such as the carabids *C. amplipennis*, *N. salina* and *S. globosus*, and the staphylinids *L. longiuscula* and *O. olens*. Contradictory results were obtained on species diversity and richness and the number of exclusive species collected in cleared dehesas for carabids and staphylinids. In this sense, shrub clearing may be regarded as negative for carabid diversity as already observed for birds (Camprodon and Brotons, 2006) while it hardly affected staphylinid diversity and richness, even providing the appropriate conditions for high number of exclusive species.

4.2. Conservation implications

Traditional extensive grazing dehesa systems of the Mediterranean Basin are human-shaped ecosystems with high conservation and socioeconomic value (Beaufoy, 1998). Like many other agroforestry systems and cultural landscapes in Europe (e.g., heathlands and semi-natural grasslands), dehesas are currently threatened by the decline and abandonment of land uses (Gómez-Limón and de Lucío Fernández, 1999; Plieninger, 2006), and require active management to ensure their preservation (Bugalho et al., 2011). Successfully managing abandoned dehesas to counteract the consequences of land use cessation (i.e., shrub encroachment and habitat homogenisation) implies the cooperative involvement of all stakeholders (Plieninger et al., 2004), and the need for monitoring and evaluating restoration actions. Understanding the determinants of ground dwelling beetle diversity in historically grazed dehesas provides important baseline information that can guide policy decisions concerning restoration management and biodiversity conservation in abandoned dehesas, as well as in many other traditional agro-forestry systems facing similar consequences of land use abandonment (e.g., Taboada et al., 2011). Also, more detailed knowledge on the functioning of the novel ecosystems created by land use changes and restoration measures, such as cleared dehesas, is crucial to determine the appropriate management priorities and policy strategies that need to be developed and implemented (Hobbs et al., 2009).

The results of this study confirmed that conservation and restoration of the historic dehesas of north-west Spain might remain an achievable goal, since mechanical shrub cutting has proven appropriate as a starting-point action to restore abandoned dehesas to a state closer to traditionally grazed ones (see also Tárrega et al., 2009). However, shrub clearance alone may not be sufficient to restore the food resources on which the functional guilds of species characteristic of grazed dehesas depend (see Tárrega et al., 2009). Prescribed grazing by domestic livestock following mechanical shrub cutting may thus constitute a necessary practice to effectively restore abandoned dehesas. Since the current socioeconomic context (i.e., depopulation trends and decline in livestock loads) makes active management conservation for all dehesas unfeasible, we recommend focusing economic efforts on (1) the maintenance of currently grazed dehesas by encouraging traditional management activities (see Plieninger, 2006), and on (2) the restoration of some selected abandoned dehesas by prescribing shrub clearance followed by low intensity grazing. Implementing these measures in the dehesas of north-west Spain might be easily achievable because they function as public rental systems where management decisions rely on the regional administration (see Plieninger et al., 2004).

To preserve biodiversity at the landscape scale, several authors have urged to maintain a mosaic of dehesas with distinct vegetation structures in a rotational cycle (Canteiro et al., 2011; Moreno and Pulido, 2009, and references therein), as well as to combine areas with different types of grazing pressure (Peco et al., 2006). Based on our findings, however, a more thorough evaluation of both abandoned and cleared dehesas is needed to confirm their biodiversity conservation value at the regional scale. Our results evidenced the high conservation value of grazed dehesas at the landscape scale in north-west Spain (see also Robles et al., 2007, 2011; Taboada et al., 2006a, 2006b; Tárrega et al., 2007, 2009), in accordance with other studies from comparable extensive grazing systems of southern Europe (Barriga et al., 2010; Martins da Silva et al., 2008, 2009; Peco et al., 2006). This underlines the necessity of specific dehesa policy strategies that acknowledge the role of traditional management for preserving an ecosystem unique for its combination of human uses, biodiversity and beauty.

Acknowledgements

The authors are grateful to Hugo Robles for his help in the location of the dehesa sites. Three anonymous referees improved the manuscript considerably. This study is part of a research project supported by the Junta de Castilla y León (Ref. LE008A06). S. García-Tejero was financed by the Junta de Castilla y León. A. Taboada is funded by Ministerio de Educación, Spain (postdoctoral fellowship EX2009-0989).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.02.017.

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Biological Conservation - Electronic Supplementary Material

Land use changes and ground dwelling beetle conservation in extensive grazing dehesa systems of north-west Spain

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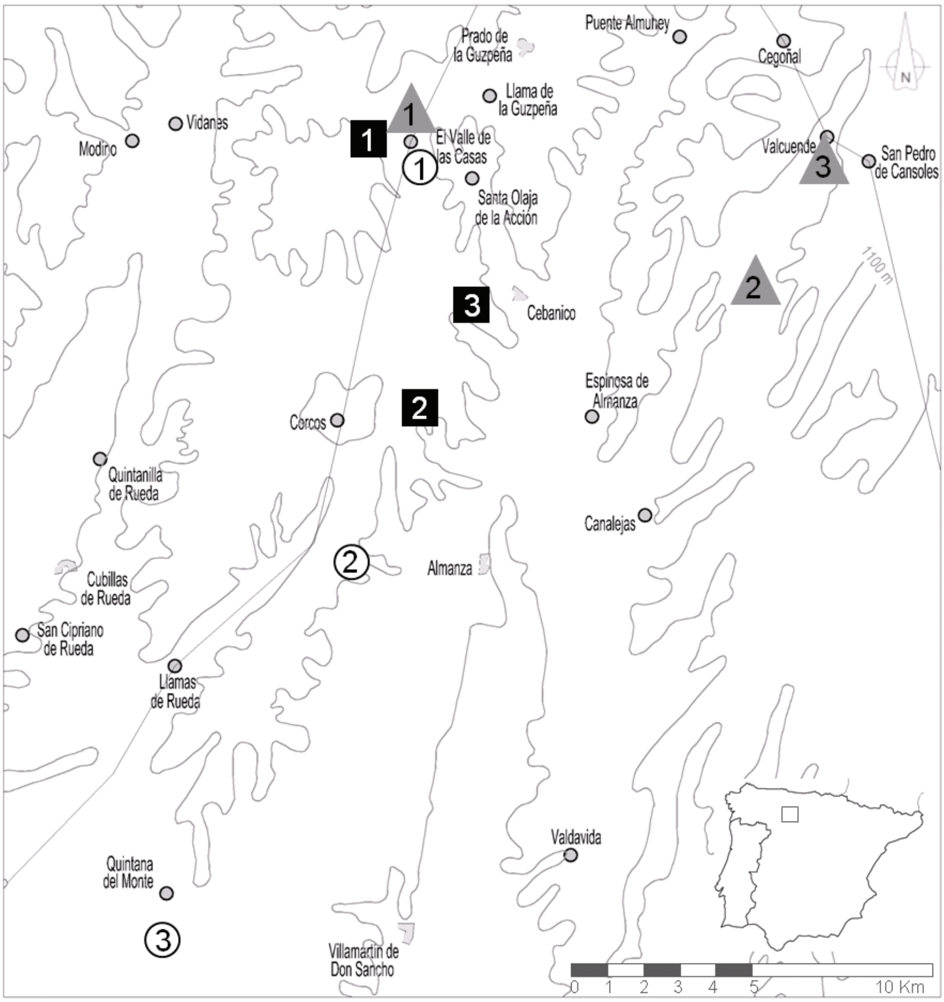

Supplementary Figure S1. Geographic layout of the sampled dehesas. Symbols represent grazed (○), abandoned (▲) and cleared (■) dehesas while numbers indicate site identity and correspond to those in the PCA plots. Contour lines represent elevation and straight lines represent the main transhumance shepherding routes ("cañadas").

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Supplementary Table S1. Reference list of the standard keys used for beetle identification, and the species catalogues adopted for carabid and staphylinid nomenclature.

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Supplementary Table S2. Carabid beetles collected at grazed, abandoned and cleared dehesas. Name abbreviations are indicated for the species shown in the PCA plot.

		Management type			Total
		Grazed	Abandoned	Cleared	
Acupalpus (*Acupalpus*) *flavicollis* (Sturm, 1825)		3	0	0	3
Amara (*Amara*) *aenea* (DeGeer, 1774)	amaraene	95	0	2	97
Amara (*Percosia*) *equestris* (Duftschmid, 1812)	amareque	0	4	5	9
Amara (*Amara*) *lucida* (Duftschmid, 1812)		1	0	0	1
Brachinus (*Brachinus*) *crepitans* (Linnaeus, 1758)		0	1	0	1
Brachinus (*Brachynidius*) *variventris* Schaufuss, 1862		1	0	1	2
Bradycellus (*Bradycellus*) *verbasci* (Duftschmid, 1812)		0	1	0	1
Calathus (*Neocalathus*) *ambiguus* (Paykull, 1790)	calaambi	7	0	2	9
Calathus (*Neocalathus*) *asturiensis* Vuillefroy, 1866	calaastu	0	0	6	6
Calathus (*Calathus*) *fuscipes* (Goeze, 1777)	calafusc	143	28	86	257
Calathus (*Neocalathus*) *granatensis* Vuillefroy, 1866		1	0	0	1
Calathus (*Neocalathus*) *melanocephalus* (Linnaeus, 1758)	calamela	0	6	1	7
Calathus (*Neocalathus*) *mollis* (Marsham, 1802)	calamoll	12	6	0	18
Calathus (*Neocalathus*) *rotundicollis* Dejean, 1828		1	1	0	2
Calathus (*Calathus*) *uniseriatus* Vuillefroy, 1866		0	2	1	3
Carabus (*Oreocarabus*) *amplipennis* Vaucher de Lapouge, 1924	caraampl	1	3	59	63
Carabus (*Archicarabus*) *nemoralis* O.F. Müller, 1764	caranemo	0	4	7	11
Cicindela (*Cicindela*) *campestris* Linnaeus, 1758		0	1	4	5
Cymindis (*Cymindis*) *etrusca* Bassi, 1834		0	1	0	1
Cymindis (*Menas*) *miliaris* (Fabricius, 1801)		0	3	0	3
Dinodes (*Dinodes*) *dives* (Dejean, 1826)	dinodive	8	9	23	40
Dixus sphaerocephalus (Olivier, 1795)		2	0	0	2
Harpalus (*Harpalus*) *anxius* (Duftschmid, 1812)	harpanxi	124	8	2	134
Harpalus (*Harpalus*) *attenuatus* Stephens, 1828	harpatte	6	0	0	6
Harpalus (*Harpalus*) *decipiens* Dejean, 1829	harpdeci	4	2	7	13
Harpalus (*Harpalus*) *distinguendus* (Duftschmid, 1812)	harpdist	148	0	0	148
Harpalus (*Harpalus*) *ebeninus* Heyden, 1870		1	0	0	1
Harpalus (*Harpalus*) *neglectus* Audinet-Serville, 1821		3	0	0	3
Harpalus (*Harpalus*) *pygmaeus* Dejean, 1829		1	0	0	1
Harpalus (*Harpalus*) *rubripes* (Duftschmid, 1812)		0	0	1	1
Harpalus (*Harpalus*) *rufipalpis* Sturm, 1818	harprufi	1	5	2	8
Harpalus (*Harpalus*) *serripes* (Quensel, 1806)		0	1	0	1
Masoreus wetterhallii (Gyllenhal, 1813)		2	0	1	3
Microlestes corticalis (Dufour, 1820)		2	0	0	2
Microlestes gallicus Holdhaus, 1912		1	0	0	1
Nebria (*Nebria*) *salina* Fairmaire & Laboulbène, 1856	nebrsali	112	6	463	581
Notiophilus biguttatus (Fabricius, 1779)		0	1	0	1
Notiophilus palustris (Duftschmid, 1812)		0	3	0	3
Notiophilus quadripunctatus Dejean, 1826		1	0	3	4
Ophonus (*Hesperophonus*) *cribricollis* (Dejean, 1829)	ophocrib	8	0	0	8
Ophonus (*Metophonus*) *puncticeps* Stephens, 1828		1	0	0	1
Orthomus (*Orthomus*) *hispanicus* (Dejean, 1828)	orthhisp	0	9	0	9
Platyderus (*Platyderus*) *leonensis* Jeanne, 1996		0	2	0	2
Poecilus (*Coelipus*) *crenulatus* (Dejean, 1828)		1	0	0	1
Poecilus (*Macropoecilus*) *kugelanni* (Panzer, 1797)	poeckuge	27	101	54	182
Poecilus (*Poecilus*) *versicolor* (Sturm, 1824)		0	0	1	1
Pseudomasoreus canigoulensis (Fairmaire & Laboulbène, 1854)		0	1	0	1
Steropus (*Steropidius*) *gallega* (Fairmaire, 1859)	stergall	0	7	16	23
Steropus (*Sterocorax*) *globosus* (Fabricius, 1792)	sterglob	302	175	1381	1858
Syntomus foveatus (Geoffroy, 1785)	syntfove	30	3	3	36
Synuchus vivalis (Illiger, 1798)	synuviva	0	4	17	21
Tachyta (*Tachyta*) *nana* (Gyllenhal, 1810)		1	0	0	1
Trechus (*Trechus*) *obtusus* Erichson, 1837	trecobtu	0	4	2	6
Trechus (*Trechus*) *quadristriatus* (Schrank, 1781)		2	0	0	2
Zabrus (*Iberozabrus*) *silphoides* Dejean, 1828	zabrsilp	20	0	7	27
Carabid individuals		1073	402	2157	3632
Carabid species		34	30	27	55
Exclusive species		16	10	3	

Supplementary Table S3. Staphylinid beetles collected at grazed, abandoned and cleared dehesas. Name abbreviations are indicated for the species shown in the PCA plot. Staphylinids identified to a higher taxonomical level than species are indicated at the end of the Table.

		Management type			Total
		Grazed	Abandoned	Cleared	
Aleochara (*Coprochara*) *bipustulata* (Linnaeus, 1761)	aleobipu	109	8	81	198
Aleochara (*Aleochara*) *curtula* (Goeze, 1777)		0	0	1	1
Aleochara (*Baryodma*) *intrincata* Mannerheim, 1831		2	0	0	2
Aleochara (*Xenochara*) *laevigata* Gyllenhal, 1810		1	0	0	1
Aleochara (*Aleochara*) *laticornis* Kraatz, 1856	aleolati	3	24	58	85
Aleochara (*Xenochara*) *moesta* Gravenhorst, 1802		0	0	1	1
Aleochara (*Heterochara*) *spissicornis* Erichson, 1840		3	0	0	3
Aleochara (*Xenochara*) *tristis* Gravenhorst, 1806		0	0	1	1
Aleochara (*Coprochara*) *verna* Say, 1836		1	0	0	1
Amarochara (*Mniobates*) *forticornis* Lacordaire, 1835	amarfort	0	10	5	15
Anaulacaspis nigra (Gravenhorst, 1802)		1	0	0	1
Anotylus inustus (Gravenhorst, 1806)	anotinus	46	0	7	53
Anotylus sculpturatus (Gravenhorst, 1806)	anotscul	5	0	1	6
Anthobium unicolor (Marsham, 1862)	anthunic	0	16	1	17
Astenus (*Astenus*) *lyonessius* (Joy, 1908)		0	0	1	1
Astenus (*Eurysunius*) *mateui* Coiffait, 1960		1	0	0	1
Atheta (*Atheta*) *nigritula* (Gravenhorst, 1802)		0	2	1	3
Atheta (*Earota*) *reyi* (Kiessenwetter, 1850)		0	2	0	2
Atheta (*Oreostiba*) *subglabra* (Sharp, 1869)		0	0	1	1
Cypha unicolor (Rosenhauer, 1856)		1	0	0	1
Dimetrota intermedia (Thomson, 1852)		0	1	0	1
Drusilla canaliculata (Fabricius, 1787)	druscana	0	22	7	29
Gabrius sp. A		0	0	1	1
Gauropterus fulgidus (Fabricius, 1787)		0	0	1	1
Leptacinus faunus Coiffait, 1956		2	0	0	2
Leptacinus guadarramus Outerelo, 1975		1	0	0	1
Liogluta alpestris (Heer, 1839)		0	3	2	5
Liogluta longiuscula (Gravenhorst, 1802)	lioglong	7	12	35	54
Lordithon (*Lordithon*) *exoletus* (Erichson, 1839)	lordexol	0	13	14	27
Medon sp. A		0	0	1	1
Micropeplus staphylinoides (Marsham, 1802)		0	2	0	2
Mycetoporus baudueri Mulsant & Rey, 1875		0	2	1	3
Mycetoporus lepidus (Gravenhorst, 1806)		0	0	1	1
Mycetoporus mulsanti Ganglbauer, 1895		0	0	4	4
Mycetoporus punctus (Gravenhorst, 1806)		0	1	0	1
Mycetoporus solidicornis Wollaston, 1864		0	0	1	1
Mycetoporus sp. A		0	0	1	1
Ocypus (*Pseudocypus*) *aethiops* (Waltl, 1835)	ocypaeth	0	10	2	12
Ocypus (*Ocypus*) *olens* (O. Müller, 1764)	ocypolen	14	29	52	95
Ocypus (*Ocypus*) *ophtalmicus* (Scopoli, 1763)		2	0	0	2
Ocypus (*Pseudocypus*) *picipennis* (Fabricius, 1793)		3	0	0	3
Oligota (*Oligota*) *punctulata* Heer, 1839		1	1	1	3
Olophrum piceum (Gyllenhal, 1810)		0	1	0	1
Omalium caesum Gravenhorst, 1806	omalcaes	0	5	1	6
Omalium nigriceps Kiesenwetter, 1850		0	4	0	4
Ontholestes murinus (Linné, 1758)		0	2	0	2
Othius laeviusculus Stephens, 1832		3	0	2	5
Othius punctulatus (Goeze, 1777)		0	0	2	2
Othius subuliformis Stephens, 1832	othisubu	0	3	11	14
Oxypoda (*Sphenoma*) *abdominalis* (Mannerheim, 1831)		2	0	0	2
Oxypoda (*Oxypoda*) *acuminata* (Stephens, 1832)		0	1	0	1
Oxypoda (*Bessopora*) *ferruginea* Erichson, 1840	oxypferr	81	6	22	109
Oxypoda (*Mycetodrepa*) *formosa* Kraatz, 1858	oxypform	0	4	4	8
Oxypoda (*Sphenoma*) *islandica* Kraatz, 1857		0	0	3	3
Oxypoda (*Oxypoda*) *opaca* (Gravenhorst, 1802)		0	0	1	1
Oxypoda (*Baeoglena*) *praecox* Erichson, 1839	oxypprae	0	22	24	46
Oxypoda (*Deropoda*) *rugulosa* Kraatz, 1856		2	0	0	2
Oxypoda (*Sphenoma*) *togata* Erichson, 1839	oxyptoga	3	17	6	26
Oxytelus (*Oxytelus*) *piceus* (Linné, 1767)		1	0	0	1
Philonthus (*Philonthus*) *cognatus* Stephens, 1832	philcogn	13	0	0	13
Philonthus (*Philonthus*) *nitidicollis* (Lacordaire, 1835)		5	0	0	5
Philonthus (*Philonthus*) *parvicornis* (Gravenhorst, 1802)		3	0	0	3
Philonthus sp. A		0	1	0	1
Platydracus (*Platydracus*) *meridionalis* (Rosenhauer, 1847)		1	0	2	3
Proteinus brachypterus (Fabricius, 1792)		1	1	3	5
Proteinus ovalis Stephens, 1834		1	0	0	1
Quedius (*Microsaurus*) *abietum* Kiesenwetter, 1858		0	4	0	4
Quedius (*Raphirus*) *asturicus* Bernhauer, 1918	quedastu	6	0	3	9
Quedius (*Raphirus*) *bonvouloiri* Brisout, 1863		0	5	0	5
Quedius (*Quedius*) *curtipennis* Bernhauer, 1908		0	0	1	1

Supplementary Table S3. (*Continued*)

		Management type			Total
		Grazed	Abandoned	Cleared	
Quedius (*Quedius*) *levicollis* (Brullé, 1832)		2	0	0	2
Quedius (*Microsaurus*) *longicornis* Kraatz, 1858		0	0	2	2
Quedius (*Raphirus*) *nigriceps* Kraatz, 1857	quednigr	0	3	5	8
Quedius (*Raphirus*) *persimilis* Mulsant & Rey, 1876		1	0	0	1
Quedius (*Raphirus*) *semiaeneus* (Stephens, 1832)	quedsemi	31	0	0	31
Quedius (*Quedius*) *simplicifrons* Fairmaire, 1862		1	0	0	1
Scopaeus (*Scopaeus*) *didymus* Erichson, 1840		0	0	1	1
Stenus (*Stenus*) *ater* Mannerheim, 1830		1	0	0	1
Stenus (*Stenus*) sp. A		1	0	0	1
Tachyporus (*Tachyporus*) *pusillus* Gravenhorst, 1806		4	0	0	4
Tinotus morion (Gravenhorst, 1802)		1	0	0	1
Xantholinus (*Xantholinus*) *linearis* (Olivier, 1795)	xantline	3	1	8	12
Xantholinus (*Xantholinus*) *gallicus* Dejean, 1821		0	1	0	1
Zyras (*Myrmoecia*) *confragosus* (Hochhuth, 1849)		0	1	0	1
Zyras (*Pella*) *limbatus* (Paykull, 1789)	zyralimb	0	5	1	6
Zyras (*Glossacantha*) *lugens* (Gravenhorst, 1802)		0	0	1	1
Stenus (*Hemistenus*) spp.		0	4	1	5
Aleocharinae		7	4	15	26
Paederinae		0	1	4	5
Pselaphinae		3	0	6	9
Staphylinid individuals		380	254	412	1046
Staphylinid species		40	36	47	86
Exclusive species		26	13	19	

IV

The role of microhabitats and their management in the functioning of wood-pastures

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Summary

1. Wood-pastures are landscapes that hold great ecological, social and cultural values, and where livestock grazing co-occurs with scattered trees and shrubs. In these landscapes, multipurpose low intensity management results in a variety of microhabitats that enhance biodiversity and wildlife conservation, but the role of the different microhabitats to ecosystem functioning remains poorly studied.

2. We investigated the impact that different wood-pasture microhabitats have on nutrient cycling and the decomposition food web. To do this, we analysed the two main microhabitats – grasslands and trees – that made up wood-pastures and three additional litter-trapping microhabitats – shrubs scattered in the grassland matrix, canopied shrubs and piles of pruning debris – in terms of topsoil nutrient content, collembolan and dipteran (detritivores) abundance, and carabid (herbivores and predators) and staphylinid (mostly predators) beetle abundance, body size, biomass, species richness and composition.

3. Grasslands were the most different microhabitats, with the lowest topsoil nutrient content and particular carabid and staphylinid species composition. Trees had the highest topsoil nutrient levels and abundance of diptera and staphylinids, and held unique staphylinid assemblages.

4. Litter-trapping microhabitats had medium to high topsoil nutrient values and shared a distinct staphylinid assemblage compared to grasslands and trees. Scattered shrubs provided shelter for large-sized carabid and staphylinid predators, while canopied shrubs held the highest carabid abundance and biomass. Pruning piles were intermediate between scattered and canopied shrubs, but they further contributed to the overall microhabitat heterogeneity in the landscape.

5. Synthesis and applications. Shrubs and pruning piles retain litter that would otherwise be lost to the wood-pasture, recovering nutrients to the system and providing new habitat, shelter and food for detritivores and unique predator assemblages, thus enhancing nutrient cycling and the decomposition process, as well as increasing biodiversity. Microhabitat heterogeneity in wood-pastures should be therefore maximized by maintaining low intensity management practices in order to achieve high wildlife conservation values.

Key-words: *Dehesa*; Detritivores; Herbivores; Leaf litter; Livestock grazing; Low intensity management; Nutrient cycling; Predators; *Quercus pyrenaica*; Shrubs

Introduction

Wood-pastures (also known as silvopastures) are multipurpose landscapes where livestock grazing co-occurs with scattered trees and shrubs, and which hold great ecological, social and cultural values (Plieninger *et al.* 2015). Since wood-pastures provide important ecosystem services such as fodder, firewood and carbon sequestration, together with biodiversity conservation (Bugalho *et al.* 2011; Campos *et al.* 2013), they are currently encouraged as a sustainable type of land use in different regions of the world (see Mosquera-Losada, Riguero-Rodriguez & McAdam 2005 for several examples). In Europe, wood-pastures occur throughout the continent as the result of traditional low-intensity management practices, but are especially common in Spain and Portugal (called *dehesas* and *montados*; Plieninger *et al.* 2015). Wood-pastures are currently threatened by both land use intensification and abandonment (Moreno & Pulido 2008; Plieninger *et al.* 2015), the latter leading to shrub encroachment that negatively affects biodiversity and ecosystem functioning (Peco *et al.* 2012; García-Tejero *et al.* 2013). The long-term preservation of European wood-pastures requires low-intensity management practices, which need to be supported by appropriate agricultural and conservation policies (Bergmeier, Petermann & Schröder 2010; Bugalho *et al.* 2011; Díaz *et al.* 2013; Plieninger *et al.* 2015).

Traditional management of wood-pastures results in a wide variety of microhabitats co-occurring in the same landscape, such as open grasslands, isolated trees, scattered shrubs, agricultural crops, hedges and water bodies (see e.g., Moreno *et al.* in press). Microhabitat heterogeneity enhances biological diversity by providing different niches, environmental conditions and resources for species that require many of these elements to live, like numerous bird and arthropod species do (DeMars, Rosenberg & Fontaine 2010; Diacon-Bolli *et al.* 2012; Hartel *et al.* 2014; Moreno *et al.* in press). In wood-pastures, grasslands constitute the dominant microhabitat type, playing the major economic role providing food for livestock and being crucial to biodiversity conservation (Taboada *et al.* 2011; Diacon-Bolli *et al.* 2012). Direct sunlight in grasslands results in (1) enhanced primary production and uptake of nutrients – which are partly returned to the ecosystem as livestock faeces and grass litter –, and in (2) sharp temperature and moisture contrasts that influence nutrient mineralisation (Köchy & Wilson 1997) and the ground dwelling arthropod fauna (Thiele 1977) . Isolated trees in wood-pastures are often considered keystone structures (Tews *et al.* 2004; Manning, Fischer & Lindenmayer 2006; Fischer, Stott & Law 2010), since they (1) create a distinct and mild microclimate owing to their shade, which affects arthropod species composition and abundance (Taboada *et al.* 2006; Lindsay & Cunningham 2009), (2) provide shelter for livestock in the warmest seasons, (3) are essential for nutrient cycling as they receive nutrients from multiple sources (leaf and grass litter, stemflow, livestock faeces, etc.) (Escudero *et al.* 1985; Gea-Izquierdo *et al.* 2010) and also pump them from deeper soil layers inaccessible to grass roots (see Vetaas 1992; Blanco Castro *et al*. 1997), and (4) constitute suitable habitats for specialized species like epiphytic flora, saproxylic fauna, birds and bats (Manning, Fischer & Lindenmayer 2006; Fischer, Stott & Law 2010).

Although scattered shrubs often constitute the third main microhabitat type in wood-pastures and savanna-like landscapes (Vetaas 1992; Bergmeier, Petermann & Schröder 2010; Bugalho *et al.* 2011; Plieninger *et al.* 2015), their importance for ecosystem functioning and wildlife conservation has rarely been studied (but see Moreno *et al*. in press). Shrubs provide roosting, nesting, resting and signing places for birds (Hartel *et al.* 2014), and shelter for reptiles (Martín & López 2002; Godinho, Santos & Sá-Sousa 2011) and butterflies (Dover, Sparks & Greatorex-Davies 1997). Moreover, in open ventilated landscapes such as many wood-pastures, scattered shrubs can retain tree leaf litter that would otherwise be blown away by the wind (Facelli & Pickett 1991), thus altering the nutrient cycle and providing new habitat for litter dwelling fauna (Sayer 2005).

In general, litter accumulation buffers soil temperatures and increases soil moisture by creating a barrier to water vapour diffusion, benefiting the abundance and activity of decomposers and detritivores (Facelli & Pickett 1991; Sayer 2005). Since up to 90% of the energy obtained in primary production goes to the decomposition pathway (Chen & Wise 1999), this food web is an essential part of the ecosystem and contributes to the provision of multiple services like water supply, nutrient cycling, soil formation and primary production (Lavelle *et al.* 2006). Among detritivores, collembola (Collembola) and diptera (Diptera) are key arthropod functional groups, which feed directly on decaying matter (including faeces in the case of diptera) or on decomposers such as fungi (Hövemeyer 1992; Rusek 1998; Frouz 1999), while at the same time serve as food to many other invertebrate predators (e.g., carabid beetles: Thiele 1977; staphylinid beetles: Thayer 2005). Among predators, carabids (Coleoptera: Carabidae) and staphylinids (Coleoptera: Staphylinidae) are predominant highly diverse ground dwelling beetles that respond to changes in habitat structure, microclimate, nutrient input, and prey abundance and composition (Bohac 1999; Rainio & Niemelä 2003). Both carabid and staphylinid beetles are important food sources for higher trophic levels and their availability and abundance can have important consequences for wildlife conservation (Vickery *et al.* 2001; Kotze *et al*. 2011).

In this study we investigate how differences among wood-pasture microhabitats regarding environmental conditions and resource provisioning influence nutrient cycling and the functioning of the decomposition food web. We surveyed topsoil nutrient content, collembolan and dipteran (detritivores) abundance, and carabid beetle (herbivores and predators) and staphylinid beetle (mostly predators) abundance, body size, biomass, species richness and composition, in five types of microhabitats: open grasslands, isolated trees, shrubs scattered in the grassland matrix, canopied shrubs, and piles of pruning debris. Opposite to open grasslands and isolated trees, tree leaves accumulate in scattered and canopied shrubs and pruning piles (i.e., litter-trapping microhabitats) providing food and favourable microclimate conditions for detritivores and their predators, which in turn influence nutrient return to the topsoil layer (Sayer 2005). With this in mind, we predict that: (i) topsoil nutrient content will be highest in litter-trapping microhabitats and lowest in grasslands, where nutrients are rapidly removed by growing grass (Otieno *et al.* 2011); (ii) better microclimate conditions and enhanced nutrient supply will foster high detritivore and predator abundances in litter-trapping microhabitats and trees (Koivula *et al*. 1999); (iii) litter-trapping microhabitats will provide shelter for large-sized predators according to the "enemy-free space hypothesis", which states that large species are favoured by complex habitat structures (Brose 2003); and (iv) grasslands will hold particular herbivore and predator assemblages due to their unique plant species composition and more severe microclimate conditions (Taboada *et al*. 2011; García-Tejero *et al*. 2013). This study sheds light on the role that litter-trapping microhabitats play in the functioning of wood-pasture ecosystems by enhancing nutrient recycling and providing new habitat and shelter for detritivores and predators, and gives practical advice to develop management guidelines aimed at maximizing biodiversity conservation.

Material and Methods

STUDY AREA

The study was conducted in three traditionally managed (i.e., sheep grazed and tree pruned) *Q. pyrenaica* wood-pastures (*dehesas*) at the lower slopes of the Cantabrian mountain range in north-west Spain. Sites are embedded in a matrix of agricultural land, dense mature oak forests and pine plantations. Specific details on location, altitude and climate can be found in García-Tejero *et al.* (2013). Five different microhabitats were studied in each wood-pasture (Fig. 1, Table 1): (i) Grasslands, which constitute the most extensive microhabitat and are lightly grazed by moderate-size sheep loads (900 - 1250 individuals; García-Tejero, personal observation). (ii) Trees are about 10-12 m high and 1-1.5 m in perimeter at breast height, and were pruned in the last two years. (iii) Scattered shrubs are formed by one or several small bushes clustered together, extending in average 1.8 m^2, separated at least 10 m from the closest tree. (iv) Canopied shrubs consist of a cluster of bushes and/or oak root sprouts, which occupied in average 16.1 m^2, located around the trunk of one or two mature trees growing together. (v) Pruning piles consist of small branches piled up in the last two years after the pruning of nearby trees, and extended 15.1 m^2. Scattered and canopied shrubs and pruning piles retained tree leaf litter underneath and are hereafter referred as litter-trapping microhabitats. Further details on microhabitat characteristics are found in Table 1. In each wood-pasture, four replicates of each microhabitat type were

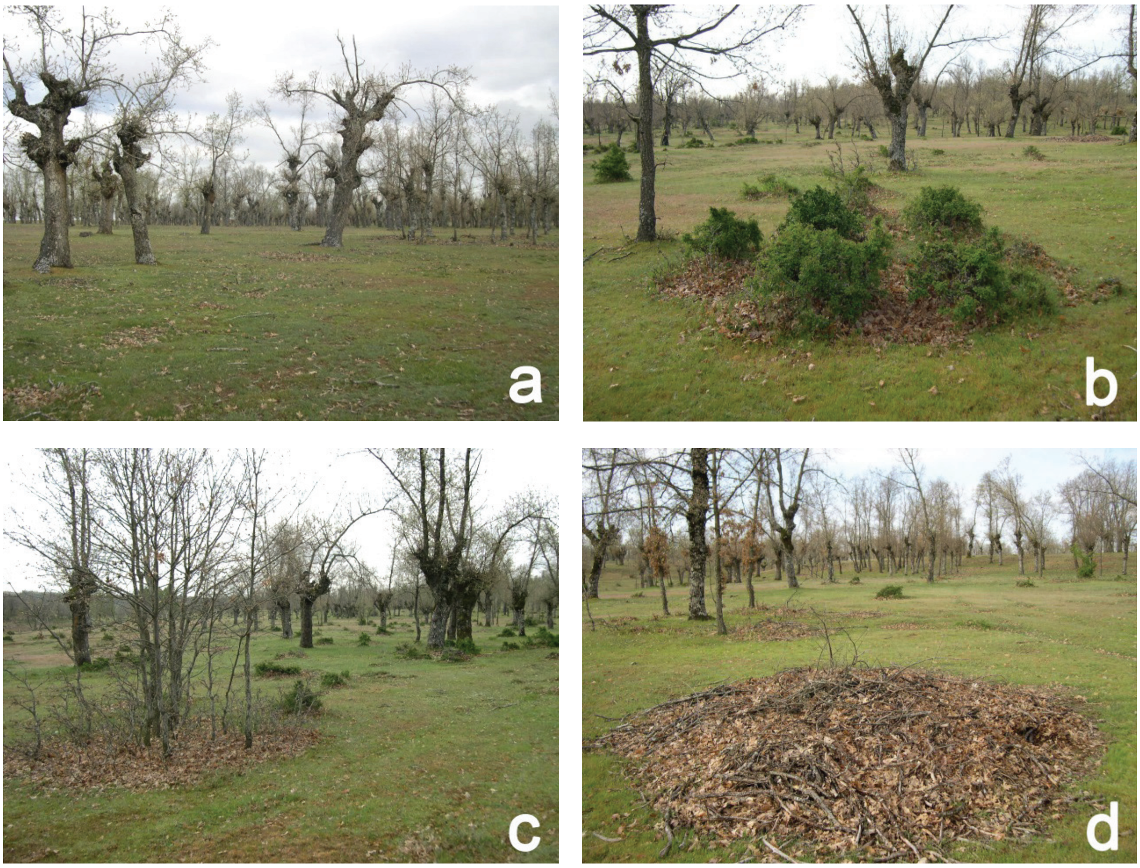

Fig. 1. The five types of microhabitats studied: (a) tree and grassland, (b) scattered shrub, (c) canopied shrub, (d) pruning pile.

selected as sampling points. Sampling points were at least 25 m apart from site edges and from each other so they could be considered independent replicates for arthropod captures (Digweed *et al.* 1995).

SOIL SAMPLING

We analysed organic matter content (O.M.), total nitrogen (N), C/N ratio and available phosphorus (P), calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and sodium (Na^+) from the first five centimetres of the topsoil layer. Five samples (1 - 2 m apart) were collected at each sampling point in June 2007 and homogenised into one that was air-dried and passed through a 2 mm mesh sieve before nutrient content analyses.

ARTHROPOD SAMPLING

We collected collembola, diptera, carabids and staphylinids using plastic pitfall traps (depth 86 mm, diameter 60 mm),covered by 10 x 10 cm roofs, partly filled with 25% propylene glycol and flush to the soil surface. In litter-trapping microhabitats, pitfall traps were covered with a 2 cm wire mesh to prevent them from getting clogged with litter. Two pitfall traps, 50-200 cm apart, were placed at each sampling point (i.e., 40 traps per site, 120 traps in total). Arthropods were collected continuously from 1 June to 20 October 2007, emptying the traps every three

Table 1. Environmental characteristics (mean ± SE) of each microhabitat type. N=12.

	Grassland	Tree	Scattered shrub	Canopied shrub	Prunning pile
Bare soil cover (%)	4.44 ± 1.73	2.25 ± 1.10	4.13 ± 1.44	3.10 ± 1.12	5.19 ± 1.74
Litter cover (%)	1.54 ± 0.67	16.50 ± 5.52	10.81 ± 1.83	65.69 ± 4.49	59.54 ± 6.23
Litter depth (cm)	0.98 ± 0.28	2.33 ± 0.48	7.23 ± 0.80	6.51 ± 0.57	11.31 ± 1.21
Coarse woody debris (%)	1.42 ± 0.61	10.04 ± 1.56	1.08 ± 0.16	8.08 ± 1.57	28.85 ± 3.67
Lower vegetation layer cover (%)	96.27 ± 1.50	94.81 ± 1.57	94.69 ± 1.34	75.81 ± 5.92	44.79 ± 6.19
Medium vegetation layer cover (%)	0.00 ± 0.00	0.40 ± 0.27	0.98 ± 0.31	25.09 ± 3.68	0.85 ± 0.54
Upper vegetation layer cover (%)	0.00 ± 0.00	85.83 ± 3.56	0.83 ± 0.56	78.61 ± 5.92	16.10 ± 7.82
Distance to nearest tree (m)	16.08 ± 2.13	0.63 ± 0.05	12.81 ± 1.50	1.10 ± 0.11	6.15 ± 0.69
Height of nearest tree (m)	11.42 ± 0.93	13.33 ± 0.47	12.25 ± 0.58	10.08 ± 0.69	11.75 ± 0.82
Area of shrub/pile (m^2)	0.00 ± 0.00	0.00 ± 0.00	1.76 ± 0.27	16.08 ± 1.01	15.07 ± 1.79
Height of shrub/pile (cm)	0.00 ± 0.00	0.00 ± 0.00	67.58 ± 7.72	49.51 ± 7.00	40.42 ± 6.99

Vegetation layer: lower (0-50 cm), medium (50-200 cm), upper (>200 cm).

weeks. Pitfall catches reflect arthropod activity-density (Thiele 1977), which will be referred hereafter as abundance or number of individuals. We counted the number of collembola and adults of diptera, carabids and staphylinids. Carabid and staphylinid beetles were identified to species level using standard keys, and named according to current species catalogues (Supplementary Table S1). Staphylinid individuals that could not be assigned to a particular species (63 individuals, 2.1%) were only included in the analysis of overall abundance. Data on average body length, carabid diet (predator, omnivore, seed-eater) and staphylinid niche preference (litter-dweller, mycophilous, coprophilous) were obtained for each species from the literature (see Supplementary Table S1). Mean biomass for each carabid and staphylinid species was estimated using family-specific length versus weight regression equations (Hódar 1996). Biomass data were included in this study because they can provide a more detailed picture of arthropod contribution to ecosystem functioning, especially in relation to resource use and energy flow (Saint-Germain *et al.* 2007).

DATA ANALYSIS

We used linear mixed models (LMMs) to look for differences between microhabitats in topsoil characteristics and mean beetle body length and generalised linear mixed models (GLMMs) with a negative binomial error distribution to compare arthropod abundances among microhabitats.. Site was included as a random factor in the models to account for the randomized block sampling design. Prior to the analyses, arthropod catches were pooled for the whole trapping period, and organic matter and nitrogen content were logit-transformed (Warton & Hui 2011).

For each carabid diet and staphylinid niche preference group in the five microhabitat types, total beetle biomass was calculated as the sum of the mean biomass values of all species multiplied by the total number of individuals collected for each species. Results were compared among microhabitats using LMMs.

We calculated sample-based rarefaction curves to compare beetle species richness between microhabitats taking into account differences in catch size. We used the 95% confidence intervals of the randomization curves to assess the significance of differences.

We used multivariate regression trees (MRT) to explore similarities and differences in beetle species composition between microhabitats. Beetle species abundance was recursively partitioned according to microhabitat types. The results are dichotomous trees that split the data in clusters that maximized between-group and minimized within-group differences in species composition. We retained the largest trees where all splits were significant ($P < 0.05$, 9999 permutations) according to permutational multivariate analyses of variance (Anderson 2001). Prior to multivariate analyses, species abundance data were pooled for each microhabitat type and wood-pasture, and then Hellinger-transformed so the model preserved Hellinger distances, which are meaningful to assess ecological patterns (see Borcard, Gillet & Legendre 2011).

Analyses were carried out with widely available free statistical programs: R (R Core Team, 2015) – packages *MASS* (Venables & Ripley 2002), *nlme* (Pinheiro *et al*. 2015), *mvpart* (De'Ath 2014) and *rpart* (Therneau, Atkinson and Ripley 2015) –, EstimateS (Colwell, 2006) and DISTLM (Anderson 2001).

Results

TOPSOIL VARIABLES

Most topsoil characteristics significantly differed between microhabitats and were highest in canopied shrubs and trees and lowest in grasslands (Fig. 2): organic

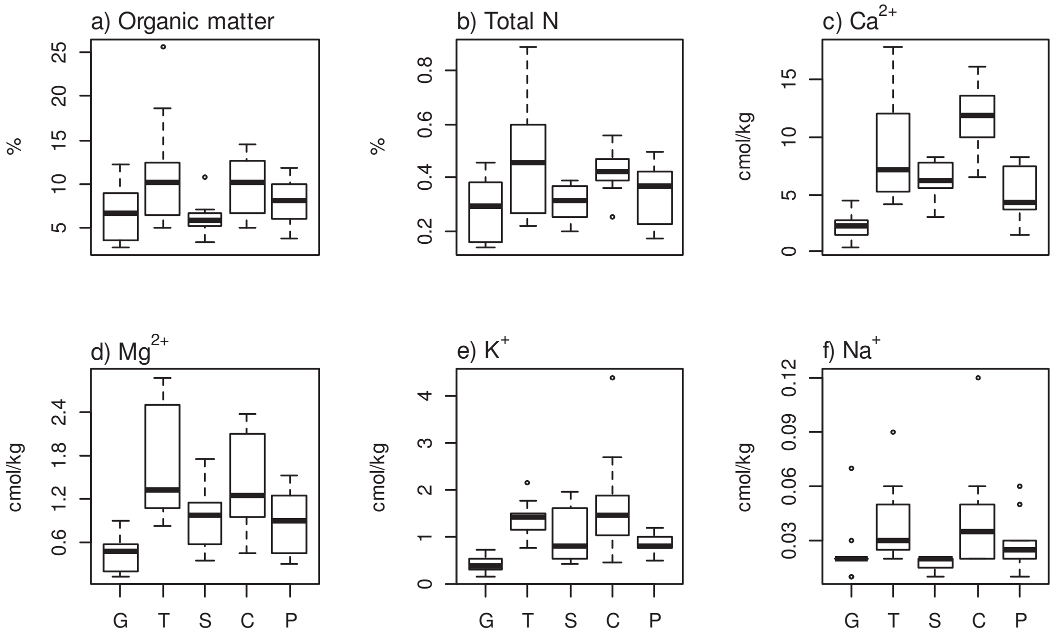

Fig. 2. Boxplots of the topsoil variables measured at the five microhabitat types: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile. Boxplots show the median (black bold line), the first and third quartiles (lower and upper limits of the box), 1.5 times the interquartile range from the box (ends of the whiskers) and values out of these limits (individual dots).

matter content (F = 5.71, $P < 0.001$), N (F = 11.07, $P < 0.001$), Ca^{2+} (F = 22.88, $P < 0.001$), Mg^{2+} (F = 23.34, $P < 0.001$), K^+ (F = 10.53, $P < 0.001$) and Na^+ (F = 3.77, $P = 0.009$). No significant differences were found in C:N ratio and P between microhabitats.

ARTHROPOD ABUNDANCE

We collected 162850 collembolan and 10315 dipteran individuals, and their abundances significantly differed between microhabitats (respectively, F = 20.75, $P < 0.001$; F = 21.99, $P < 0.001$). Collembola were very abundant in grasslands and scarce in litter-trapping microhabitats (Fig. 3a). Dipteran abundance was highest

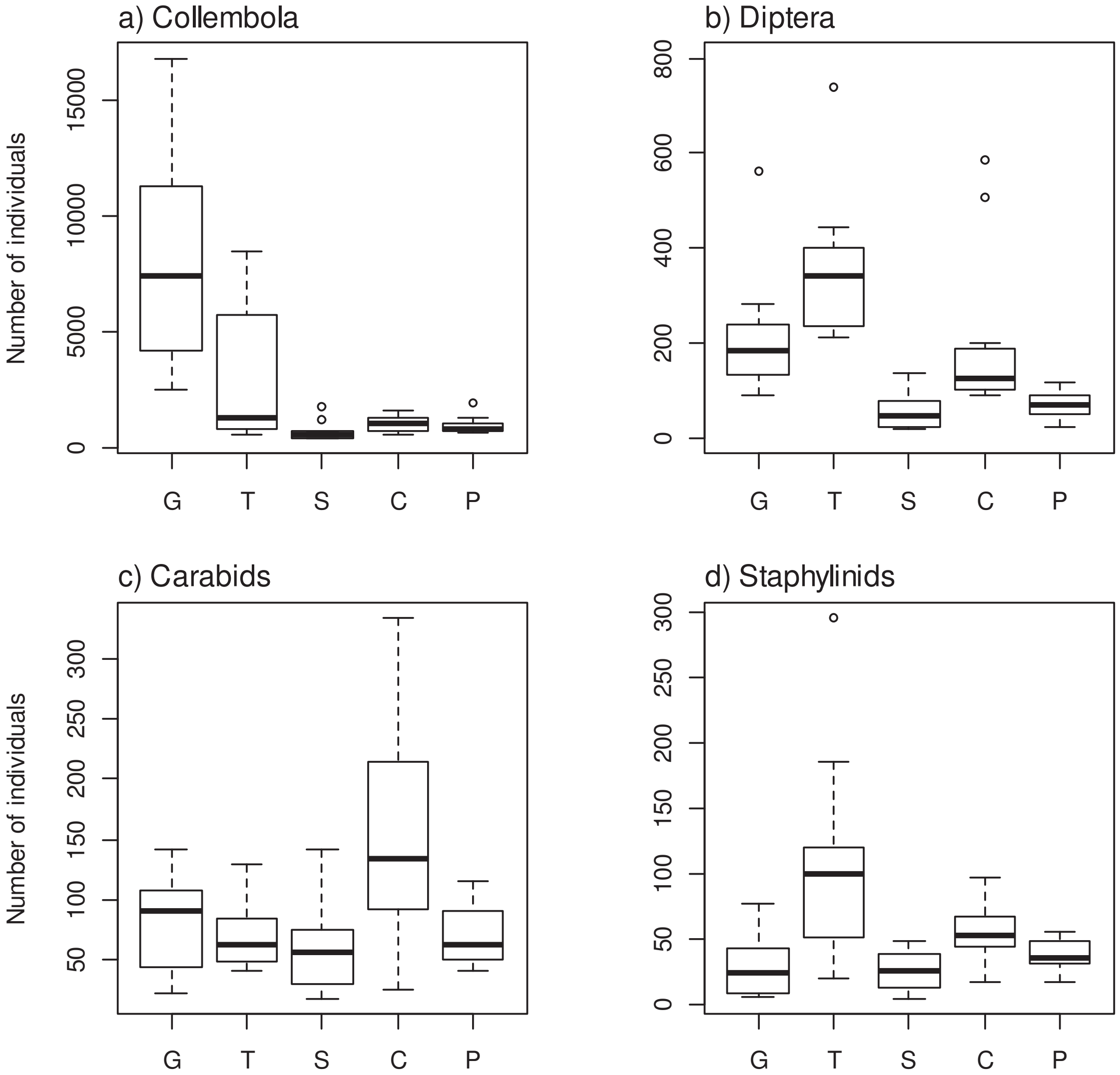

Fig. 3. Boxplots of the number of individuals of (a) collembola, (b) dipteran adults, (c) carabids and (d) staphylinids captured at each sampling point of the five microhabitat types: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile. The number of captured individuals was standardised to the median number of days the traps were active at each sampling point (282 days) prior to plotting. Boxplots show the median (black bold line), the first and third quartiles (lower and upper limits of the box), 1.5 times the interquartile range from the box (ends of the whiskers) and values out of these limits (individual dots).

under trees and lowest in scattered shrubs and pruning piles (Fig. 3b).

We collected 5128 carabid and 2981 staphylinid individuals, whose numbers differed between microhabitats (respectively, F = 7.20, P = 0.009; F = 4.17, P = 0.041). Carabids were more abundant in canopied shrubs and staphylinids in trees and canopied shrubs than in the other microhabitats (Fig. 3c, d).

BEETLE LENGTH AND BIOMASS

Mean carabid body length was highest in scattered shrubs (F = 5.73, $P < 0.001$; Fig. 4a). Staphylinids differed in size between microhabitats (F = 23.88, $P < 0.001$) and were in average bigger in scattered shrubs and smaller in grasslands and trees (Fig. 4b). Total carabid biomass was highest in canopied shrubs and mainly composed of predators and omnivores (Fig. 4c). Carabid biomass significantly differed between microhabitat types for

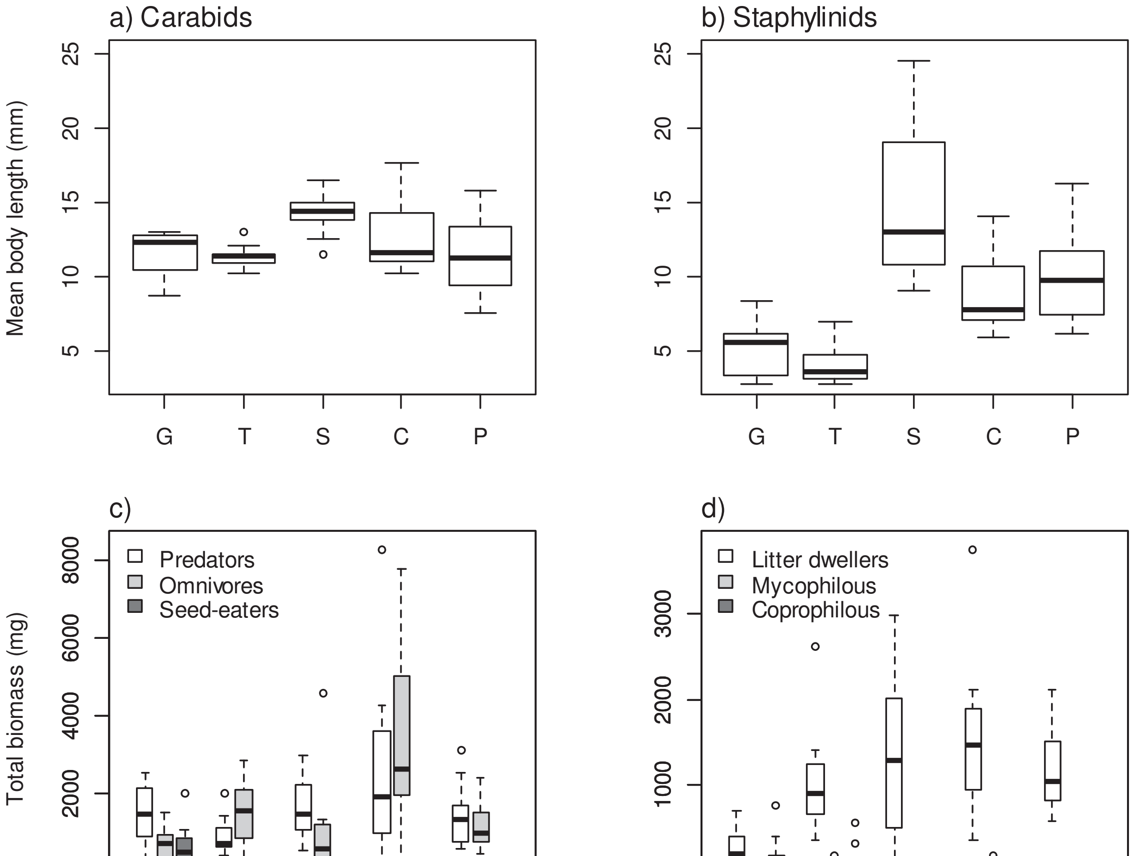

Fig. 4. Boxplots of the mean body length and total biomass of (a, c) carabids and (b, d) staphylinids at the five microhabitat types: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile. Total biomass was calculated separately for each carabid diet group (predators, omnivores, seed-eaters) and each staphylinid niche preference group (litter dwellers, mycophilous, coprophilous). Boxplots show the median (black bold line), the first and third quartiles (lower and upper limits of the box), 1.5 times the interquartile range from the box (ends of the whiskers) and values out of these limits (individual dots).

all diet groups (predators: F = 3.09, *P* = 0.023; omnivores: F = 12.1, *P* < 0.001; seed-eaters: F = 18.7, *P* <0.001). Biomass of predators and omnivores was highest in canopied shrubs and that of seed-eaters in grasslands. Total staphylinid biomass was lowest in grasslands and similar in all other microhabitat types, where it was mainly composed of litter dwellers. Staphylinid biomass significantly differed between microhabitat types for all niche preference groups (litter dwellers: F = 6.43, *P* < 0.001; coprophilous: F = 3.86, *P* = 0.008; mycophilous: F = 3.94, *P* = 0.007). Biomass of litter dwellers and mycophilous species was highest in canopied shrubs and that of coprophilous in grasslands (although it did not differ from trees).

BEETLE DIVERSITY AND COMPOSITION

We collected 51 carabid and 116 staphylinid species (Supplementary Tables S2 and S3). Rarefied carabid species richness was significantly higher in scattered shrubs and grasslands compared to the other microhabitat types (Fig. 5a). Rarefied staphylinid richness did not significantly differ between microhabitats (Fig. 5b).

The multivariate regression tree on carabid species composition first separated grasslands from the other microhabitats, this split accounting for 24.2% of the total variation of the data. The remaining microhabitats were then split in two groups according to canopy presence, which explained 12.3% of the total variation: trees and canopied shrubs versus scattered shrubs and pruning piles (Fig. 6a). Staphylinid assemblages were first separated into those of litter-trapping microhabitats and the rest, which accounted for 32.9% of the total variation. Grasslands and trees further split,

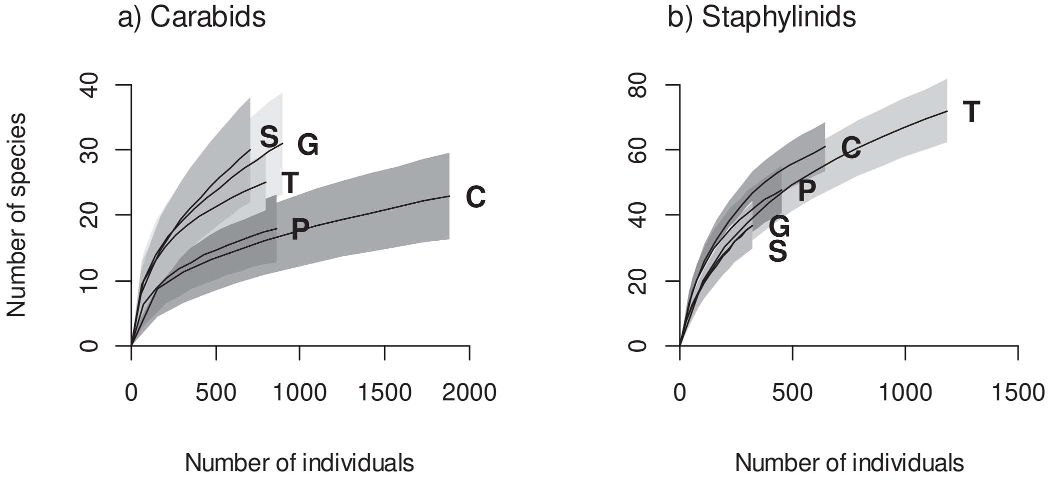

Fig. 5. Curves of the rarefied number of species for (a) carabids and (b) staphylinids at the five microhabitat types: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile. Rarefaction curves represent the number of species relative to the number of individuals for each microhabitat type. 95% confidence intervals for each curve are indicated in light grey shading.

explaining 8.7% of the total variation in the data (Fig. 6b).

Discussion

Differences in resources and environmental conditions provided by each microhabitat type influenced the topsoil characteristics and ground dwelling arthropod fauna of wood-pastures. Grasslands had low topsoil organic matter and nutrient content, very abundant collembola, high carabid species richness, and particular carabid and staphylinid beetle assemblages. Trees had high topsoil organic matter and nutrient content, abundant diptera and staphylinids, and a distinct assemblage of small-sized staphylinids. Litter-trapping microhabitats shared intermediate to high topsoil nutrient content and a common assemblage of medium to large staphylinids. However, scattered shrubs held high carabid species richness and large-sized carabid and staphylinid beetles; while canopied shrubs high carabid and staphylinid abundance and carabid beetle biomass.

DIFFERENCES BETWEEN MICROHABITATS

Topsoil nutrient content was lowest in grasslands, which agrees with our prediction (i) and the results of previous studies (Gallardo 2003; Gea-Izquierdo *et al.* 2010). Grasslands receive nutrients from livestock faeces and grass litter (Escudero *et al.* 1985; Otieno *et al.* 2011), which mineralise faster than tree leaves (Begon, Townsend & Harper 2006), and even more when exposed to the sharp changes in moisture that occur in this microhabitat type (Vetaas 1992; Köchy & Wilson 1997). Fast mineralisation and direct sunlight promote primary production in grasslands, accelerating the nutrient cycle (Otieno *et al.* 2011) and resulting in low nutrient accumulation at the topsoil

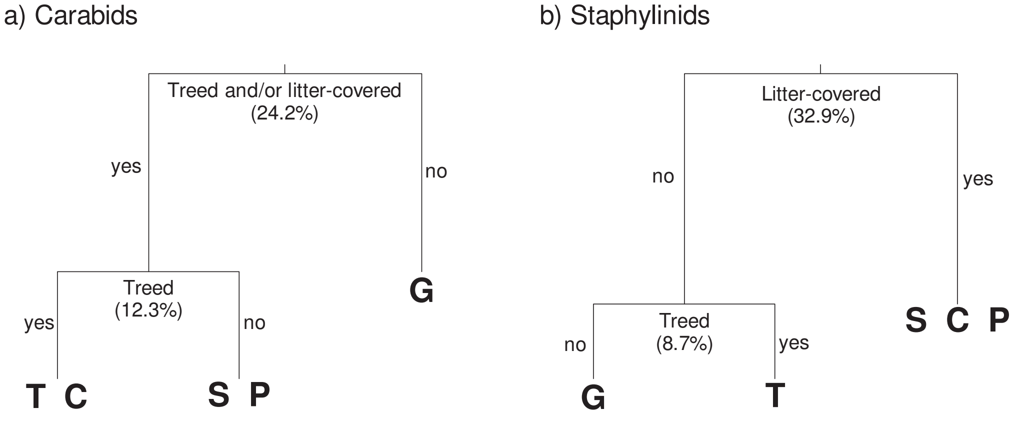

Fig. 6. Multivariate regression trees on species composition data of (a) carabids (Error = 0.545; CV Error = 0.951; SE = 0.100) and (b) staphylinids (Error = 0.501; CV Error = 0.817; SE = 0.059). The criteria for partitioning and the percentages of explained variance (R^2_{adj}) are indicated below each split. Only significant splits, according to a permutational multivariate analysis of variance ($P < 0.05$; 9999 permutations), were retained. Microhabitat types: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile.

layer (Wardle *et al.* 2004). Although nutrient cycling may also be rapid under trees as primary production is usually as high as in grasslands (Rivest *et al.* 2013), the nutrient content of the topsoil layer is high under trees, where the input of nutrients comes from many different sources [e.g., livestock faeces, bird droppings, stemflow, throughfall, leaf litter (Escudero *et al.* 1985; Vetaas 1992; Gallardo 2003; Gea-Izquierdo *et al.* 2010) and grass litter]. Furthermore, tree roots bring up nutrients from deep soil layers where they are inaccessible to grassland herbaceous vegetation, and posteriorly return them as leaf litter (Vetaas 1992; Moreno & Pulido 2008), thus enhancing nutrient recycling. In the studied wood-pastures, the majority of leaf litter produced by trees was blown away by the wind and only retained under scattered and canopied shrubs and pruning piles, where such accumulation of litter may increase decomposition rates (Chen *et al.* 2014). Topsoil organic matter and nutrient content was highest in canopied shrubs, probably because these microhabitats persist longer than pruning piles and are of greater size and less exposed to litter renewal by wind and to nutrient uptake by the surrounding grassland than scattered shrubs. These results show that two rather distinct nutrient cycles occur in wood pastures: a faster one in grasslands and trees, where easily decomposable grass litter and livestock faeces return nutrients to the topsoil that are rapidly used in primary production; and a slower one in litter-trapping microhabitats, where recalcitrant tree leaf litter is slowly decomposed and organic matter and nutrients are stored in the topsoil layer (Wardle *et al.* 2004).

Contrary to our expectations, collembola were much more abundant in grasslands than in litter-trapping microhabitats. Collembola may have preferred grasslands to the other microhabitat types (see Rusek 1998), but our results may have as well been greatly influenced by differences in collembolan activity among microhabitat types. Collembola thriving in grasslands where sharp changes in moisture conditions occur may have been attracted by the humid environment inside the traps, thus overestimating abundance (Joosse & Groen 1970). But it may as well be that collembola did not particularly favour litter accumulation (Ponge, Arpin & Vannier 1993), or that the great structural complexity of the litter layer may have hindered their capture in litter-trapping microhabitats (Melbourne 1999). The abundance of diptera, carabids and staphylinids was highest under treed microhabitats (i.e., isolated trees and/or canopied shrubs), which partly agrees with our prediction (ii) and with previous studies (Taboada *et al.* 2006; Lindsay & Cunningham 2009). Treed microhabitats provide food, shelter, leaf litter (particularly canopied shrubs), logs and shade for invertebrates (Lindsay & Cunningham 2009). For diptera, large amounts of fresh livestock faeces under trees may have attracted abundant coprophilous species, while the moister conditions beneath the thick litter layer of canopied shrubs may have favoured hemi-edaphic species (Hövemeyer 1992; Frouz 1999). The combination of tree shade and leaf litter accumulation especially benefited carabids, which were twice as abundant under canopied shrubs as in the other microhabitat types (see Koivula *et al.*

1999). Finally, tree presence also favoured staphylinids, which dominated under trees and canopied shrubs, where they could benefit from favourable environmental conditions and feed on abundant diptera, one of their preferred preys (Thayer 2005).

Mean carabid and staphylinid body length was highest under scattered shrubs; a result that partly agrees with our prediction (iii) and complies with the "enemy-free space" hypothesis that large-sized species may prefer complex habitat structures to avoid predation (Brose 2003). Scattered shrubs embedded in the grassland matrix can be very important for large predators that hunt in grasslands and take shelter in dense vegetation or under stones (Coiffait 1974; Bohac 1999; Morris 2000). In turn, small-sized species, particularly staphylinids, can escape predation in grasslands and under trees by hiding into crevices, thanks to their slender and flexible body form (Bohac 1999). The great abundance of medium- and large-sized individuals collected in canopied shrubs resulted in high beetle biomass (especially for carabids), which was mostly made up of omnivorous and predatory carabid species and litter-dwelling staphylinid species. High biomass of predatory beetles probably reflects the substantial energy flow through the decomposition food web in canopied shrubs, which very likely held high biomass of decomposers and detritivores at lower trophic levels (Chen & Wise 1999; Ponsard, Arditi & Jost 2000). A few mycophilous staphylinids were also present in canopied shrubs and trees, where moist conditions, mild temperatures and copious decomposing matter (including woody debris from fallen branches) may favour fungi development and fructification (Nordén *et al.* 2004; Pinna *et al.* 2010).

Open grasslands were richest in carabid species and, as predicted (iv), held particular carabid and staphylinid beetle assemblages different from the other microhabitat types. Grassland beetle assemblages included guilds of species that were rare elsewhere like seed-eating carabids that usually thrive in warm and sun exposed habitats (Thiele 1977), and coprophilous staphylinids that depend closely on livestock faeces. Also, great carabid species richness was found for scattered shrubs, a fact that suggests that this microhabitat type may be a keystone structure for these beetles as occurs in drier biotopes (Mazía, Chaneton & Kitzberger 2006). Differences in carabid beetle assemblages of the remaining microhabitats were determined by the presence of trees, stressing the influence that shade has on carabid species distribution (Taboada *et al.* 2006). On the other hand, staphylinid beetle assemblages responded strongly to litter accumulation, to which many species are particularly adapted (Mckenna *et al.* 2015), causing all litter-trapping microhabitats to share a common staphylinid assemblage. Although grasslands and trees offered similar resources to staphylinids, such as coprophilous diptera, they held distinct staphylinid assemblages, maybe due to the different environmental conditions provided by tree shade.

CONSERVATION AND MANAGEMENT IMPLICATIONS

The differences found in topsoil nutrient content and in arthropod abundance and distribution among the five microhabitat types most likely affect wood-pasture ecosystem functioning and service provisioning (de Bello *et al.* 2010). The accumulation of organic matter in litter-trapping microhabitats, especially under canopied shrubs, may enhance soil carbon sequestration (Wardle *et al.* 2004; Howlett *et al.* 2011), an important ecosystem service of wood-pastures (Bugalho *et al.* 2011). Litter-trapping microhabitats proved to be essential for the arthropod fauna, providing new habitat and shelter for large-sized beetles, and enhancing biodiversity, similarly to other complex vegetation structures embedded in grazed grasslands (Vickery *et al.* 2001; Woodcock *et al.* 2009). Scattered shrubs may also serve as shelter for butterflies (Dover, Sparks & Greatorex-Davies 1997) and lizards (Martín & Lopez 2002; Godinho, Santos & Sá-Sousa 2011) and stand as resting, roosting, singing and nesting places for birds (Hartel *et al.* 2014). Shrubs may thus be considered keystone structures for species requiring multiple microhabitats to live, in the same way as birds and bats benefit from tree presence in open landscapes (DeMars, Rosenberg & Fontaine 2010; Fischer, Stott & Law 2010). Furthermore, great arthropod biomass under canopied shrubs implies enhanced prey availability for higher trophic levels such as lizards, rodents, shrews and birds (Thiele 1977), very likely contributing to overall wildlife conservation (Vickery *et al.* 2001; Woodcock *et al.* 2009).

According to these results, a certain density of shrubs should be preserved and promoted in wood-pastures to enhance heterogeneity, but shrub encroachment should be avoided due to its negative effects on biodiversity and ecosystem functioning (Tárrega *et al.* 2009; Peco *et al.* 2012; García-Tejero *et al.* 2013). Even though shrub encroachment frequently promotes oak tree regeneration (Plieninger, Pulido & Konold 2003; Canteiro *et al.* 2011), it does not maintain the functioning and provision of services of wood-pastures in the long-term (Moreno & Pulido 2008; Ramírez & Díaz 2008; Moreno *et al.* 2013). Abandoned wood-pastures where shrubs proliferated can be firstly cleared by mechanical shrub cutting, while preserving several scattered shrub patches to promote heterogeneity. After cutting, grazing by low livestock loads should be implemented to restore the grassland habitat and resources (livestock faeces and grass seeds) on which arthropod assemblages depend (Morris 2000; Diacon-Bolli *et al.* 2012; García-Tejero *et al.* 2013). Since low-intensity grazing can limit the expansion of shrubs without suppressing them (Álvarez-Martínez, Gómez-Villar & Lasanta 2013), the cost of preserving shrubs may be lower compared to more delicate microhabitats that require fencing such as tall swards (Woodcock *et al.* 2009).

In all cases, the proportion and extent of the different microhabitats in a wood-pasture should be balanced according to the services they provide, and considering that the relative importance of different habitat structures decreases as their density increases (see Hartel *et al.* 2014). With this in mind, trees may be favoured over canopied shrubs since they render unique productive services such as resting places for livestock and, in some cases, tree shade may enhance grass production during dry summers (Hartel *et al.* 2014). Trees, particularly old ones, are of outstanding importance for fauna conservation (Kirby 1992; Manning, Fischer & Lindenmayer 2006; Robles *et al.* 2007; Sebek *et al.* 2013). Tree management is essential to maintain wood-pastures and their values (Plieninger *et al.* 2015) and trees are often pruned or pollarded (i.e., pruned removing the upper branches of the tree) to obtain firewood, fodder for livestock and to encourage horizontal canopy growth (Taboada *et al.* 2006; Moreno & Pulido 2008). Pollarding is also the most effective way to ensure tree longevity (Kirby 1992) and promotes the formation of tree hollows that favour saproxylic invertebrates, secondary cavity nesting birds and bats (Robles, Ciudad & Matthysen 2011; Sebek *et al.* 2013). Moreover, the habit of piling pruning debris may contribute to nutrient recycling and habitat provisioning for reptiles (Godinho, Santos & Sá-Sousa 2011) and arthropods, even though, for the latter, these structures may be of lower conservation value compared to other microhabitats (Kirby 1992). Whatever their contribution, pruning piles add up to promote landscape heterogeneity, further underlying the necessity of maintaining low-intensity management practices to preserve natural values in wood-pastures (Bugalho *et al.* 2011; Plieninger *et al.* 2015).

In conclusion, every microhabitat type in wood-pastures influenced the nutrient cycle and rendered important resources for the arthropod fauna (detritivores, herbivores and predators), emphasizing the relevance of preserving microhabitat heterogeneity to maximize the values of these traditional man-made ecosystems (Diacon-Bolli *et al.* 2012). Litter-trapping microhabitats (i.e., canopied and scattered shrubs and pruning piles) provided shelter and new habitat for arthropods, increasing their biomass and underlying the contribution of complex vegetation structures in promoting invertebrate diversity and conservation (Woodcock *et al.* 2009). Shrubs may thus be considered as an essential component of wood-pastures and should be therefore promoted and maintained in order to enhance microhabitat heterogeneity and overall biodiversity. However, this must be carried out without detriment to grasslands and trees, which play the main productive roles in wood-pastures (Moreno *et al*. 2013) and are crucial for the conservation of specialized arthropods (Manning, Fischer & Lindenmayer 2006; García-Tejero *et al.* 2013). Low-intensity management practices, such as livestock grazing and tree pruning or pollarding, are necessary to preserve the microhabitat mosaic that characterises wood-pastures, but such practices need to be supported by adequate agricultural and conservation policies to assure long-term sustainability (Bergmeier, Petermann & Schröder 2010; Díaz *et al.* 2013; Plieninger *et al.* 2015). Now that the social, cultural, aesthetic and conservation values of wood-pastures are sufficiently recognized by the scientific community, it is time to enhance public appreciation and political concern in order to preserve these outstanding landscapes.

Acknowledgements

We are grateful to Hugo Robles for help locating the sites, to José María Salgado for help identifying carabid beetles and to Reyes Tárrega García-Mares for her contribution to previous versions of the manuscript. This study is part of a research project supported by the Junta de Castilla y León (Ref. LE008A06). S.G-T. was funded by Junta de Castilla y León (doctoral fellowship EDU/918/2006).

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Supporting Information

The role of microhabitats and their management in the functioning of wood-pastures

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Supplementary Table S1. Identification keys and catalogues used to identify and name carabid and staphylinid beetles, and literature from which carabid species diet and staphylinid species niche preferences were obtained.

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Supplementary Table S2. Carabid beetles collected at the five different microhabitats: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile. Species body length and diet (P = predator, O = omnivore, SE = seed-eater) were obtained from the litterature (see Supplementary Table S1). Body weight was calculated using regression equations on body length (Hódar 1996)*.

	Body length (mm)	Body weight (mg)	Diet	Microhabitat					Total
				G	T	S	C	P	
Acupalpus (*Acupalpus*) *flavicollis* (Sturm, 1825)	3.1	9.8	SE	3	0	0	0	0	3
Amara (*Amara*) *aenea* (DeGeer, 1774)	7.0	22.5	O	74	23	12	7	2	118
Amara (*Bradytus*) *apricarius* (Paykull, 1790)	7.3	23.3	O	0	0	1	0	0	1
Amara (*Amara*) *eurynota* (Panzer, 1796)	10.0	32.1	O	0	0	1	0	0	1
Amara (*Amara*) *lucida* (Duftschmid, 1812)	5.5	17.7	O	1	1	2	0	1	5
Bembidion (*Phyla*) *tethys* Netolitzky, 1926	3.1	10.0	O	0	0	0	1	0	1
Brachinus (*Brachinoaptinus*) *bellicosus* Dufour, 1820	8.0	25.7	P	0	0	4	0	0	4
Brachinus (*Brachynidius*) *variventris* Schaufuss, 1862	6.0	19.3	P	1	3	0	0	0	4
Calathus (*Neocalathus*) *ambiguus* (Paykull, 1790)	10.5	33.8	O	3	1	2	0	1	7
Calathus (*Calathus*) *fuscipes* (Goeze, 1777)	12.5	40.2	O	122	241	186	498	156	1203
Calathus (*Neocalathus*) *granatensis* Vuillefroy, 1866	10.8	34.6	O	1	182	70	464	176	893
Calathus (*Neocalathus*) *melanocephalus* (Linnaeus, 1758)	7.0	22.5	O	0	35	9	35	23	102
Calathus (*Neocalathus*) *mollis* (Marsham, 1802)	7.5	24.1	O	8	11	7	3	1	30
Calathus (*Neocalathus*) *rotundicollis* Dejean, 1828	10.5	33.8	O	1	13	1	176	18	209
Carabus (*Oreocarabus*) *amplipennis* Vaucher de Lapouge, 1924	20.0	64.3	P	0	23	14	252	29	318
Carabus (*Mesocarabus*) *macrocephalus* Dejean, 1826	27.5	88.4	P	0	0	1	3	0	4
Carabus (*Archicarabus*) *nemoralis* O.F. Müller, 1764	23.0	73.9	P	0	0	0	0	1	1
Cymindis (*Cymindis*) *alternans* Rambur, 1837	8.3	26.5	P	0	1	0	0	0	1
Dinodes (*Dinodes*) *dives* (Dejean, 1826)	11.5	37.0	P	8	0	0	0	0	8
Dixus sphaerocephalus (Olivier, 1795)	6.5	20.9	SE	1	0	1	0	0	2
Harpalus (*Harpalus*) *anxius* (Duftschmid, 1812)	7.4	23.8	SE	112	4	5	0	0	121
Harpalus (*Harpalus*) *attenuatus* Stephens, 1828	8.0	25.7	SE	5	0	0	0	0	5
Harpalus (*Harpalus*) *decipiens* Dejean, 1829	9.0	28.9	SE	2	0	1	0	0	3
Harpalus (*Harpalus*) *distinguendus* (Duftschmid, 1812)	10.0	32.1	SE	120	0	0	0	0	120
Harpalus (*Harpalus*) *ebeninus* Heyden, 1870	11.0	35.4	SE	1	0	0	0	0	1
Harpalus (*Harpalus*) *neglectus* Audinet-Serville, 1821	8.0	25.7	SE	3	0	0	0	0	3
Harpalus (*Harpalus*) *oblitus* Dejean, 1829	10.5	33.8	SE	0	0	2	0	0	2
Harpalus (*Harpalus*) *pygmaeus* Dejean, 1829	6.3	20.1	SE	1	0	0	0	0	1
Harpalus (*Harpalus*) *rufipalpis* Sturm, 1818	8.0	25.7	SE	1	0	0	1	0	2
Masoreus wetterhallii (Gyllenhal, 1813)	4.8	15.3	P	2	1	0	0	0	3
Microlestes corticalis (Dufour, 1820)	2.7	8.5	P	1	0	0	0	0	1
Microlestes gallicus Holdhaus, 1912	3.0	9.7	P	1	0	0	0	0	1
Microlestes luctuosus Holdhaus, 1904	2.8	8.8	P	0	1	1	0	0	2

Supplementary Table S2. *(Continued)*

	Body length (mm)	Body weight (mg)	Diet	Microhabitat					Total
				G	T	S	C	P	
Nebria (*Nebria*) *brevicollis* (Fabricius, 1792)	12.0	38.6	P	0	3	0	3	0	6
Nebria (*Nebria*) *salina* Fairmaire & Laboulbène, 1856	11.0	35.4	P	96	137	15	277	32	557
Notiophilus quadripunctatus Dejean, 1826	5.3	16.9	P	1	2	1	7	1	12
Notiophilus substriatus Waterhouse, 1833	5.3	16.9	P	0	0	0	4	0	4
Olisthopus fuscatus Dejean, 1828	6.0	19.3	P	0	1	0	1	0	2
Ophonus (*Hesperophonus*) *azureus* (Fabricius, 1775)	8.0	25.7	SE	0	0	1	1	0	2
Ophonus (*Hesperophonus*) *cribricollis* (Dejean, 1829)	8.0	25.7	SE	4	0	0	0	0	4
Poecilus (*Coelipus*) *crenulatus* (Dejean, 1828)	11.3	36.3	O	1	0	0	0	0	1
Poecilus (*Macropoecilus*) *kugelanni* (Panzer, 1797)	13.0	41.8	O	25	2	20	1	12	60
Pseudomasoreus canigoulensis (Fairmaire & Laboulbène, 1854)	6.5	20.9	P	0	0	1	4	0	5
Steropus (*Steropidius*) *gallega* (Fairmaire, 1859)	14.5	46.6	P	0	0	1	0	3	4
Steropus (*Sterocorax*) *globosus* (Fabricius, 1792)	16.8	53.8	P	251	69	322	53	215	910
Syntomus foveatus (Geoffroy, 1785)	3.3	10.5	P	25	22	5	1	2	55
Synuchus vivalis (Illiger, 1798)	8.0	25.7	P	0	2	1	1	1	5
Tachyta (*Tachyta*) *nana* (Gyllenhal, 1810)	2.4	7.7	P	1	0	0	0	0	1
Trechus (*Trechus*) *obtusus* Erichson, 1837	3.6	11.6	P	0	8	6	73	182	269
Trechus (*Trechus*) *quadristriatus* (Schrank, 1781)	3.6	11.6	O	0	7	2	18	0	27
Zabrus (*Iberozabrus*) *silphoides* Dejean, 1828	13.8	44.2	SE	16	3	5	0	0	24
Carabid individuals				892	796	700	1884	856	5128
Carabid species				31	25	30	23	18	51
Exclusive species				12	1	4	2	1	

* Hódar, J.A. (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica*, **17**, 421–433.

Supplementary Table S3. Staphylinid beetles collected at the five different microhabitats: G = grassland, T = tree, S = scattered shrub, C = canopied shrub, P = pruning pile. Species body length and niche preference (L = litter-dweller, C = coprophilous, M = mycophilous) were obtained from the litterature (see Supplementary Table S1). Body weight was calculated using regression equations on body length (Hódar 1996)*.

	Body length (mm)	Body weight (mg)	Niche preference	Microhabitat					Total
				G	T	S	C	P	
Acrolocha sulcula (Stephens, 1834)	2.5	8.3	C	0	1	0	0	0	1
Acrotona clientula (Erichson, 1840)	2.6	8.7	L	0	36	5	15	40	96
Aleochara (*Coprochara*) *bipustulata* (Linnaeus, 1761)	3.5	11.7	C	105	33	0	2	12	152
Aleochara (*Baryodma*) *intrincata* Mannerheim, 1831	4.5	15.0	C	2	0	0	0	0	2
Aleochara (*Xenochara*) *laevigata* Gyllenhal, 1810	4.0	13.3	C	1	0	0	0	0	1
Aleochara (*Aleochara*) *laticornis*, Kraatz, 1856	5.0	16.7	L	3	1	2	4	8	18
Aleochara (*Heterochara*) *spissicornis*, Erichson, 1840	2.3	7.5	L	2	0	0	0	0	2
Aleochara (*Xenochara*) *stichai* Likovsky, 1965	4.5	15.0	L	0	5	0	1	0	6
Aleochara (*Coprochara*) *verna* Say, 1836	3.0	10.0	C	1	1	0	0	0	2
Amarochara (*Mniobates*) *forticornis* Lacordaire, 1835	3.3	10.8	L	0	1	0	0	0	1
Anotylus inustus (Gravenhorst, 1806)	3.5	11.7	C	44	19	0	0	0	63
Anotylus sculpturatus (Gravenhorst, 1806)	4.0	13.3	C	5	32	0	0	0	37
Anotylus tetracarinatus (Block, 1799)	1.9	6.3	C	0	0	1	0	0	1
Anthobium unicolor (Marsham, 1862)	3.3	10.8	L	0	0	0	0	1	1
Astenus (*Astenus*) *lyonessius* (Joy, 1908)	3.8	12.5	L	0	1	0	0	0	1
Astenus (*Astenognathus*) *macrocephalus* Coiffait, 1960	4.5	15.0	L	0	0	0	0	1	1
Astenus (*Eurysunius*) *mateui* Coiffait, 1960	4.3	14.3	L	1	0	0	0	0	1
Atheta (*Atheta*) *castanoptera* (Mannerheim, 1830)	3.9	13.0	L	0	4	0	1	0	5
Atheta (*Atheta*) *crassicornis* (Fabricius, 1792)	3.0	10.0	M	0	1	0	2	0	3
Atheta (*Datomicra*) *nigra* (Kraatz, 1856)	1.8	5.8	L	0	1	0	0	0	1
Atheta (*Atheta*) *nigritula* (Gravenhorst, 1802)	2.8	9.2	M	0	0	0	5	3	8
Atheta (*Atheta*) *pertyi* (Heer, 1839)	3.4	11.3	M	0	1	2	2	0	5
Atheta (*Earota*) *reyi* (Kiessenwetter, 1850)	4.0	13.2	L	0	0	1	4	1	6
Bolitobius castaneus (Stephens, 1832)	6.5	21.7	L	0	1	0	1	0	2
Cypha bifida Assing, 2004	1.1	3.7	L	0	15	0	0	0	15
Cypha unicolor (Rosenhauer, 1856)	1.0	3.3	L	1	0	0	1	0	2
Drusilla canaliculata (Fabricius, 1787)	4.8	15.8	L	0	1	0	0	0	1
Gabrius sp. A			L	0	0	0	1	0	1
Gauropterus fulgidus (Fabricius, 1787)	9.8	32.5	L	0	1	0	0	0	1
Gyrohypnus (*Gyrohypnus*) *fracticornis* (O. Müller, 1776)	7.0	23.3	L	0	0	0	1	0	1
Gyrohypnus (*Gyrohypnus*) *punctulatus* (Paykull, 1789)	7.0	23.3	L	0	0	0	0	1	1
Habrocerus capillaricornis (Gravenhorst, 1806)	3.5	11.7	L	0	0	0	0	8	8
Hesperus (*Hesperus*) *rufipennis* (Gravenhorst, 1802)	9.0	30.0	L	0	1	0	0	0	1
Leptacinus faunus Coiffait, 1956	5.0	16.7	L	2	0	0	0	1	3
Leptacinus guadarramus Outerelo, 1975	4.5	15.0	L	1	0	0	0	0	1
Liogluta alpestris (Heer, 1839)	4.2	13.8	L	0	25	0	8	1	34
Liogluta longiuscula (Gravenhorst, 1802)	3.8	12.5	L	7	100	42	151	67	367

Supplementary Table S3. (*Continued*).

	Body length (mm)	Body weight (mg)	Niche preference	Microhabitat					Total
				G	T	S	C	P	
Lomechusa emarginata (Paykull, 1780)	4.3	14.2	L	0	6	0	1	0	7
Lordithon (*Lordithon*) *exoletus* (Erichson, 1839)	4.5	15.0	M	0	15	0	25	4	44
Lordithon (*Bobitobus*) *lunulatus* (Linnaeus, 1760)	6.5	21.7	M	0	0	0	1	0	1
Medon castaneus (Gravenhorst, 1802)	6.5	21.7	L	0	0	0	1	0	1
Megarthrus sp. A			L	0	1	0	0	0	1
Metopsia clypeata (P. Müller, 1821)	2.6	8.7	L	0	0	1	0	4	5
Micropeplus staphylinoides (Marsham, 1802)	2.1	7.1	L	0	1	2	0	7	10
Mycetoporus angularis Mulsant & Rey, 1875	3.3	10.8	L	0	1	1	0	0	2
Mycetoporus baudueri Mulsant & Rey, 1875	3.3	10.8	L	0	2	1	3	2	8
Mycetoporus rufescens (Stephens, 1832)	4.5	15.0	L	0	0	1	1	5	7
Nehemitropia lividipennis (Mannerheim, 1830)	3.1	10.3	L	0	1	0	0	2	3
Ocypus (*Ocypus*) *olens* (O. Müller, 1764)	25.0	83.3	L	8	12	148	68	74	310
Ocypus (*Ocypus*) *ophtalmicus* (Scopoli, 1763)	17.0	56.6	L	2	2	1	0	0	5
Ocypus (*Pseudocypus*) *aeneocephalus* (DeGeer, 1774)	13.0	43.3	L	0	3	0	0	0	3
Ocypus (*Pseudocypus*) *aethiops* (Waltl, 1835)	16.0	53.3	L	0	3	35	112	53	203
Ocypus (*Pseudocypus*) *fortunatarum* Wollaston, 1871	12.5	41.7	L	0	0	1	0	0	1
Ocypus (*Pseudocypus*) *obscuroaeneus* Fairmaire, 1852	16.5	55.0	L	0	2	0	3	0	5
Ocypus (*Pseudocypus*) *picipennis* (Fabricius, 1739)	15.5	51.6	L	3	6	3	1	3	16
Oligota (*Oligota*) *punctulata* Heer, 1839	1.1	3.8	L	1	67	1	4	1	74
Omalium caesum Gravenhorst, 1806	3.0	10.0	L	0	15	7	3	3	28
Omalium excavatum Stephens, 1834	3.5	11.7	L	0	2	0	6	0	8
Omalium nigriceps Kiesenwetter, 1850	2.4	7.8	L	0	0	2	0	0	2
Othius laeviusculus Stephens, 1832	5.8	19.2	L	1	8	3	0	0	12
Othius piceus Scriba, 1870	8.1	27.0	L	0	0	0	4	1	5
Othius punctulatus (Goeze, 1777)	12.0	40.0	L	0	6	1	11	7	25
Othius subuliformis Stephens, 1832	5.8	19.2	L	0	7	0	13	2	22
Oxypoda (*Sphenoma*) *abdominalis* (Mannerheim, 1831)	3.3	10.8	L	2	11	0	0	1	14
Oxypoda (*Mycetodrepa*) *alternans* (Gravenhorst, 1802)	3.5	11.7	M	0	5	0	1	2	8
Oxypoda (*Bessopora*) *annularis* (Mannerheim, 1839)	2.3	7.5	L	0	9	1	6	0	16
Oxypoda (*Bessopora*) *ferruginea* Erichson, 1840	2.0	6.5	L	57	486	13	5	9	570
Oxypoda (*Mycetodrepa*) *formosa* Kraatz, 1858	3.0	10.0	M	0	1	0	4	0	5
Oxypoda (*Oxypoda*) *opaca* (Gravenhorst, 1802)	4.0	13.3	L	0	1	1	5	1	8
Oxypoda (*Baeoglena*) *praecox* Erichson, 1839	1.9	6.3	L	0	12	5	35	23	75
Oxypoda (*Sphenoma*) *rufa* Kraatz, 1858	3.8	12.5	L	0	20	0	0	0	20
Oxypoda (*Deropoda*) *rugulosa* Kraatz, 1856	2.0	6.7	L	2	0	0	0	0	2
Oxypoda (*Bessopora*) *testacea* Erichson, 1837	2.8	9.2	L	0	0	2	4	1	7
Oxypoda (*Sphenoma*) *togata* Erichson, 1839	3.3	10.8	L	3	3	0	4	0	10
Oxypoda (*Podoxya*) *umbrata* (Gyllenhal, 1810)	2.9	9.5	L	0	4	0	7	4	15
Oxypoda sp. A			L	0	6	0	0	0	6
Oxypoda sp. B			L	0	1	0	0	0	1

Supplementary Table S3. (*Continued*).

	Body length (mm)	Body weight (mg)	Niche preference	Microhabitat					Total
				G	T	S	C	P	
Oxypoda (*Sphenoma*) *assimilis* Kraatz, 1855	2.5	8.3	L	0	2	0	0	0	2
Oxypoda (*Sphenoma*) *islandica* Kraatz, 1857	2.3	7.5	L	0	5	0	6	0	11
Oxytelus (*Oxytelus*) *piceus* (Linnaeus, 1767)	4.3	14.2	C	1	0	0	0	0	1
Philonthus (*Philonthus*) *cognatus* Stephens, 1832	9.5	31.7	L	13	7	0	1	0	21
Philonthus (*Philonthus*) *nitidicollis* (Lacordaire, 1835)	7.0	23.3	L	5	0	0	0	0	5
Philonthus (*Philonthus*) *parvicornis* (Gravenhorst, 1802)	5.8	19.2	C	3	0	0	0	0	3
Philonthus (*Philonthus*) *splendens* (Fabricius, 1792)	12.5	41.7	C	0	1	0	0	0	1
Phloeonomus (*Phloeonomus*) *pusillus* (Gravenhorst, 1806)	1.9	6.2	L	0	0	0	0	1	1
Phyllodrepa (*Dropephylla*) *palpalis* Luze, 1906	2.5	8.3	L	0	2	0	0	0	2
Platydracus (*Platydracus*) *meridionalis* (Rosenhauer, 1847)	15.0	50.0	C	1	0	2	0	0	3
Proteinus brachypterus (Fabricius, 1792)	1.6	5.3	M	1	0	1	0	0	2
Proteinus ovalis Stephens, 1834	2.2	7.2	M	1	1	0	1	2	5
Quedius (*Raphirus*) *asturicus* Bernhauer, 1918	5.8	19.2	L	5	4	0	2	0	11
Quedius (*Raphirus*) *humeralis* Stephens, 1832	6.8	22.5	L	0	0	0	0	6	6
Quedius (*Raphirus*) *latinus* Gridelli, 1938	13.0	43.3	L	0	2	5	22	41	70
Quedius (*Quedius*) *levicollis* (Brullé, 1832)	12.5	41.7	L	1	8	1	4	0	14
Quedius (*Microsaurus*) *longicornis* Kraatz, 1858	8.5	28.3	L	0	0	0	1	0	1
Quedius (*Raphirus*) *nemoralis* Baudi, 1848	6.5	21.7	L	0	0	5	0	1	6
Quedius (*Raphirus*) *nigriceps* Kraatz, 1857	7.8	25.8	L	0	11	9	11	13	44
Quedius (*Microsaurus*) *nigrocaeruleus* Fauvel, 1876	9.0	30.0	L	0	2	0	0	0	2
Quedius (*Raphirus*) *persimilis* Mulsant & Rey, 1876	5.3	17.5	L	1	5	0	2	1	9
Quedius (*Raphirus*) *pineti* Brisout, 1866	7.5	25.0	L	0	0	0	5	6	11
Quedius (*Raphirus*) *semiaeneus* (Stephens, 1832)	6.8	22.5	L	29	19	1	4	5	58
Quedius (*Raphirus*) *semiobscurus* (Marsham, 1802)	8.0	26.7	L	0	3	3	0	0	6
Quedius (*Quedius*) *simplicifrons* Fairmaire, 1862	11.5	38.3	L	1	0	0	0	0	1
Rugilus (*Rugilus*) *erichsoni* (Fauvel, 1867)	4.0	13.3	L	0	0	0	1	0	1
Rugilus (*Rugilus*) *orbiculatus* (Paykull, 1789)	4.0	13.3	L	0	0	0	2	6	8
Sepedophilus lusitanicus Hammond, 1973	4.9	16.3	M	0	0	0	0	5	5
Sepedophilus nigripennis (Stephens, 1832)	2.3	7.5	L	0	0	2	3	6	11
Stenus (*Hemistenus*) *cordatus* Gravenhorst, 1802	7.0	23.3	L	1	0	0	0	0	1
Sunius fagniezi (Peyerimhoff, 1916)	3.5	11.5	L	0	0	0	2	0	2
Tachyporus (*Tachyporus*) *pusillus* Gravenhorst, 1806	2.5	8.3	L	2	59	6	14	1	82
Tasgius (*Tasgius*) *ater* (Gravenhorst, 1802)	16.0	53.3	L	0	1	0	0	0	1
Tinotus morion (Gravenhorst, 1802)	1.8	5.8	C	0	1	0	0	0	1
Xantholinus (*Polyodontophallus*) *elegans* (Olivier, 1795)	10.5	35.0	L	0	1	0	1	0	2
Xantholinus (*Xantholinus*) *gallicus* Dejean, 1821	7.0	23.3	L	0	0	0	1	0	1
Xantholinus (*Xantholinus*) *linearis* (Olivier, 1795)	7.5	25.0	L	2	45	1	27	4	79
Zyras (*Pella*) *limbatus* (Paykull, 1789)	5.0	16.7	L	0	3	0	3	1	7
Zyras (*Glossacantha*) *lugens* (Gravenhorst, 1802)	4.5	15.0	L	0	0	0	4	0	4

Supplementary Table S3. (*Continued*).

	Body length (mm)	Body weight (mg)	Niche preference	Microhabitat					Total
				G	T	S	C	P	
Mycetoporus sp.				0	1	0	0	0	1
Stenus (Hemistenus) spp.				0	3	4	5	1	13
Aleocharinae				7	25	2	4	2	40
Paederinae				0	1	0	4	1	6
Pselaphinae				2	1	0	0	0	3
Staphylinid individuals				330	1213	325	657	456	2981
Staphylinid species				37	72	37	61	48	116
Exclusive species				10	20	3	9	7	

* Hódar, J.A. (1996) The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica*, **17**, 421–433.

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