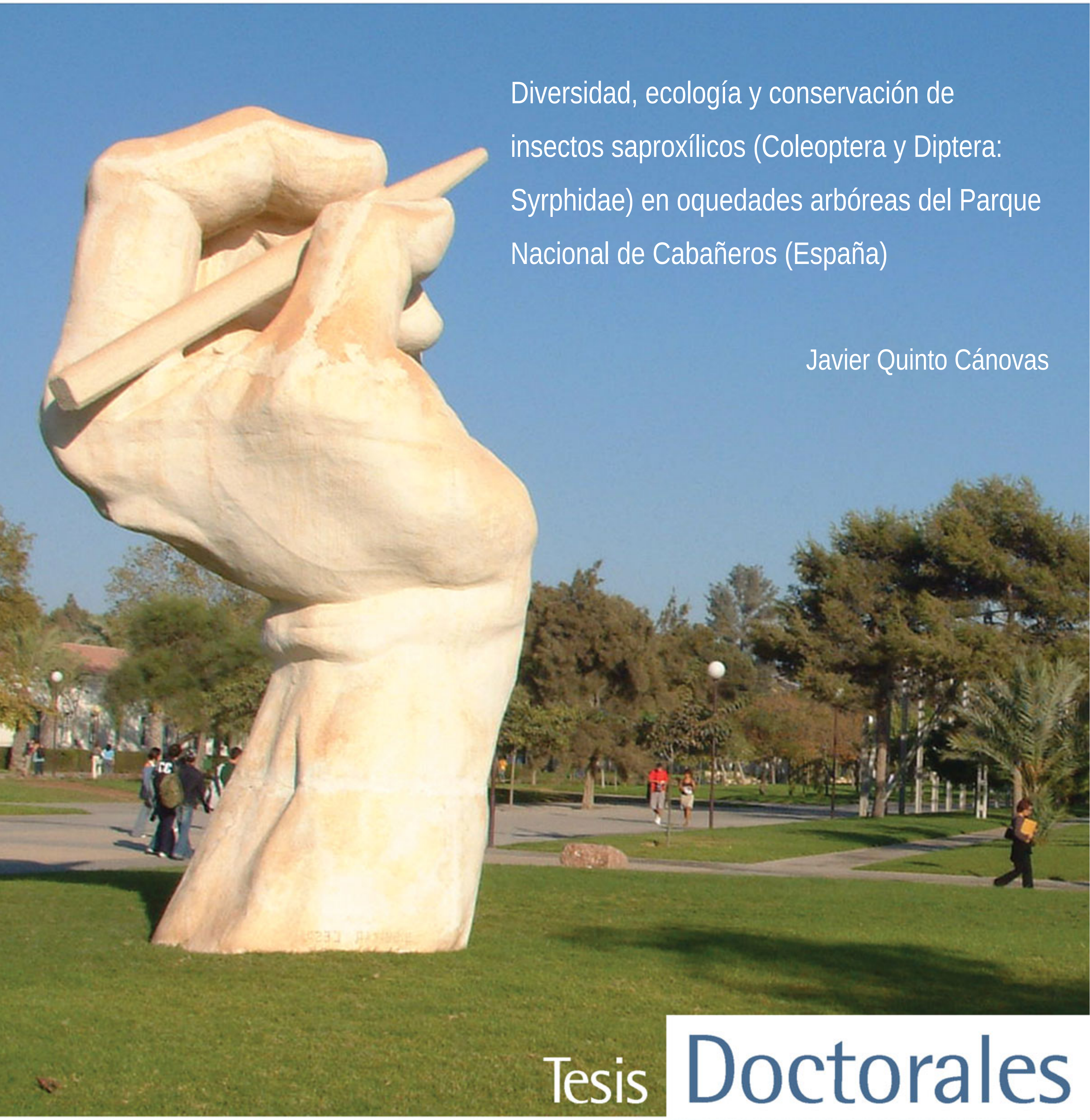

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Javier Quinto Cánovas

Tesis doctoral

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CIBIO
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Diversidad, ecología y conservación de insectos saproxílicos (Coleoptera y Diptera: Syrphidae) en oquedades arbóreas del Parque Nacional de Cabañeros (España)

Memoria presentada por el Licenciado Javier Quinto Cánovas para optar al título de Doctor en Biología por la Universidad de Alicante

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Universidad de Alicante

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Con orden y tiempo se encuentra el secreto de
hacerlo todo, y de hacerlo bien

Pitágoras

A mi familia y amigos

A mis abuelos

INDICE

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RESUMEN

Resumen y estructura de la tesis

Los insectos saproxílicos representan una gran biodiversidad en Europa, y participan en procesos ecológicos clave en los ecosistemas de bosque, siendo fundamentales en la descomposición y reciclado de nutrientes. La reducción y fragmentación de las masas forestales a lo largo de cientos de años ha provocado la extinción local de insectos saproxílicos en toda Europa, desembocando en la necesidad de un marco legal de protección de especies saproxílicas a través de su inclusión en Listas Rojas europea o nacionales, o al desarrollo de programas de conservación específicos de la entomofauna saproxílica y sus hábitats. Los bosques mediterráneos son el producto del manejo antrópico, abarcando desde las prácticas tradicionales hasta recientes cambios de uso de suelo. A pesar de la importancia ecológica de la fauna saproxílica y de su grado de amenaza en Europa, existe un bajo conocimiento de la diversidad, biología y ecología de este grupo funcional en los bosques mediterráneos.

En los últimos años, los bosques mediterráneos han suscitado un gran interés científico, ya que encierran una diversa fauna de insectos saproxílicos. La diversidad de insectos saproxílicos en los bosques mediterráneos está en gran medida condicionada por la escasez de árboles viejos y de sus microhábitats asociados, siendo las oquedades uno de los más importantes en términos de biodiversidad. Sin embargo, apenas existen estudios en bosques mediterráneos de la Península Ibérica, existiendo un desconocimiento general de su biodiversidad saproxílica y, por ende, de su estatus de conservación. Estudios recientes dejan ver la existencia de una gran diversidad de insectos saproxílicos en distintos bosques mediterráneos de la Península Ibérica, con un alto componente de especies raras o endémicas, y donde confluyen especies de distribución centroeuropea y norteafricana. Por tanto, resulta de gran interés estudiar la fauna saproxílica asociada a un microhábitat tan particular y limitado como son las oquedades de los árboles en bosques mediterráneos ibéricos.

Esta tesis doctoral en primer lugar busca conocer qué especies de Coleoptera y Diptera: Syrphidae constituyen la comunidad saproxílica de las oquedades de los bosques mediterráneos presentes en el Parque Nacional de Cabañeros (España). En segundo lugar, se persigue evaluar qué métodos de muestreo son más efectivos para realizar inventarios y seguimientos de la fauna saproxílica ligada a las oquedades de bosques mediterráneos. Por último, buscamos determinar qué factores ecológicos influyen en la distribución y diversidad de los insectos saproxílicos. La selección del Parque Nacional de Cabañeros como área de estudio se debe a que es un ejemplo de ecosistemas mediterráneos bien preservados, que cuenta con 20000 hectáreas de bosques. Hemos trabajado con tres de los bosques mediterráneos más representativos de Cabañeros: 1) bosque caducifolio mixto de robles acidófilos *Quercus pyrenaica* y *Q. faginea*, 2) bosque de ribera de fresno *Fraxinus angustifolia*, y 3) bosque esclerófilo de encina *Q. rotundifolia*, donde seleccionamos 30, 27 y 30 oquedades, respectivamente. A partir de esta selección inicial se han desarrollado la totalidad de los capítulos de esta tesis.

Esta tesis doctoral está estructurada en cuatro capítulos seguidos de una discusión y de las conclusiones generales.

En el **capítulo 1** se realiza una introducción general sobre los insectos saproxílicos, los grupos taxonómicos más representativos y los tipos de gremios saproxílicos en función de sus hábitos tróficos, así como su importancia ecológica en los ecosistemas forestales. Del mismo modo, se facilita información acerca del conocimiento actual y estrategias de conservación del grupo en Europa y en la Península ibérica. De acuerdo con esta información de partida se establecen la justificación y objetivos propuestos en esta tesis. En este capítulo también se describe el área donde se desarrollan nuestras investigaciones, así como los grupos taxonómicos seleccionados para responder a los objetivos planteados.

En los **capítulos 2 al 4** y en los **Apéndices 1-4** se recogen los principales resultados derivados de esta tesis, los cuales presentan una estructura de artículos científicos y se encuentran ya publicados o en distintas fases de revisión.

En el **capítulo 2** se evalúa la efectividad de tres métodos de muestreo para capturar coleópteros saproxílicos en los bosques mediterráneos más maduros del área de estudio. La finalidad es conocer qué son más adecuados para estudiar la diversidad de familias y especies de coleópteros saproxílicos, así como para evaluar la diversidad ecológica de los distintos gremios saproxílicos dentro de las oquedades. El conocimiento del método que proporciona una mejor caracterización de la comunidad saproxílica ligada a las oquedades, ha permitido su aplicación en el desarrollo de los capítulos subsiguientes.

En el **capítulo 3** se analiza qué propiedades o patrones típicos de redes ecológicas especializadas están presentes en la interacción oquedad arbórea-insecto saproxílico, considerando tres diferentes grados de interacción: 1) red completa; 2) subredes de acuerdo al uso de los recursos tróficos de la madera; y 3) subredes de acuerdo al gremio saproxílico. Además, se analizan las diferencias en la arquitectura y patrones de interacción entre las subredes consideradas, y se estudian sus posibles implicaciones en la estabilidad de estas redes ante perturbaciones ambientales, a través de la simulación de extinciones aleatorias y dirigidas del microhábitat oquedad en el bosque mediterráneo. El análisis de redes ecológicas nos permite profundizar sobre cómo afectan las relaciones interespecíficas en la biodiversidad, estructura, dinámica y estabilidad de esta comunidad saproxílica.

En el **capítulo 4** se estudia la diversidad y composición de los gremios de insectos saproxílicos: xilófagos, saprófagos, saproxilófagos, xilomicetófagos, depredadores y comensales en las oquedades seleccionadas en los diferentes tipos de bosque mediterráneo. También se analiza cómo distintas variables microambientales (ecológicas y biológicas) difieren entre los tipos de bosques, y cómo éstas determinan diferencias en la distribución de los gremios saproxílicos.

En los **capítulos 2 y 4** se describen diferentes medidas de conservación de la fauna saproxílica asociada a los boques mediterráneos y sus oquedades a escala local.

De acuerdo al conjunto de resultados obtenidos se realiza una **discusión general**. En el apartado de **conclusiones generales**, se compendian las principales conclusiones derivadas de cada capítulo.

En los **Apéndices 1-4** quedan recogidos otros trabajos científicos que se han desarrollado dentro del contexto de esta tesis, y que aportan

información complementaria sobre la distribución, hábitats de desarrollo o status de conservación de algunos insectos saproxílicos.

CAPÍTULO 1

Introducción general

Capítulo 1. Introducción general

1.1. Los insectos saproxílicos y su importancia ecológica

Los organismos saproxílicos son aquellos que, en al menos una parte de su ciclo biológico, dependen de la madera muerta o en proceso de descomposición asociada tanto a árboles moribundos o muertos (en pie o caídos) como a árboles vivos, o de hongos que colonizan dicha madera, o bien se encuentran asociadas a la presencia de otras especies estrictamente saproxílicas (Speight, 1989; Alexander, 2008). Dentro de esta amplia definición se incluyen especies que habitan multitud de microhábitats ligados a la madera, como oquedades, corteza, savia, acumulaciones de agua, etc. (Speight, 1989), así como aquellas que dependen de diferentes fases de descomposición particulares, de sus productos, o de sus agentes causantes (Stokland *et al*., 2012). La diversidad de microhábitats que ofrece la madera es muy heterogénea entre tipos de bosques, dentro de un mismo bosque o incluso dentro de un mismo árbol (Irmler *et al*., 1996; Schmidl *et al*., 2008; Winter & Möller, 2008). Entre los organismos que explotan estos recursos se encuentran numerosos grupos taxonómicos (Alexander, 2002), siendo los insectos el grupo más diversificado. En particular, Coleoptera y Diptera (junto con los Hymenoptera) son considerados los dos órdenes más diversos dentro de este grupo funcional, y un alto número de familias de coleópteros y dípteros presentan representantes saproxílicos (Bouget & Brustel, 2009; Stokland *et al*., 2012).

Los insectos saproxílicos pueden agruparse en distintos gremios según su régimen alimenticio: xilófago, saprófago/saproxilófago, xilomicetófago, detritívoro, depredador y comensal (Dajoz, 1998), existiendo una gran variabilidad de requerimientos biológicos dentro de cada uno de estos gremios tróficos. De manera general, los estados larvarios presentan régimen saproxílico mientras que los adultos son florícolas (Figura 1), aunque existen numerosas excepciones en las que tanto la larva como el adulto presentan el mismo régimen alimenticio, especialmente entre xilomicetófagos y depredadores (Bouget *et al*., 2008). Las comunidades de insectos saproxílicos juegan un papel ecológico decisivo en los ecosistemas de bosque, dado que las fases larvarias favorecen la descomposición y reciclaje del material vegetal (Davies *et al*., 2008), degradando compuestos orgánicos con estructuras químicas complejas (como polisacáridos o lignina) en un sustrato más fácilmente asimilable (Micó *et al*., 2011), mientras que los adultos participan en la polinización de las especies vegetales. Por último, su elevada diversidad contribuye en gran medida al mantenimiento de las cadenas tróficas en los ecosistemas forestales (Dajoz, 1998; Thompson & Rotheray, 1998).

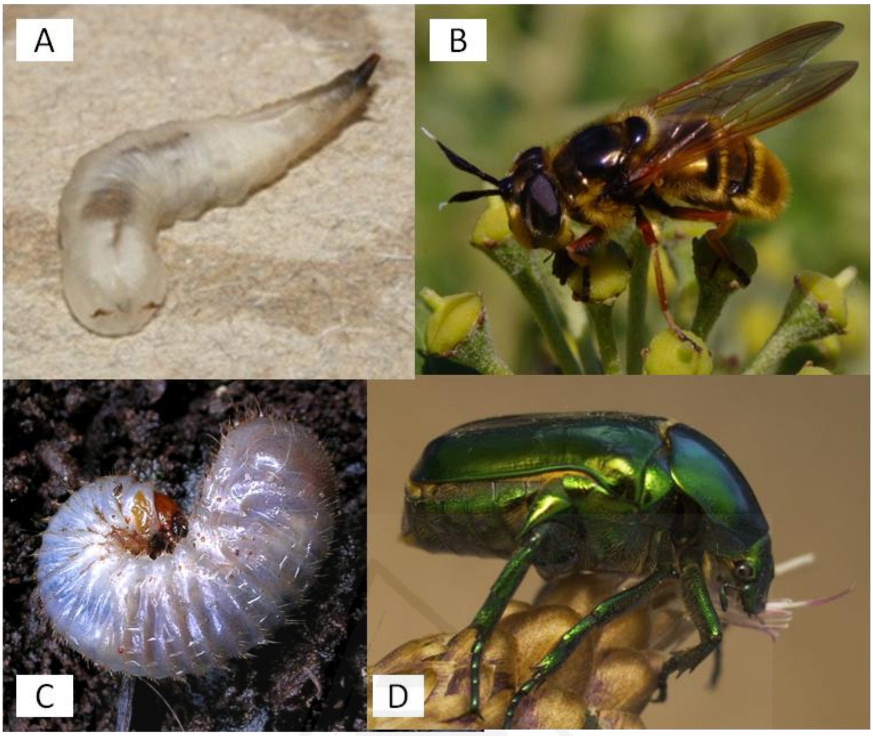

Figura 1. A-B: larva saprófaga y adulto florícola de *Callicera spinolae* Rondani, 1844. C-D: larva saproxilófaga y adulto florícola de *Cetonia aurataeformis* Curti, 1913 (Fotos: M.A. Marcos, E. Micó, J. Ordóñez).

1.2. Situación en Europa y en la Península Ibérica

La necesidad de conservar la biodiversidad de invertebrados saproxílicos en Europa queda por primera vez manifiesta en el Consejo de Europa de 1989. Es en este Consejo donde se define el concepto de saproxílico, y se pone de manifiesto la problemática y la necesidad de conservación de las comunidades saproxílicas en Europa, reconociendo además el papel que este grupo funcional tiene como bioindicador de la calidad/estado de conservación de los bosques, así como su importancia ecológica en la dinámica de los ecosistemas forestales (Speight, 1989).

Los Coleoptera son sin duda el grupo de insectos saproxílicos más conocido en Europa, y se estima que entre el 22-56% del total de especies de coleópteros presentan hábitos saproxílicos (Grove, 2002), siendo además el grupo de insectos con más representantes saproxílicos protegidos de Europa. La Lista Roja Europea contempla 436 especies de coleópteros saproxílicos, e incluye especies pertenecientes a los distintos biotopos de Europa, abarcando desde las áreas más secas de bosque mediterráneo en el sur a la tundra ártica en el extremo norte (Nieto & Alexander, 2010). Entre los Diptera, la familia Syrphidae es una de las más estudiadas, registrando más de 100 especies saproxílicas con distintas áreas de distribución en Europa (Speight *et al*., 2010). Sus representantes presentan notorias diferencias en sus requerimientos tróficos y en los microhábitas que habitan (Speight *et al*., 2010; Rotheray & Gilbert, 2011; Radenković *et al*., 2013).

Durante los últimos siglos se ha producido un progresivo cambio de los usos del bosque que ha conllevado una profunda transformación del paisaje y fragmentación de los hábitats en el norte de Europa. Como consecuencia de ello se ha producido un negativo impacto en la comunidad de invertebrados (Speight, 1989), provocando la desaparición local de insectos saproxílicos (Siitonen & Martikainen, 1994; Hambler & Speight, 1996) y la inclusión de muchas otras en listados nacionales de especies amenazadas (Gärdenfors, 2005; Farkac *et al*., 2005). En la Región Mediterránea, los incendios forestales, el sobrepastoreo y los cambios de uso de suelo como el abandono de las actividades tradicionales continúan reduciendo drásticamente la superficie de los bosques mediterráneos (Haslett, 2007). Aunque la necesidad de conservar este grupo funcional también se ha hecho patente en España a través de la incorporación de varias especies saproxílicas en el Libro Rojo de Invertebrados de España (Verdú & Galante, 2005), en general existen muy pocos estudios sobre la fauna saproxílica de los bosques mediterráneos ibéricos.

La cuenca del Mediterráneo es considerada como un 'punto caliente' de biodiversidad animal y vegetal a escala global (Mittermeier *et al*., 2004, van Swaay *et al*., 2010), y a pesar de ello, apenas existen estudios sistemáticos que evalúen la biodiversidad saproxílica de los bosques mediterráneos en Europa (Brin & Brustel, 2006; Buse *et al*., 2008; Jansson & Coskum, 2008; Da Silva *et al*., 2009; Ricarte *et al*., 2009; Micó *et al*., en prensa). La Península Ibérica es la región mediterránea más estudiada en cuanto a invertebrados, y cada año son descritas nuevas especies (Haslett, 2007), muchas de ellas con biologías saproxílicas (algunos ejemplos en Alonso-Zarazaga *et al*., 2009; Otero *et al*., 2010; Viñolas, 2011; Zapata de la Vega & Sánchez-Ruiz, 2012). Sin embargo, los estudios sobre este grupo funcional se han centrado en algunos taxones saproxílicos, o bien se ha documentado cualitativamente la fauna saproxílica de algunas zonas o especies arbóreas concretas, careciendo de un listado nacional de especies saproxílicas y presentando una ecología prácticamente desconocida (citas recogidas en Méndez Iglesias, 2009).

Los bosques ibéricos reúnen una serie de características que los hacen únicos frente a los del resto del continente europeo y por lo que resulta esencial el estudio de su fauna saproxílica. Por una parte, la Península Ibérica constituye el origen y centro de distribución de varios tipos de bosque, como los robledales de *Quercus pyrenaica*, que sólo alcanzan el sur de Francia y Norte de Marruecos fuera del territorio peninsular. Por otra parte, su posición geográfica permite la presencia de bosques de distribución íberomagrebí de gran singularidad en el contexto europeo pues se trata del único país donde están presentes, como es el caso de los quejigares de *Quercus faginea* subsp. *broteroi* (Sainz Ollero y Sánchez de Dios, 2011). Además, otras formaciones vegetales son exclusivas de países de la Región Mediterránea, como las fresnedas de *Fraxinus angustifolia* (distribución holártica submediterránea) (de Bolós y Vigo, 1990b), o los encinares de *Quercus rotundifolia* (Mediterráneo SW) (de Bolós y Vigo, 1990a). Por último, la explotación y manejo de los bosques mediterráneos en España se remonta al siglo VI (Bignal & McCracken, 2000), lo que ha contribuido notoriamente a la diversificación del paisaje mediterráneo y de los hábitats donde se integra la fauna (Rodà *et al*., 2009; Ortuño & Martínez-Pérez, 2011).

1.3. Justificación

Estudios pioneros han señalado que los bosques mediterráneos más representativos del Parque Nacional de Cabañeros albergan una rica fauna de especies de Coleoptera y Diptera (Syrphidae) saproxílicas con distribuciones Centroeuropeas y Norteafricanas, concentrando un alto número de endemismos, especies raras o poco conocidas (Ricarte *et al*., 2007; Ricarte *et al*., 2009; Micó *et al*., en prensa). Sin embargo, apenas existen estudios que permitan comparar estos resultados con otros bosques mediterráneos de la Península Ibérica. Los bosques mediterráneos estudiandos en otras partes de Europa presentan una rica fauna saproxílica (Brin & Brustel, 2006; Buse *et al*., 2008; Jansson & Coskum, 2008; Da Silva *et al*., 2009) que en gran medida está condicionada por la escasez de árboles viejos (Speight & Good, 2003) y de sus microhábitats asociados, siendo las oquedades uno de los más importantes en términos de biodiversidad (Sirami *et al*., 2008; Atay *et al*., 2012). Además, en estas oquedades se dan cita numerosas especies saproxílicas exclusivas de coleópteros y sírfidos (Ranius, 2002; Speight *et al*., 2010; Gouix *et al*., 2012), muchas de las cuales se encuentran protegidas a nivel europeo (Nieto & Alexander, 2010). Por tanto, la fauna saproxílica en las oquedades de distintos bosques mediterráneos debe ser estudiada de un modo sistemático con el fin de conocer la biodiversidad saproxílica total en un área actualmente bien preservada como es el Parque Nacional de Cabañeros, y posteriormente poder comparar con los resultados obtenidos en otros bosques mediterráneos ibéricos. Del mismo modo, resulta importante discernir qué factores ecológicos determinan diferentes ensambles saproxílicos en diferentes tipos de bosque mediterráneo, estableciendo así estrategias de conservación aplicables a escala local.

1.4. Área de estudio: El Parque Nacional de Cabañeros

El Parque Nacional de Cabañeros fue declarado como tal en 1995 (Figura 2). Se trata de uno de los 14 Parques Nacionales que existen en España, y abarca 40.586 ha repartidas entre las provincias de Ciudad Real y Toledo (MAAM, 2012). El tipo de clima es Mediterráneo (con inviernos suaves y largos periodos de sequía), comprendiendo los pisos bioclimáticos mesomediterráneo y supramediterráneo. La temperatura media anual oscila entre 12.9 y 15.6 ºC, y la precipitación media anual fluctúa entre 500 y 750 mm (Vaquero de la Cruz, 1997a).

Figura 2. Panorámica del Parque Nacional de Cabañeros (Foto: J. Ordóñez).

El Parque está constituido por paisajes mediterráneos, donde las distintas masas forestales están contenidas dentro de una matriz predominante herbácea y arbustiva (Figura 3). Este paisaje vegetal es el resultado de una compleja trama de relaciones entre sus características ambientales, pasadas y actuales, y la determinante actividad desarrollada durante siglos por el hombre y sus animales. Una de las principales actuaciones transformadoras del hombre en Cabañeros ha sido el adehesamiento del bosque, aunque estas actividades cesaron en gran parte de su extensión desde que fue declarado Parque Nacional en 1995, por lo que hoy podemos encontrar formaciones forestales maduras. Entre las principales formaciones arbóreas destacan (Figura 4): 1) Formaciones puras o mixtas de quejigo (*Quercus faginea*) y roble melojo (*Q. pyrenaica*) en el piso mesomediterráneo; 2) Formaciones de ribera dominada por fresnos (*Fraxinus angustifolia*); 3) Formaciones arbóreas dominadas por especies esclerófilas como el alcornoque (*Q. suber*) o la encina (*Q. rotundifolia*), o bien formaciones mixtas con quejigo (Vaquero de la Cruz, 1997b).

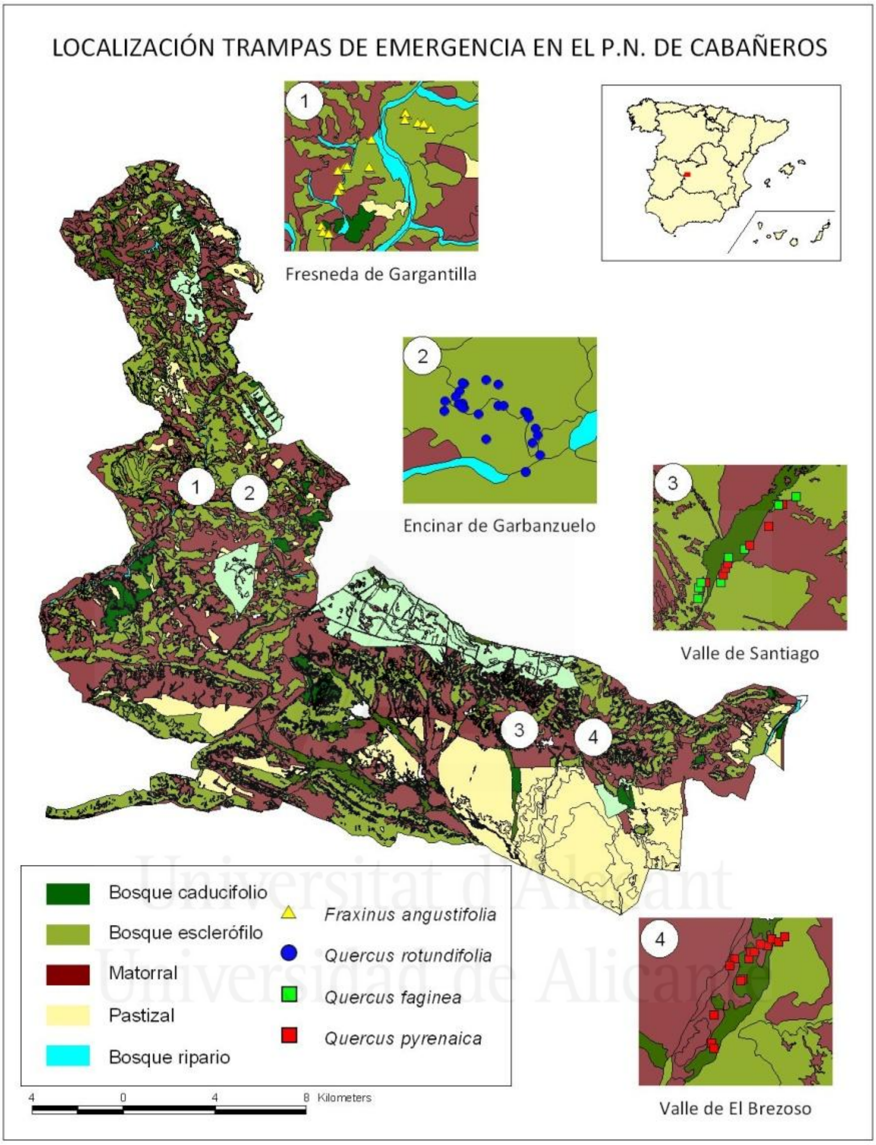

Figura 3. Principales tipos de vegetación, puntos de muestreo y localización de las trampas de emergencia en P.N. de Cabañeros.

Figura 4. Algunas de las formaciones forestales más representativas: robledales caducifolios mixtos de melojo y quejigo, bosque ripario de fresno y encinares perennifolios (Fotos: E. Micó, J. Ordóñez).

1.5. Grupos taxonómicos objeto de estudio

Los grupos de insectos considerados en esta tesis fueron:

a) Coleoptera saproxílicos. Las 42 familias de coleópteros consideradas en esta tesis fueron: Aderidae, Anobiidae, Biphyllidae, Buprestidae, Cerambycidae, Cerylonidae, Cetoniidae, Ciidae, Clambidae, Cleridae, Cryptophagidae, algunos Curculionidae, Curculionidae Scolytinae, Dasytidae, Dermestidae, Dynastidae, Elateridae, Endomychidae, Eucinetidae, Helodidae, Histeridae, Laemophloeidae, Latridiidae, Leiodidae, Lucanidae, Malachiidae, Melandryidae, Melyridae, Mycetophagidae , Nitidulidae, Oedemeridae, Platypodidae, Pselaphidae, Ptiliidae, Ptinidae, Rhizophagidae, Scraptiidae, Scydmaenidae, Silvanidae, Tenebrionidae, Trogossitidae, Zopheridae, abarcando representantes pertenecientes a distintos gremios saproxílicos: xilófagos, saproxilófagos, xilomicetófagos, depredadores y comensales.

b) Dípteros saprófagos/saproxilófagos (Diptera: Syrphidae). Dentro de los sírfidos, se conocen tres tipos de alimentación larvaria: 1) micofagia/fitofagia, 2) entomofagia (depredadores), y 3) el grupo funcional objeto de estudio, saprofagia/saproxilofagia (Cole *et al*., 2002). Los sírfidos saprófagos/saproxilófagos explotan condiciones húmedas o acuáticas en un amplio rango de hábitats ligados a la madera: exudados de savia, en madera o material vegetal en descomposición, o en galerías de otros insectos barrenadores (Speight *et al*., 2010). Además, muchas de estas especies son raras y/o están amenazadas de extinción, constituyéndose en importantes indicadores de la calidad de bosques (Speight, 1986).

El creciente conocimiento que se tiene sobre la taxonomía y diversidad, así como los hábitats y microhábitats a los que se asocian estos grupos taxonómicos saproxílicos, permite que los utilicemos en estudios ecológicos como especies bioindicadoras de la calidad de los bosques (Speight, 1989), y en estudios de conservación como especies bandera de comunidades saproxílicas completas (New, 2007; Ricarte *et al*., 2007).

1.6. Objetivos de la tesis doctoral

El objetivo general de esta tesis es conocer la biodiversidad saproxílica de Coleoptera y Diptera (Syrphidae) que albergan las oquedades de los árboles en bosques mediterráneos más representativos del Parque Nacional de Cabañeros, y determinar qué factores ecológicos y biológicos influyen en la diversidad, distribución y estructura de las comunidades saproxílicas mediterráneas ibéricas. Estos resultados permitirán establecer o/y optimizar estrategias de manejo y conservación a escala local basadas en el conocimiento empírico de la comunidad saproxílica asociada a las oquedades de los árboles. Con este fin, se han desarrollado los siguientes objetivos específicos:

- Evaluar la eficacia de tres métodos de muestreo para caracterizar la fauna de coleópteros saproxílicos en el bosque mediterráneo. Determinar qué métodos son más adecuados para muestrear la diversidad taxonómica del ensamble de escarabajos de las oquedades, así como la diversidad ecológica de los gremios saproxílicos.

Tras conocer qué método de muestreo resulta más adecuado para caracterizar el ensamble saproxílico en los bosques seleccionados, se evaluaron diferentes factores ecológicos y biológicos que aparecen recogidos en los objetivos específicos subsiguientes.

- Averiguar cómo se establecen las relaciones multitróficas en la comunidad saproxílica de coleópteros y sírfidos en el microhábitat oquedad. Se examinan qué tipos de patrones de redes especializados están presentes en la interacción oquedad-insecto saproxílico a lo largo de las distintas subredes de interacción que tienen lugar en esta red: 1) red completa; 2) subredes de acuerdo al uso de los recursos de la madera; 3) subredes de acuerdo al grupo funcional.

  Una vez conocidas las diferencias entre las diferentes subredes consideradas, evaluar las posibles implicaciones de éstas sobre la estabilidad de la interacción oquedad-insecto saproxílico y a través de simulaciones de extinciones aleatoria y dirigidas del microhábitat oquedad.

- Estudiar cómo varía la diversidad y composición de los distintos gremios tróficos en las oquedades de los principales tipos de bosque mediterráneo. Del mismo modo, evaluar las diferencias a nivel de microescala entre tipos de bosque, considerando diversas variables ecológicas y biológicas de las oquedades, y discernir qué variables afectan en mayor medida a la distribución de cada gremio saproxílico.

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CAPÍTULO 2

Effectiveness of three sampling methods to survey saproxylic beetle assemblages in Mediterranean woodland

Efectividad de tres métodos de muestreo para evaluar el ensamble de escarabajos saproxílicos en el bosque mediterráneo

Quinto, J., Marcos-García, M.A., Brustel, H., Galante, E., Micó, E. Journal of Insect Conservation, en revision.

Abstract

The choice of sampling methods to survey saproxylic beetles is a key aspect to set conservation strategies for one of the most endangered assemblages in Europe. We evaluated the efficiency of three sampling methods: baited tube traps (TT), window traps in front of a hollow opening (WT), and emergence traps covering tree hollows (ET) to study richness and diversity of saproxylic beetle assemblages at species and family levels in Mediterranean woodlands. We also examined trap efficiency to report ecological diversity, and changes in the relative richness and abundance of species forming trophic guilds: xylophagous, saprophagous/saproxylophagous, xylomycetophagous, predators and commensals. WT and ET were similarly effective in reporting species richness and diversity at species and family levels, and provided an accurate profile of both the flying active and hollow-linked saproxylic beetle assemblages. WT and ET were the most complementary methods, together reporting more than 90% of richness and diversity at both species and family levels. Diversity, richness and abundance of guilds were better characterized by ET, which indicates higher efficiency in outlining the ecological community of saproxylics that inhabit tree hollows. TT were the least effective method at both taxonomic levels, sampling a biased portion of the beetle assemblage attracted to trapping principles, however they could be used as a specific method for families such as Bostrichiidae, Biphyllidae, Melyridae, Mycetophagidae or Curculionidae Scolytinae species. Finally, ET and WT combination allows a better characterization of saproxylic assemblages in Mediterranean woodland, by recording species with different biology and linked to different microhabitat types.

Keywords

Trap efficiency, tube trap, window trap, emergence trap, Mediterranean woodland, Coleoptera

Introduction

Saproxylic insects – *sensu* Speight 1989, updated by Alexander 2008– are considered to be the most important group in woodland ecosystems because they depict the highest richness and abundance of species, with Coleoptera as one of the most representative orders (Dajoz 2001; Schlaghamersky 2003; Bouget et al. 2008a). Nevertheless, forestry practices carried out in Europe during the last centuries have jeopardized their habitats (Speight 1989; Dajoz 2001; Siitonen 2001), and forest fires, grazing (Haslett 2007) or local changes in land uses still continue to devastate woodlands in the Mediterranean region. Consequently, saproxylic species are one of the most threatened groups of organisms (Jonsell et al. 1998; Alexander 2004). They also perform a crucial ecological role, by contributing to the maintenance of trophic chains (Schlaghamersky 2003), and participating in the decomposition of woody material (Davies et al. 2008; Micó et al. 2011a). Despite their importance, saproxylic beetles are so diverse taxonomically and inhabit in so many woody substrates and microhabitats within woodlands that few studies involve an accurate representation of the whole community, resulting in little attention to community attributes such as species richness, diversity and evenness or abundance of trophic guilds.

Many saproxylic beetles present low dispersal ability (Thomas 2000; Ranius and Hedin 2001; Ewers and Didham 2006), and some are small and cryptic (Bouget et al. 2008a), or specific to microhabitats offered by dead wood or living trees within the woodland matrix (Dajoz 1980, Sirami et al. 2008; Winter and Möller 2008; Marcos-García et al. 2010). This is why combined method techniques are usually required to obtain reliable information on saproxylic communities (Martikainen and

Kouki 2003; Ozanne 2005; Alinvi et al. 2007). Many combinations of methods surveying saproxylic beetle assemblages have already been used by other authors (Økland 1996; Ranius and Jansson 2002; Hyvärinen et al. 2006; Alinvi et al. 2007; Bouget et al. 2009), leading to the conclusion that trunk-window traps are suitable for comparisons of substrates within forest environments (Økland 1996), baited-window traps for comparing communities from different forest environments (Bouget et al. 2009), or pitfall traps for collecting beetles associated with tree hollows (Ranius and Jansson 2002; Hyvärinen et al. 2006).

The choice of pertinent standardized sampling techniques is crucial not only to obtain more complete inventories, but also to acquire information about species status (Bouget and Brustel 2009a; Sverdrup-Thygeson and Birkemoe 2009), species interactions (Quinto et al. 2012), biotic requirements or phenologies (Ranius and Jansson 2002; Hyvärinen et al. 2006; Alinvi et al. 2007; Gouix and Brustel 2011), and in general to develop ecological studies addressed to suitable woodland management based on saproxylic assemblages. Moreover, standardized sampling techniques are essential for comparing species diversity and abundance patterns across different studies and sites (Larsen and Forsyth 2005). However, although many studies have taken into account method effectiveness for several saproxylic families or target species in Northern (Økland 1996; Ranius and Jansson 2002; Martikainen and Kalia 2004; Hyvärinen et al. 2006; Alinvi et al. 2007) and Western Europe (Sirami et al. 2008; Bouget et al. 2009; Gouix and Brustel 2011), very few studies have been centred on the Southern region (Jansson and Coskum 2008). As the majority of saproxylic insect diversity, in terms of species richness, occurs in more southern regions of Europe (Nieto and Alexander 2010), and with Coleoptera as one of the most diversified orders among insects (Dajoz 1980), it is of vital importance to evaluate trapping techniques to monitor beetle communities in Mediterranean woodlands for conservation purposes. This consideration should cover several sampling methods and taxonomic levels to enable comparison with previous research.

The aim of this work was to assess the effectiveness of three sampling methods: window, emergence and baited-tube traps, used to study saproxylic beetle community patterns (relative richness and abundance) at species and family levels in Mediterranean woodlands. We also examine changes in the relative abundance of trophic guilds: xylophagous, saprophagous/saproxylophagous, xylomycetophagous, predators and commensals in relation to each sampling method. The following questions were addressed: i) Which sampling method captures the greatest abundance and richness of Coleoptera saproxylic species and families? and ii) Are there differences in the ecological diversity of guilds among sampling methods?

Methods

Study area

The study was conducted in Cabañeros National Park (Spain), a protected area of 40,856 ha. The annual temperature average fluctuates between 12.9 and 15.6 ºC and annual precipitation averages between 500 and 750 mm. The park constituted a well-preserved Mediterranean landscape, where heterogeneous forest patches appear inside a matrix of grassland and scrubland (Vaquero de la Cruz 1997).

Fieldwork was carried out in the most mature woodlands of the National Park (Micó et al. in prep.), selecting one mixed deciduous woodland of Pyrenean oak *Quercus pyrenaica* Willd. and the native oak *Quercus faginea* Lam., and one riparian woodland dominated by narrow-leafed ash *Fraxinus angustifolia* Vahl. The oak stand (N39 21.338 W4 23.715) presented a mean altitude of 760 m., and the riparian stand (N39 26.944 W4 33.788) a mean altitude of 550 m.

Sampling methods

We tested three sampling techniques used to collect saproxylic beetles: tube traps (TT), window traps (WT), and emergence traps (ET) (Figure 1):

- TT (Fig. 1a) are an active method traditionally used to evaluate and control woodland insect pests (Guerrero 1988; Pérez Moreno 1997). They have also been successfully used to detect rare saproxylic species that are difficult to obtain using other sampling methods in woodland environments (Alonso-Zarazaga et al. 2002). Some chemical compounds such as ethanol or acetates act as kairomones (Pérez Moreno 1997; Jonsell et al. 2003; Bouget et al. 2009), and are common bait for baited-trap designs (Alonso-Zarazaga et al. 2002; Bouget et al. 2009). We followed a similar model to that described by Alonso-Zarazaga et al. (2002), composed of an orange PVC tube with a length of 150 cm and a diameter of 20 cm that was attached to a collecting pot containing ethylene glycol as preservative. We perforated three equidistant rows of ten holes along the tube to facilitate bait dispersion. Inside the tube we hung two 25 ml glass bottles, one with 70% ethanol and the other with ethyl acetate as active bait. Consequently, several trapping principles were combined in this method: attractant, colour and silhouette. Two traps were set in the deciduous woodland and one in the riparian woodland.

- WT (Fig. 1b) are interception traps designed to capture flying active insects (Økland 1996). WT installed in front of a hollow opening are usually preferred among sampling methods to study saproxylic assemblages living in tree hollows (Økland 1996; Ranius and Jansson 2002) (Økland 1996; Ranius and Jansson 2002). The trap is made up of three convergent methacrylate plates mounted above a 20 cm brown plastic funnel that flows into a brown collecting pot containing ethylene glycol as preservative. Traps were hung just in front of the hollow openings, 1.5–2 m above the ground, a suitable height to obtain a better characterization of beetle fauna (Bouget et al. 2008a). We selected 21 trees: 14 in the deciduous woodland and 7 in the riparian woodland.
- ET (Fig. 1c) specially modified from Colas (1974) are traps for collecting species that inhabit tree hollow microhabitats (Gouix and Brustel 2011; Quinto et al. 2012), and allow recording of saproxylic species shortly after their emergence from immature stages. The use of modified ET covering and sealing the hollow opening is quite recent (Gouix and Brustel 2011; Micó et al. 2011b; Quinto et al. 2012), and their use provides accurate information about species assemblages inhabiting microhabitats (Bouget and Brustel 2009a). Tree hollows were covered with black acrylic mesh and sealed up with staples. Specimens emerged and came into a white collecting pot containing ethylene glycol as preservative. We selected 15 hollow trees in the deciduous woodland, and 27 in the riparian woodland. In the selection of tree hollows we considered the real

heterogeneity and abundance of tree hollows in each woodland type, always taking into account the high degree of protection of this National Park and the inherent need to protect and conserve this important and limited microhabitat (Quinto et al. 2012).

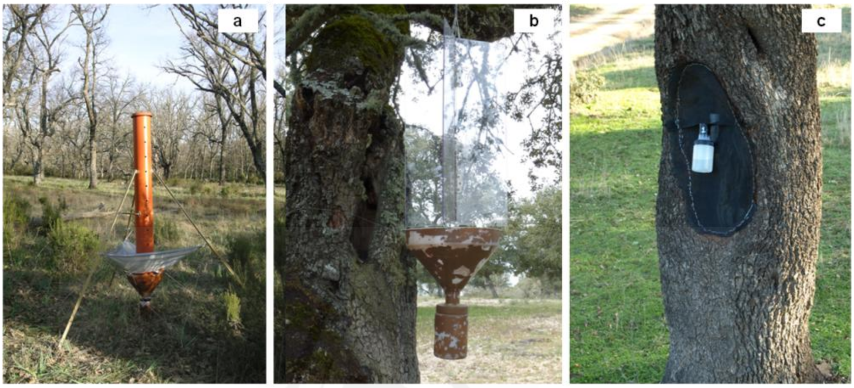


Figure 1. Tube trap (a), window trap (b) and emergence trap (c) designs. (Picture authorship: E. Micó, J. Quinto and J. Ordóñez, respectively).

The sampling period spanned eight months, which is the typical active period of Mediterranean insect communities (Ricarte et al. 2009). We took different years into consideration in order to avoid interference among sampling methods: TT and ET were active from April to November in 2006 and 2009, respectively, and WT were active from September-December 2004 to April-August 2005. In all cases, traps were revisited monthly at each selected stand.

Species identification and classification into trophic guilds

We were assisted by an external taxonomist for species identification of many families (see Acknowledgments). We included as many saproxylic families as were identified at species level, arriving to morphospecies with few exceptions. Classification into trophic guilds: xylophagous, saprophagous/saproxylophagous, xylomycetophagous, predators and commensals, was based on biological/ecological information available in the bibliography, the 'Frisbee' data base (Bouget et al. 2008b) and information from taxonomists (pers. com.).

Data analysis

In order to check that each selected stand could be considered as a true replicate, we assessed the similarities between woodland types and among sampling methods using ANOSIM tests for differences between groups (Faith et al. 1987). Moreover, we performed two-way ANOVA analyses to elucidate which factor (stand or type trap) influences total species richness, by means of Statistica 8.0 (StatSoft 2007).

The completeness of each sampling method was calculated as the percentage of observed species/families in relation to the number of predicted species/families, obtained with ACE and Chao1 estimators, using EstimateS 8.0 (Colwell 2005).

Species/family richness and diversity were compared for each sampling method and rarefaction curves with 95% confidence intervals were used for species/family richness, using the minimum abundance value at each site as a standard sampling size for comparison with

Species Diversity and Richness 3.02 software (Henderson and Seaby 2002). We calculated the number of effective species for species/family diversity, using the measure of true diversity order 1 (Jost 2006), which weights each species exactly according to its frequency in the community (i.e. favouring neither rare nor common species). Given the presence of rare species (singletons) in all communities, we calculated estimated diversity using the Chao and Shen estimator (Chao and Shen 2003), with the program SPADE (Chao and Shen 2010). The same procedure was followed for trophic guilds.

We compared total species/family richness and abundance registered for each sampling method with a Kruskal-Wallis with multiple comparisons test, carried out with Statistica 8.0 (StatSoft 2007). Moreover, we assessed the efficiency of each method to record any beetle family separately, conducting ANOVA with Tukey post hoc tests or Kruskal-Wallis with multiple comparisons tests (depending on the normality or not of the data). We also assessed the differences in relative species richness and abundance of trophic guilds among methods.

Similarities among sampling methods were calculated with the incidence-based Sorensen similarity index (Magurran 2004) at species and family levels. A similarity analysis ANOSIM (Faith et al. 1987) was performed to test the significance of these differences using Primer v.6 software (Clarke and Gorley 2006). Complementarity was studied using Venn diagrams with *VennDiagram* package for R-Project (Chen and Boutros 2011).

To discover differences among methods in saproxylic species, the species distribution distribution was analyzed using a multivariate detrended correspondence analysis (DCA) with Past software (Hammer et al. 2001). This software enables to draw convex hulls, which are the smallest convex set that contains the whole set of points of each trap type in the Euclidean space, easily visualizing which species/families tend to be better sampled by each hull/sampling method.

Results

Species/family/guild richness and abundance per method

Woodland types did not affect trap efficiency (trapping techniques did not differ in species richness between woodland types neither using two way ANOVA test, F = 0.429, df = 1, p = 0.51 nor using ANOSIM analyses, R = -0.041, p = 0.733), which mean that trap efficiency was assessed only according to sampling methods (two-way ANOVAS test, F = 4.41, df= 2, p = 0.018; ANOSIM analyses, R = 0.423, p < 0.001).

A total of 5,084 saproxylic beetles belonging to 206 species and 46 families were found (Online Resource). ET and WT were the most effective methods for collecting species richness (125 species each), capturing a similar number of families (35 and 34, respectively). TT recorded the highest number of individuals (2,151 individuals), but also collected the lowest species and family richness (71 species and 29 families). The WT captured the lowest species abundance (1,207 individuals). Differences in species richness and abundance among sampling methods can be seen in the Online Resource.

The richness estimators showed high sampling completeness for all three methods, with an accurate replication and sampling effort, higher than 70% for each of the three methods at species level (ACE, TT = 73.16%, WT = 90.76%, ET = 75.83%; Chao 1, TT = 75.47%, WT = 85.75%, ET = 75.02%), and higher than 90% at family level (Chao 2, TT = 96.03%, WT = 95.34%, ET = 94.44%; Chao 1, TT = 91.69%, WT = 92.82%, ET = 96.45%).

When sampling size was standardized for 1,244 individuals at species level, the WT saproxylic community significantly had the greatest species richness, followed by ET, whereas TT reported the lowest species richness, as seen in the rarefaction curves (Figure 2). Moreover, at the lowest abundance value at family level (34 families), WT and ET reported statically similar values of family richness, whereas TT again offered the lowest value. We found the same pattern when we compared true diversity at species and family level, ET presenting the highest number of effective species/families (Figure 2), followed closely by WT, whereas TT reported the lowest number of effective species/families, which means that ET is the best method to study the diversity of both species and families.

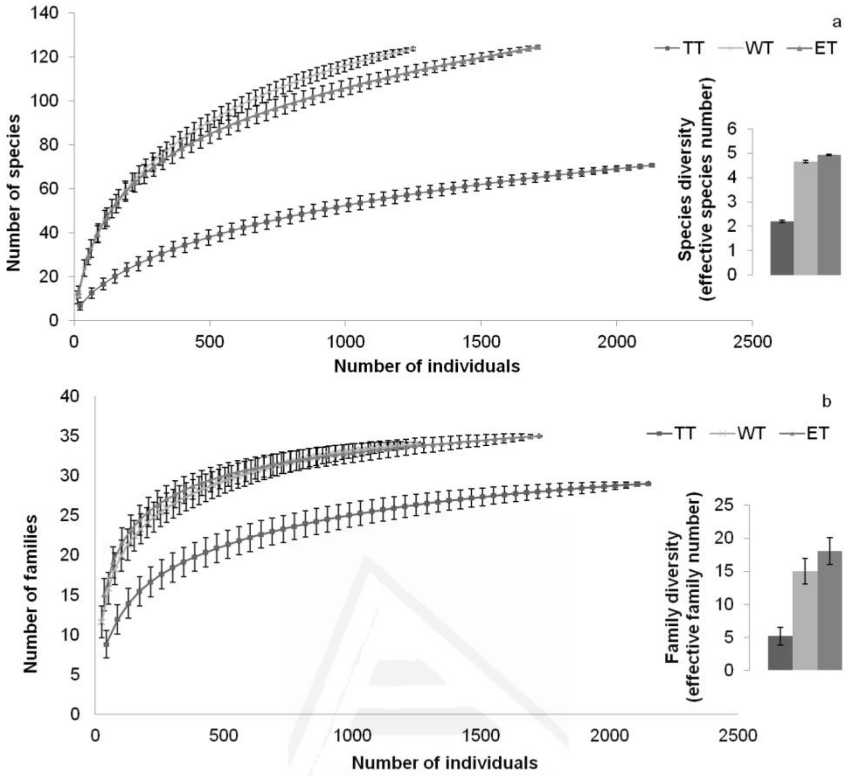


Figure 2. Rarefaction curves showing the differences among sampling methods in inventory the saproxylic species richness (a) and species families (b).

The Kruskal-Wallis test indicated significant differences in species richness only between TT and ET (H (2, N = 24) = 6.48, p = 0.034). Regarding species abundance, no differences were found among methods, nor did the total family richness and abundance present significant differences (H (2, N = 24) = 0.77, p = 0.681). The analysis of species abundance for each beetle family showed differences among sampling methods (Table 1), where ET was more effective in monitoring the family abundance of Aderidae, Cetoniidae, Helodidae, Ptiliidae , Scraptiidae and Scydmaenidae with both WT and TT being statistically different. TT and ET were statically different in recording Latridiidae, Lucanidae, Nitidulidae and Tenebrionidae families. Finally, TT and WT differently recorded Ptinidae and Curculionidae Scolytinae families. The variation of the total species richness and abundance of beetle families per sampling method is shown in Figure 3.

FAMILY	TT	WT	ET
Aderidae	0 (0)a	0 (0)a	8 (3.6)b
Anobiidae	0 (0)a	6 (3.8)a	5.3 (3.7)a
Biphyllidae	11.8 (8.2)a	0.3 (0.2)a	3.1 (2.1)a
Bostrichidae	3.8 (2.7)a	0.1 (0.1)a	0 (0)a
Bothrideridae	0 (0)a	0.1 (0.1)a	0 (0)a
Buprestidae	2.8 (1.5)a	0.8 (0.4)a	0 (0)a
Cerambycidae	1 (0.4)a	1.4 (0.6)a	3.9 (2.4)a
Cerylonidae	0 (0)a	0 (0)a	0.1 (0.1)a
Cetoniidae	0.1 (0.1)a	1.6 (0.7)a	17.9 (7.4)b
Ciidae	0.1 (0.1)a	0 (0)a	0 (0)a
Clambidae	0.1 (0.1)a	0 (0)a	0.1 (0.1)a
Cleridae	0.3 (0.3)a	2.3 (1.6)a	0.1 (0.1)a
Corylophidae	0.4 (0.2)a	0.3 (0.2)a	0 (0)a
Cryptophagidae	3.9 (2.8)a	7.1 (3.4)a	23.3 (9.3)a
Curculionidae Scolytinae	153 (66.7)a	10.1 (6.4)b	26.8 (11.9)ab
Dasytidae	1.8 (1.1)a	12.9 (10.3)a	0.3 (0.2)a
Dermestidae	9.1 (5.2)a	20 (10.9)a	9.4 (5.2)a
Dynastidae	0 (0)a	0 (0)a	0.9 (0.7)a
Elateridae	0.5 (0.4)a	6.4 (4)a	15.6 (7.8)a
Endomychidae	0.1 (0.1)a	0.3 (0.2)a	0.9 (0.4)a
Helodidae	0 (0)a	0 (0)a	20.9 (8.4)b
Histeridae	6.3 (3.1)a	2.4 (1.5)a	11 (4)a
Laemophloeidae	1.9 (1.3)a	0 (0)a	0.8 (0.4)a
Latridiidae	0 (0)a	0.4 (0.3)ab	2.6 (0.9)b
Lucanidae	0.3 (0.2)a	0.8 (0.4)ab	4.5 (1.8)b
Malachiidae	0 (0)a	1.1 (0.6)a	2.4 (1.6)a
Melandryidae	0 (0)a	0.4 (0.3)a	0.6 (0.5)a

Melyridae	19.6 (19.5)a	5.6 (3)a	0 (0)a
Mordellidae	3.5 (2.3)a	1.9 (0.9)a	0 (0)a
Mycetophagidae	42.4 (22.6)a	1.4 (0.9)a	1.8 (0.9)a
Nitidulidae	1.3 (0.6)a	5.9 (1.5)ab	13.8 (5.6)b
Oedemeridae	0.3 (0.2)a	0.1 (0.1)a	0.8 (0.4)a
Platypodidae	0 (0)a	0.3 (0.2)a	0 (0)a
Prionoceridae	0 (0)a	2.8 (2)a	0 (0)a
Pselaphidae	0 (0)a	0 (0)a	0.4 (0.3)a
Ptiliidae	0 (0)a	0 (0)a	1.4 (0.7)b
Ptinidae	2.3 (0.8)a	26.8 (8.3)b	9.9 (3.5)ab
Rhizophagidae	0 (0)a	0 (0)a	0.1 (0.1)a
Salpingidae	0 (0)a	0.3 (0.3)a	0 (0)a
Scraptiidae	0.4 (0.4)a	5 (2.9)a	7.5 (5.1)b
Scydmaenidae	0 (0)a	0 (0)a	1 (0.3)b
Silvanidae	0.3 (0.3)a	0.4 (0.2)a	1 (0.4)a
Tenebrionidae	0.9 (0.7)a	23.4 (16.4)ab	18.1 (9.7)b
Tetratomidae	0 (0)a	0.1 (0.1)a	0 (0)a
Trogossitidae	0.6 (0.4)a	0 (0)a	0.3 (0.3)a
Zopheridae	0.4 (0.3)a	2.6 (1.2)a	1.8 (0.7)a

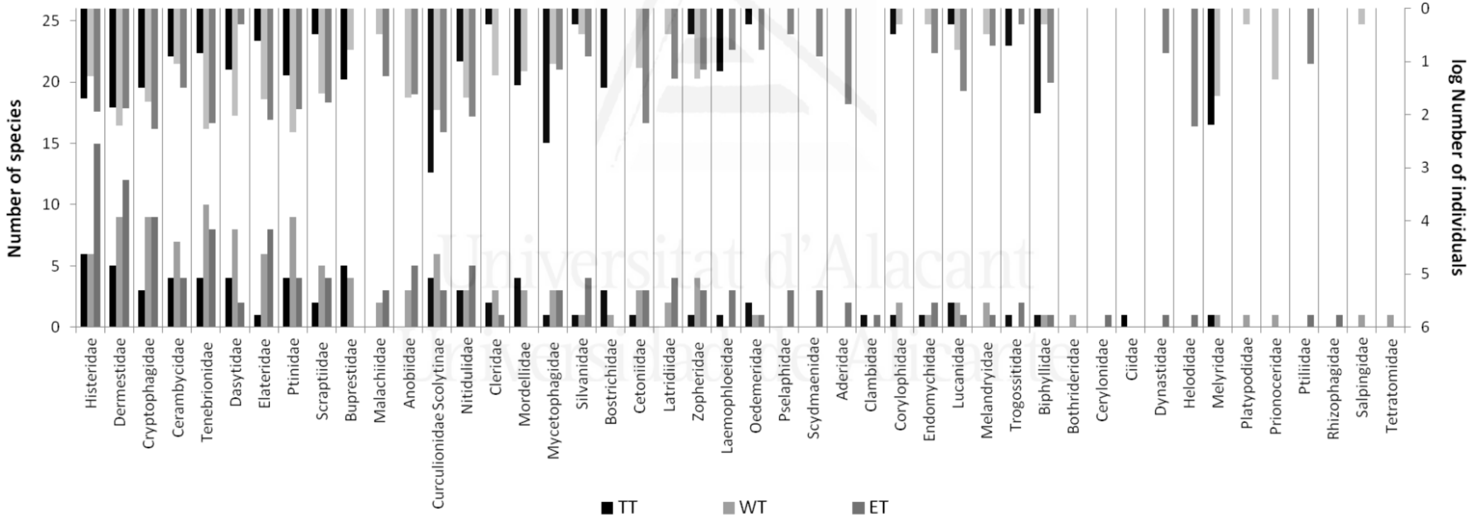
Table 1. Mean number (SE) of species abundance for each beetle family per trap type, and statistic differences among methods ($p < 0.05$).

Clear differences in the ability of sampling techniques to report ecological diversity of guilds were found (Table 2), Moreover, ET performed the best characterization of saproxylic assemblage functional diversity (4.92 ± 0.02; CI: 4.88, 4.97), closely followed by WT (4.65 ± 0.05; CI: 4.56, 4.75), whereas TT reported the lowest functional diversity (2.19 ± 0.05; CI: 2.09, 2.29) (see Table 2 for more detail in this respect).

Table 2. Mean number (SE) of species richness and abundance of saproxylic guilds per trap type, and statistic differences among methods ($p < 0.05$). x: xylophagous, sx: saprophagous/saproxylophagous, xm: xylomycetophagous, p: predators, c: commensals.

	Richness			Abundance		
	TT	WT	ET	TT	WT	ET
x	5.6 (2.4)a	16.8 (6)ab	21.5 (4.4)b	11.5 (5.3)a	24.6 (9.2)ab	46.4 (15.2)b
sx	3.5 (1.4)a	22.3 (7)b	19.9 (5.8)b	6.3 (3.6)a	49.5 (19.1)b	40 (12.4)b
xm	10 (3.1)a	9.6 (3.8)a	26.8 (7)b	211.8 (91.6)a	16.9 (8.2)b	49.1 (15.7)ab
p	5.1 (2.3)a	23.4 (12.3)a	18.3 (6.2)a	29 (23.4)a	33.3 (18.4)a	33.9 (13.9)a
c	2.5 (0.9)a	14.4 (4.2)b	15.4 (4.1)b	10.4 (5.4)a	26.6 (11.1)ab	46.5 (13.4)b

Figure 3. Differences in species richness and abundance per family and sampling method. The number of species is reflected in the first vertical axis (left), and the number of individual (expressed as logarithm) in the second vertical axis (right).



Similarity and complementarity

The ANOSIM showed strong differences among sampling methods in monitoring species/family composition (R = 0.383, p < 0.001 and R = 0.389, p < 0.001, respectively). At species level, TT and ET presented the lowest similarity (34.87%), whereas ET-WT and TT-WT pairs were more similar (48.8% and 43.08%, respectively). At family level, WT-ET and TT-ET were the most dissimilar pairs (69.57% and 71.88%, respectively), and TT-WT pairs were the most alike (79.37%). The Venn diagram showed the main dissimilarities in species/family composition among sampling methods (Figure 4), ET were the method that reported the highest number of unique species/families (57 species/8 families), followed by WT (46 species/5 families). The number of unique species captured with TT was also high (21 species), whereas one unique family was recorded. This representation also revealed that the most complementary method for monitoring species/family richness was the WT-ET pair (90.43% and 97.83%, respectively), followed by TT-ET (78.47% and 89.13%, respectively) and TT-WT pairs (73.21% and 84.44%, respectively). Almost 12% of the species and 44% of the families (25 species and 20 families) were shared by the three sampling methods. Regarding European Red List saproxylic beetles (Nieto and Alexander 2010), the Endangered *Limoniscus violaceus* was effectively recorded using ET and the Vulnerable *Ischnodes sanguinicollis* (Elateridae) with ET and WT.

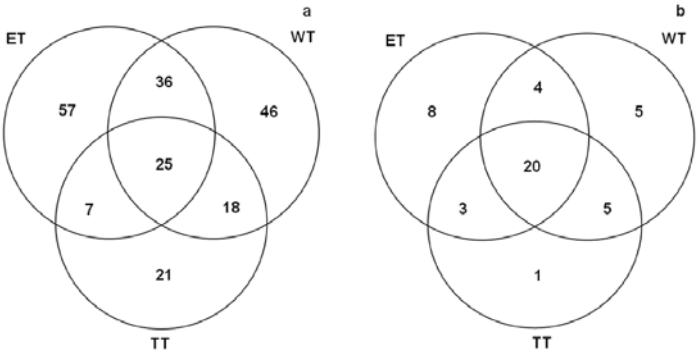
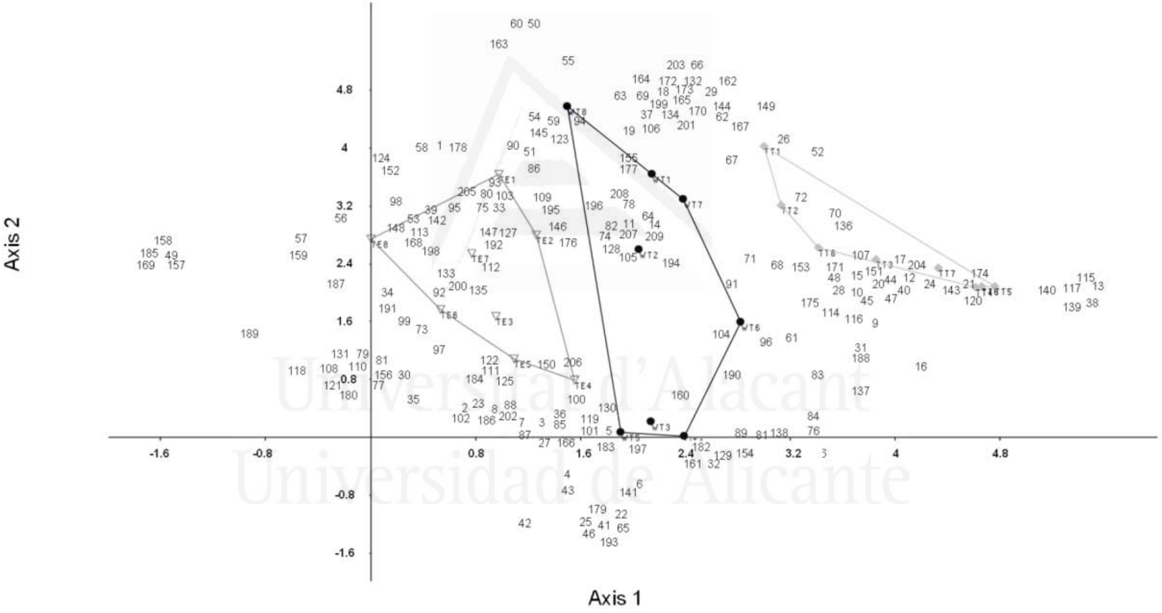


Figure 4. Venn diagrams showing the main differences in species (a) and family (b) richness among sampling methods.

Species distribution among methods

DCAs showed differences among sampling methods in monitoring the distribution of saproxylic assemblages of Coleoptera at species level (Figure 5), and the cumulative percentage of the variance explained 23.61% of the distribution.

Figure 5. Detrended correspondence analyses according to species distribution. The species names for the labels of the species distribution are included in the Online Resource.



The DCA spaced the convex hulls (one per method) out in the ordination, clearly embracing different sections of the species distribution (species falling into them). The ET hull embraced higher numbers of species; mainly species only recorded using this method, and included species with high numbers of individuals such as *Soronia oblonga*, *Epuraea fuscicollis* (Nitidulidae), *Pseudocistela ceramboides*, *Probaticus anthracinus* (Tenebrionidae), *Ptinus timidus* (Ptinidae), *Megapenthes lugens* (Elateridae), and *Troglops furcatus* (Malachiidae). WT were effective in monitoring species presenting high numbers of individuals such as *Attagenus trifasciatus* (Dermestidae), *Isomira hispanica, Mycetochara quadrimaculata* (Tenebrionidae), *Dignomus dilophus* (Ptinidae), and *Lobonyx aeneus* (Prionoceridae). Finally, only TT were widely effective for monitoring *Xyleborinus saxesenii* (Curculionidae Scolytinae) and *Falsomelyris granulata* (Melyridae).

Moreover, species surrounding one or two hulls may also be associated with one or two methods. Accordingly, *Prionocyphon serricornis* (Helodidae), *Aderus populneus* (Aderidae), *Anaspis regimbarti*, *Scraptia testacea* (Scraptiidae), *Cetonia aurateiformis* (Cetoniidae), *Cryptophagus punctipennis*, *C. reflexus*, *C. saginatus* (Cryptophagidae), *Dorcus parallelepipedus* (Lucanidae), *Enicmus brevicornis*, *Latridius assimilis* (Latridiidae) and *Ischnomera xanthoderes* (Oedemeridae) were mainly associated with ET, whereas *Cryptophagus pallidus* (Cryptophagidae), *Dasytes pauperculus*, *Mauroania bourgeoisi* (Dasytidae), *Dignomus irroratus* (Ptinidae), *Scraptia ophthalmica* (Scraptiidae) were associated with WT, and *Litargus connexus* (Mycetophagidae), *Placonotus testaceus* (Laemophloeidae) and *Scobicia chevrieri* (Bostrichidae) with TT. Considering species linked to two hulls, *Ampedus aurilegulus*, the Vulnerable *Ischnodes sanguinicollis* (Elateridae), *Cryptophagus aurelii*, *C. micaceus*, *C. scanicus* (Cryptophagidae), *Mycetochara linearis* (Tenebrionidae), *Mycetophagus quadriguttaus* (Mycetophagidae), and *Xyleborus monographus* (Curculionidae Scolytinae) were similarly recorded with both ET and WT. These results enhanced the specificity of each trap type in monitoring different sections of the saproxylic community at species level.

Discussion

Effectiveness of traps for monitoring species richness and diversity

The information that samples provide about rarity, population density, activity of insects or differences in the quality of habitats used to be a common source of error inherent to the design and purpose of each sampling method (Martikainen and Kaila 2004), affecting their results and interpretation (Longino et al. 2002; Hyvärinen et al. 2006). The use of different trap types in different years also can lead to a misinterpretation of results due to the known year variation of the saproxylic species between years (Martikainen and Kalia 2004). Therefore, it is necessary take into account that the results from this study may be partially biased. However, the selected stands and sampling period was the same, so we expect less effect of inter-year variation at family level, whereas at species level is more expectable that species abundance was more variable than species richness between years. All the three sampling methods showed high completeness effort (estimators over 70 and 90 % at species and family levels, respectively). Instead, clear differences in the performance of the three trap types at species, family and guild levels were found.

Sampling methods for monitoring microhabitats tend to capture a greater proportion of specialist species. Examples of these are direct sampling (Ranius and Jansson 2002; Alinvi et al. 2007), trunk-window traps (Hyvärinen et al. 2006; Sverdrup-Thygeson and Birkemoe 2009), pitfall traps inside tree hollows (Ranius and Jansson 2002; Hyvärinen et al. 2006; Brin et al. 2012), or ET covering parts of logs (Alinvi et al. 2007), deadwood pieces (Brin et al. 2011), stumps (Brin et al. 2012) or tree hollows (Gouix and Brustel 2011). ET effectively monitored species richness and diversity at species and family levels, and reported a high proportion of species/families strongly linked to tree hollow microhabitats as well as presenting different life cycles, trophic habits, behaviour or phenology, such as many Aderidae, Cryptophagidae, Cetoniidae, Elateridae, Helodidae, Histeridae, Latridiidae, Ptiliidae, Scraptiidae or Tenebrionidae species. These results highlighted ET efficiency in characterizing the saproxylic beetle fauna developing, coexisting or interacting inside tree hollows.

In contrast, WT clearly respond to habitat surroundings (Bouget et al. 2009; Sverdrup-Thygeson and Birkemoe 2009; Sverdrup-Thygeson et al. 2010), and the presence of tourist species is also possible (Bouget and Brustel 2009b). This trap predominantly catch flying adults (Saint-Germain et al. 2006; Alinvi et al. 2007) arriving from a wide range of woody resources within the woodland environment, such as dead wood on the ground, decaying aerial branches, bark or tree hollows (Ranius and Jansson 2002; Hyvärinen et al. 2006; Saint-Germain et al. 2006; Alinvi et al. 2007; Sverdrup-Thygeson and Birkemoe 2009). Accordingly, WT were the most effective method for reporting species richness and diversity with least sampling effort, and many Cryptophagidae, Dasytidae, Elateridae, Malachiidae, Prionoceridae, Ptinidae, Scraptiidae, Tenebrionidae and Zopheridae species were correctly monitored, matching up with species usually reported using this method (Ranius and Jansson 2002, Hyvärinen et al. 2006; Brin 2008; Viñolas et al. 2012), and heterogeneously linked to many woody resources. In many cases species were closely bound to tree hollow microhabitats (Bouget et al. 2008b; Viñolas et al. 2012). Therefore, not only a general outline of the flying active species of the woodland was obtained using this method, but also of the dispersive species emerging from tree hollows.

Finally, the combined effect of bait and visual cues such as colour or silhouette of the TT strongly attract a wide variety of dead wood and hardwood associated beetles (Jonsell et al. 2003; Bouget et al. 2008a; Bouget et al. 2009), consequently severely affecting the capture frequency of a biased proportion of the community (Allemand and Aberlenc 1996; Bouget et al. 2008a). The TT was the least effective method at both species and family levels and mainly recorded a few species that were highly abundant, which suggested that they are all attracted to similar chemical/visual cues. Many Curculionidae Scolytinae and Cerambycidae species, and their associated fauna are attracted to volatiles such as isoprenoid monoterpenes (kairomones) and the alcohol or acetate derivates emitted by stressed, dead or dying host trees (Shibata et al. 1996; Erbilgin and Raffa 2001; Jonsell et al. 2003; Allison et al. 2004; Schlyter 2007; Miller and Rabaglia 2009), and are similarly attracted to bait imitating these chemical compounds (Berti and Flechtmann 1986; Allemand and Aberlenc 1996; Pérez Moreno 1997;

Bouget et al. 2009). Moreover, many predator species prey on adults of several species of bark beetles, and their larvae feed on bark beetle progeny (Erbilgin and Raffa 2001), which explains to a great extent the strong attraction of Melyridae, Histeridae and Trogossitidae species to the chemical compounds that were used.

The effective number of species allows for a more intuitive interpretation, and offers easily comparable values of species diversity (Moreno et al. 2011). The functional diversity of trophic guilds in terms of effective numbers was most efficiently reported using ET, closely followed by WT, which also recorded the highest species richness and abundance of all the saproxylic trophic guilds (except predators). ET cutting off tree hollows are a specific method directed at recording the saproxylic fauna that inhabit tree hollows (Gouix and Brustel 2011), by capturing an accurate number of species and individuals that coexist in this microhabitat, whereas WT installed in front of tree hollows also provides wide saproxylic diversity (Økland 1996), performing a good characterization of mobile saproxylics linked both to hollows or surrounding microhabitats. These results highlight that the combination of ET and WT provide a more complete outline of the functional heterogeneity of saproxylic assemblages in Mediterranean woodland, by recording species with different biology and linked to different microhabitat types.

Complementarity among methods

Combined method techniques are usually required to obtain reliable and complementary information on saproxylic communities (Martikainen and Kouki 2003; Ozanne 2005; Alinvi et al. 2007). The saproxylic species/families richness and diversity recorded for the three sampling methods showed a different structure of the local saproxylic assemblage. ET and WT recorded similar numbers of species/family richness but also presented a high number of unique species/families, and therefore they were the most dissimilar and complementary methods. The main determinant was the ability of both methods to capture a high proportion of species of the community (Økland 1996; Ranius and Jansson 2002; Martikainen and Kalia 2004; Hyvärinen et al. 2006; Alinvi et al. 2007; Jansson 2009; Sverdrup-Thygeson et al. 2010 for WT, and Gouix 2011 for ET), because each method was originally designed to study different woodland environments: WT for woodland patches (Økland 1996; Ranius and Jansson 2002; Martikainen and Kalia 2004; Hyvärinen et al. 2006), and ET for tree hollow microhabitats (Bouget and Brustel 2009a; Gouix and Brustel 2011; Gouix 2011). These results suggest that depending on the target species/families, the WT installed in front of hollow openings and the ET covering tree hollows are highly complementary methods for studying this beetle assemblage, and provide more accurate studies on population dynamics, dispersive behaviour, habitat and microhabitat preferences, etc.

In contrast, TT determined lower complementarity with both ET and WT, revealing a generally low performance of this method for studying species and family richness. The multiple attractive principles that occur in this TT design model these notable differences, due to the fact that they tend to capture species particularly attracted to bait, colour and/or silhouette effects (Pérez Moreno 1997; Erbilgin and Raffa 2001; Jonsell et al. 2003; Allison et al. 2004; Schlyter 2007; Bouget et al. 2009; Miller and Rabaglia 2009). Therefore, they can only report and/or provide higher frequency of captures of species/families susceptible to trapping principles. Nevertheless, our results showed that a relatively high number of species were only captured using TT (21 species), indicating the affinity of TT for collecting those beetle fauna.

Selection of sampling methods

WT are widely considered to be the most efficient method for standardized studies concerning saproxylic beetle assemblages because they provide the most individuals and/or species richness (Økland 1996; Ranius and Jansson 2002; Martikainen and Kalia 2004; Hyvärinen et al. 2006; Alinvi et al. 2007; Jansson 2009; Sverdrup-Thygeson et al. 2010), and give an outline of the local species pool (Ranius and Jansson 2002) without requiring a long sampling period (Bouget et al. 2008a). However, tree hollows house a wide range of microhabitats (Alexander 2008; Sirami et al. 2008; Winter and Möller 2008; Marcos-García et al. 2010) that support a high proportion of hollow-specialist species (Dajoz 1980) with low dispersive behaviour (Thomas 2000; Ranius and Hedin 2001; Ewers and Didham 2006) that WT could not report. ET make it possible to conduct standardized and replicable studies to monitor or detect target saproxylic species occurring in tree hollows (Gouix and Brustel 2011; Micó et al. 2011b) and also to survey entire saproxylic communities and their ecological interactions (Gouix 2011; Quinto et al. 2012). Our approach represents the first occasion that the efficiency of this ET model has been tested in comparison with other sampling methods, and is more effective in reporting species/family richness and diversity than conventional WT models and offers deeper knowledge of beetle assemblages related to tree hollows.

The selection or combination of methods for monitoring saproxylic beetle assemblages for conservation purposes should be thorough, without negatively affecting their habitat and populations (Bußler and Müller 2009), and should comprise an optimized number of traps/methods adapted to the target species/family and reflect the heterogeneity of the studied woodland environment. This choice may determine the recording of a particular species. As an example, the Endangered *Limoniscus violaceus* (Elateridae) has only been captured with ET in the studied area, in agreement with Gouix and Brustel (2011) who showed that ET was the most efficient method to capture this species, whereas other trapping techniques were inefficient.

In addition, species abundance is more powerful than species lists for understanding community dynamics and distribution patterns in ecological studies (Larsen and Forsyth 2005) and, for instance, the addition of shared and unique species from ET and WT held a special complementarity to report higher richness and abundance of many species-rich families such as Cryptophagidae, Elateridae, Ptinidae, Scraptiidae and Tenebrionidae. Due to these arguments, we recommend a combination of the easily standardized and replicable ET and WT to suitably characterize and compare the saproxylic fauna developing in tree hollows and their subset of flying active species. These non-intrusive methods also avoid interference with the habitat, and allow urgent decisions to be taken when any protected species appear in order to safeguard their populations, such as the removal of traps when the required presence for any protected species has been achieved at a location (Gouix and Brustel 2011), preserving habitat and populations in this way.

Our results showed how trap efficiency varies according to the target beetle species and families, therefore the selection and/or combination of methods should consider this sensitivity, adapting the sampling technique/s to the section of the saproxylic beetle assemblage under study. These findings will be fundamental to carry out rigorous ecological studies and to establish conservation strategies in Mediterranean woodlands and in other woodland types taking into account this important saproxylic functional group.

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Online Resource. Appendix. Relative species/family richness and abundance of saproxylic beetles. TT: tube trap; WT: window trap; ET: emergence trap. The trophic guild for each species is reflected in the eighth column, being x: xylophagous, sx: saprophagous-saproxylophagous, xm: xylomycetophagous, p: predators, c: commensals. The DCA labels are presented in the last column.

Family	Species	TT	WT	ET	Total	Guild	dca
Aderidae	*Aderus populneus*	0	0	18	18	x	*1*
	Otoletus neglectus	0	0	46	46	x	*2*
Anobiidae	*Dorcatoma ajenjoi*	0	0	4	4	xm	*3*
	Oligomerus brunneus	0	20	19	39	x	*4*
	Rhamna semen	0	2	10	12	xm	*5*
	Stagetus andalusiacus	0	26	0	26	x	*6*
	Stagetus elongatus	0	0	7	7	x	*7*
	Stagetus micoae	0	0	2	2	x	*8*
Biphyllidae	*Diplocoelus fagi*	94	2	25	121	xm	*9*
Bostrichidae	*Bostrichus capucinus*	3	0	0	3	x	*10*
	Lichenophanes numida	0	1	0	1	x	*11*
	Scobicia chevrieri	27	0	0	27	x	*12*
	Xylopertha praeusta	1	0	0	1	x	*13*
Bothrideridae	*Bothrideres interstitialis*	0	1	0	1	p	*14*
Buprestidae	*Acmaeodera degener*	9	2	0	11	x	*15*
	Acmaeoderella adspersula	5	1	0	6	x	*16*

	Agrilus hastulifer	1	0	0	1	x	*17*
	Anthaxia chaerodrys	0	1	0	1	x	*18*
	Anthaxia salicis	0	2	0	2	x	*19*
	Anthaxia scutellaris	1	0	0	1	x	*20*
	Chrysobothris affinis	6	0	0	6	x	*21*
Cerambycidae	*Alocerus moesiacus*	0	3	0	3	x	*22*
	Cerambyx welensii	0	1	3	4	x	*23*
	Chlorophorus pilosus	2	0	0	2	xm	*24*
	Chlorophorus ruficornis	0	1	0	1	x	*25*
	Phymatodes testaceus	3	3	0	6	x	*26*
	Prinobius myardi	0	0	11	11	x	*27*
	Stenopterus ater	1	0	0	1	xm	*28*
	Stenurella nigra	0	1	0	1	x	*29*
	Stictoleptura trisignata	0	1	16	17	x	*30*
	Trichoferus fasciculatus	2	0	1	3	x	*31*
	Trichoferus pallidus	0	1	0	1	x	*32*
Cerylonidae	*Cerylon histeroides*	0	0	1	1	xm	*33*
Cetoniidae	*Cetonia aurataeformis*	1	8	124	133	sx	*34*
	Potosia cuprea	0	0	13	13	sx	*35*
	Potosia opaca	0	3	6	9	sx	*36*
	Valgus hemipterus	0	2	0	2	sx	*37*
Ciidae	*Cis striatulus*	1	0	0	1	xm	*38*

Clambidae	*Calyptomerus* sp	0	0	1	1	xm	*39*
	Cybocephalus rufifrons	1	0	0	1	xm	*40*
Cleridae	*Korynetes geniculatus*	0	1	0	1	p	*41*
	Opilo abeillei	0	4	0	4	p	*42*
	Opilo domesticus	0	13	1	14	p	*43*
	Pseudoclerops mutillarius	1	0	0	1	p	*44*
	Thanasimus formicarius	1	0	0	1	p	*45*
Corylophidae	*Arthrolips indescreta*	0	1	0	1	xm	*46*
	Arthrolips obscura	3	1	0	4	xm	*47*
Cryptophagidae	*Atomaria fuscata*	3	0	0	3	xm	*48*
	Atomaria pusilla	0	0	1	1	xm	*49*
	Cryptophagus angustus	0	1	0	1	x	*50*
	Cryptophagus aurelioi	0	2	7	9	sx	*51*
	Cryptophagus dentatus	26	9	16	51	sx	*52*
	Cryptophagus distinguendus	0	0	1	1	sx	*53*
	Cryptophagus micaceus	0	9	31	40	p	*54*
	Cryptophagus pallidus	0	18	0	18	sx	*55*
	Cryptophagus punctipennis	0	0	17	17	x	*56*
	Cryptophagus reflexus	0	0	66	66	xm	*57*
	Cryptophagus saginatus	0	2	12	14	xm	*58*
	Cryptophagus scanicus	2	14	35	51	xm	*59*
	Cryptophagus spadiceus	0	1	0	1	c	*60*

	Micrambe micoae	0	1	0	1	sx	*61*
Curculionidae Scolytinae	*Dryocoetes villosus*	3	1	0	4	x	*171*
	Hylesinus crenatus	0	1	0	1	x	*172*
	Hylesinus fraxini	0	4	0	4	x	*173*
	Xyleborinus saxesenii	1198	12	25	1235	xm	*174*
	Xyleborus dryographus	12	4	8	24	xm	*175*
	Xyleborus monographus	11	59	181	251	xm	*176*
Dasytidae	*Aplocnemus brevis*	2	7	0	9	p	*62*
	Aplocnemus limbipennis	0	6	1	7	p	*63*
	Danacea lata	0	3	0	3	p	*64*
	Danacea pici	0	2	0	2	p	*65*
	Dasytes pauperculus	0	45	0	45	p	*66*
	Dasytes terminalis	1	2	0	3	p	*67*
	Enicopus rugosicollis	1	0	0	1	p	*68*
	Mauroania bourgeoisi	0	36	1	37	p	*69*
	Psilothrix illustris	10	2	0	12	p	*70*
Dermestidae	*Anthrenus angustefasciatus*	2	6	2	10	c	*71*
	Anthrenus festivus	57	44	6	107	c	*72*
	Anthrenus minutus	0	2	39	41	c	*73*
	Anthrenus scrophulariae	0	1	0	1	c	*74*
	Anthrenus verbasci	0	0	3	3	c	*75*
	Attagenus incognitus	8	17	1	26	c	*76*

	Attagenus schaefferi	0	0	1	1	c	*77*
	Attagenus trifasciatus	0	83	14	97	c	*78*
	Dermestes bicolor	0	0	1	1	c	*79*
	Dermestes erichsonii	0	0	1	1	c	*80*
	Dermestes undulatus	0	0	5	5	c	*81*
	Globicornis nigripes	0	2	0	2	c	*82*
	Orphilus niger	5	3	2	10	c	*83*
	Trogoderma versicolor	1	2	0	3	c	*84*
Dynastidae	*Oryctes nasicornis*	0	0	7	7	sx	*85*
Elateridae	*Ampedus aurilegulus*	0	19	43	62	p	*86*
	Ectamenogonus montandoni	0	0	7	7	p	*87*
	Elater ferrugineus	0	0	22	22	p	*88*
	Elathous platiai	0	3	0	3	p	*89*
	Ischnodes sanguinicollis	0	8	15	23	p	*90*
	Lacon punctatus	4	4	9	17	p	*91*
	Limoniscus violaceus	0	0	2	2	sx	*92*
	Megapenthes lugens	0	3	17	20	p	*93*
	Procraerus tibialis	0	14	10	24	p	*94*
Endomychidae	*Mycetaea hirta*	0	0	4	4	xm	*95*
	Symbiotes gibberosus	1	2	3	6	xm	*96*
Helodidae	*Prionocyphon serricornis*	0	0	167	167	c	*97*
Histeridae	*Abraeus perpusillus*	0	0	17	17	p	*98*

	Aeletes atomarius	0	0	6	6	p	*99*
	Atholus corvinus	1	0	11	12	p	*100*
	Atholus duodecimstriatus	0	0	1	1	p	*101*
	Eubrachium hispidulum	0	0	2	2	p	*102*
	Euspilotus perrisi	0	0	1	1	p	*103*
	Gnathoncus communis	7	0	21	28	p	*104*
	Gnathoncus nannetensis	0	9	6	15	p	*105*
	Gnathoncus rotundatus	0	2	0	2	p	*106*
	Kissister minimus	36	3	3	42	p	*107*
	Margarinotus brunneus	0	0	1	1	p	*108*
	Margarinotus merdarius	0	3	7	10	p	*109*
	Margarinotus uncostriatus	0	0	2	2	p	*110*
	Merohister ariasi	0	1	2	3	p	*111*
	Paromalus flavicornis	0	1	5	6	p	*112*
	Platylomalus complanatus	0	0	1	1	p	*113*
	Platylomalus gardineri	1	0	1	2	p	*114*
	Platysoma elongatum	1	0	0	1	p	*115*
	Platysoma filiforme	2	0	1	3	p	*116*
	Teretrius parasita	2	0	0	2	p	*117*
Laemophloeidae	*Cryptolestes ferrugineus*	0	0	4	4	xm	*118*
	Laemophloeus nigricollis	0	0	1	1	xm	*119*
	Placonotus testaceus	15	0	1	16	xm	*120*

Latridiidae	*Corticaria obscura*	0	0	1	1	c	*121*
	Enicmus brevicornis	0	0	3	3	xm	*122*
	Enicmus rugosus	0	2	2	4	xm	*123*
	Latridius assimilis	0	1	15	16	xm	*124*
Lucanidae	*Dorcus parallelepipedus*	1	4	36	41	x	*125*
	Pseudolucanus barbarossa	1	2	0	3	x	*126*
Malachiidae	*Anthocomus fenestratus*	0	3	6	9	p	*127*
	Attalus anticus	0	1	0	1	p	*128*
	Axinotarsus marginalis	0	1	0	1	p	*129*
	Cyrtosus cyanipennis	0	3	0	3	p	*130*
	Hypebaeus albifrons	0	0	1	1	p	*131*
	Malachius bipustulatus	0	1	0	1	p	*132*
	Troglops furcatus	0	0	12	12	p	*133*
Melandryidae	*Conopalpus brevicollis*	0	1	0	1	xm	*134*
	Orchesia micans	0	2	5	7	xm	*135*
Melyridae	*Falsomelyris granulata*	157	45	0	202	p	*136*
Mordellidae	*Mediimorda batteni*	9	6	0	15	x	*137*
	Mordella brachyura	3	7	0	10	x	*138*
	Mordellistena confinis	2	0	0	2	x	*139*
	Variimorda fagniezi	14	0	0	14	x	*140*
	Variimorda theryi	0	2	0	2	x	*141*
Mycetophagidae	*Litargus balteatus*	0	0	1	1	xm	*142*

	Litargus connexus	339	3	4	346	xm	*143*
	Mycetophagus fulvicollis	0	1	0	1	xm	*144*
	Mycetophagus quadriguttatus	0	7	9	16	xm	*145*
Nitidulidae	*Amphotis marginata*	0	2	1	3	c	*146*
	Epuraea fuscicollis	3	0	27	30	c	*147*
	Epuraea ocularis	0	0	2	2	c	*148*
	Meligethes reitteri	1	4	0	5	c	*149*
	Soronia oblonga	6	41	79	126	c	*150*
Oedemeridae	*Chrysanthia reitteri*	1	0	0	1	x	*151*
	Ischnomera xanthoderes	0	1	6	7	x	*152*
	Oedemera barbara	1	0	0	1	x	*153*
Platypodidae	*Platypus cylindrus*	0	2	0	2	p	*154*
Prionoceridae	*Lobonyx aeneus*	0	22	0	22	x	*155*
Pselaphidae	*Euplectus* sp	0	0	1	1	c	*156*
	Geopsephalus sp	0	0	1	1	c	*157*
	sp1 (Goniaceritae tribe)	0	0	1	1	p	*158*
Ptiliidae	sp2	0	0	11	11	xm	*159*
Ptinidae	*Dignomus dilophus*	2	22	0	24	x	*160*
	Dignomus irroratus	10	154	4	168	sx	*161*
	Dignomus lusitanus	0	1	0	1	x	*162*
	Ptinus bidens	0	9	2	11	sx	*163*
	Ptinus hirticornis	1	8	1	10	sx	*164*

	Ptinus palliatus	0	1	0	1	x	*165*
	Ptinus pyrenaeus	0	2	0	2	c	*166*
	Ptinus spitzyi	5	9	0	14	sx	*167*
	Ptinus timidus	0	8	72	80	x	*168*
Rhizophagidae	*Rhizophagus unicolor*	0	0	1	1	p	*169*
Salpingidae	*Salpingus aeneus*	0	2	0	2	p	*170*
Scraptiidae	*Anaspis incognita*	0	4	0	4	x	*177*
	Anaspis regimbarti	0	0	3	3	x	*178*
	Anaspis trifasciata	0	1	0	1	x	*179*
	Pentaria defarguesi	0	0	1	1	x	*180*
	Scraptia dubia	2	9	0	11	x	*181*
	Scraptia ophthalmica	0	24	0	24	x	*182*
	Scraptia schotti	0	0	2	2	x	*183*
	Scraptia testacea	1	2	54	57	x	*184*
Scydmaenidae	*Paleostigus palpalis*	0	0	1	1	c	*185*
	Scydmaenus cornutus	0	0	2	2	c	*186*
	Stenichus godarti	0	0	5	5	c	*187*
Silvanidae	*Ahasverus advena*	2	0	1	3	xm	*188*
	Airaphilus sp	0	0	1	1	xm	*189*
	Airaphilus elongatus	0	3	0	3	xm	*190*
	Silvanus bidentatus	0	0	2	2	xm	*191*
	Uleiota planata	0	0	4	4	xm	*192*

Tenebrionidae	*Corticeus fasciatus*	0	1	0	1	c	*193*
	Isomira hispanica	3	59	1	63	sx	*194*
	Mycetochara linearis	0	22	20	42	sx	*195*
	Mycetochara quadrimaculata	2	78	51	131	sx	*196*
	Prionychus fairmairei	1	10	13	24	sx	*197*
	Probaticus anthracinus	0	3	20	23	sx	*198*
	Probaticus granulatus	0	1	0	1	sx	*199*
	Pseudocistela ceramboides	0	2	30	32	sx	*200*
	Stenohelops sublinearis	1	9	1	11	sx	*201*
	Tenebrio sp	0	2	9	11	c	*202*
Tetratomidae	*Tetratoma baudueri*	0	1	0	1	xm	*203*
Trogossitidae	*Temnochila caerulea*	5	0	1	6	p	*204*
	Tenebroides marrocanus	0	0	1	1	p	*205*
Zopheridae	*Colobicus hirtus*	0	4	2	6	p	*206*
	Colydium elongatum	0	5	2	7	p	*207*
	Endophloeus marcovichianus	3	11	10	24	xm	*208*
	Synchita variegata	0	1	0	1	xm	*209*
	TOTAL ABUNDANCE	2151	1207	1726	5084		

CAPÍTULO 3

Breaking down complex saproxylic communities: Understanding sub-networks structure and implications to network robustness

Explorando las comunidades saproxílicas: Un acercamiento a la estructura de las subredes y sus implicaciones en la estabilidad

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Abstract

Saproxylic insect communities inhabiting tree hollow microhabitats correspond with large food webs which simultaneously are constituted by multiple types of plant-animal and animal-animal interactions, according to the use of trophic resources (wood- and insect-dependent sub-networks), or to trophic habits or interaction types (xylophagous, saprophagous, xylomycetophagous, predators and commensals). We quantitatively assessed which properties of specialised networks were present in a complex networks involving different interacting types such as saproxylic community, and how they can be organised in trophic food webs. The architecture, interacting patterns and food web composition were evaluated along sub-networks, analysing their implications to network robustness from random and directed extinction simulations. A structure of large and cohesive modules with weakly connected nodes was observed throughout saproxylic sub-networks, composing the main food webs constituting this community. Insect-dependent sub-networks were more modular than wood-dependent sub-networks. Wood-dependent sub-networks presented higher species degree, connectance, links, linkage density, interaction strength, and were less specialised and more aggregated than insect-dependent sub-networks. These attributes defined high network robustness in wood-dependent sub-networks. Finally, our results emphasise the relevance of modularity, differences among interacting types and interrelations among them in modelling the structure of saproxylic communities and in determining their stability.

Keywords

Coleoptera, Syrphidae (Diptera), types of interaction, tree hollow microhabitats, modularity, interacting patterns, ecological patterns, extinction simulations

Introduction

Network analysis is a valuable tool for studying the diversity of species and interactions in large trophic networks [1]. A high number of ecological communities have been studied under this perspective, discovering specialised interacting patterns as nestedness in mutualistic networks [2,3] or modularity in antagonistic networks [4], providing insight into the function and evolution of the components of the system [5]. Specialized interacting patterns act like a variable modelling the network structure of interactions, reducing the effective interspecific competition and enhancing the number of coexisting species [6]. The biotic environment of co-occurring species critically determines the way in which species adapt to new environments [7], as antagonistic and facilitative interactions between species determining the response to environmental perturbations [8].

Research on ecological communities has been dominated by small-scale studies [9], and restricted to a single type of interaction [4], while only recently, spatio-temporal scales of ecological communities [10-12] or complex networks with different types of interaction [13,14] have been addressed with network analysis. Ecological network studies are largely focussed on qualitative data, assuming that all interacting species are equally important [15]. However, specialised network patterns are best defined at quantitative scale in both mutualistic and antagonistic communities [16], and the relative abundances of the components of the networks influences structural patterns as asymmetry [17].

One of the most complex communities in terrestrial environments develops inside tree hollows, which provide a diverse range of microhabitats within forest ecosystems [18-21]. In each tree hollow, saproxylic insect assemblages with a high number of species with several types of interaction coexist: dependence or not of woody resources or/and feeding guilds. Moreover, from a functional perspective, saproxylic insects include a large number of taxa that play a key role in the decomposition of woody material in forest ecosystems [22]. Nevertheless, the diversity of their interactions is poorly understood [23] and consequently saproxylic insect communities [24] have to be studied form the point of view of interacting networks.

Here we provide a first approach to characterise and to analyse specialized interacting patterns occurring in quantitative tree hollow-saproxylic insect food webs, using network analyses. We used empirical data related to trophic structure of the complex community to break down quantitative saproxylic food webs inhabiting hollow microhabitats of Mediterranean forests in Cabañeros National Park (Spain). Mediterranean forests have a large number of woody species compared to central or northern Europe [25] and host a high animal diversity [26], where saproxylic insects make up the highest percentage of their biodiversity. In order to incorporate the high amount of the components of the tree hollow/saproxylic insect interaction, we have included the most representative tree species of the woodland in the studied area. Among the Coleoptera and Diptera (Syrphidae) saproxylic species coexisting in tree hollows, we considered three levels of interaction: 1) complete network (the 'whole' saproxylic community), 2) sub-networks defined according to the use or not of woody resources (direct or indirect saproxylics), and 3) sub-networks according to their feeding guild (xylophagous, saprophagous, xylomycetophagous, predators and commensals). In particular we addressed the following questions: i) How are saproxylic sub-networks organized either defined by the use of resource and by the feeding guild or according to specialised patterns of interaction, as nestedness or modularity? ii) Are there differences in interacting and ecological patterns among sub-networks; and iii) Which are the implications of these properties in network robustness, from random and directed simulations of the lost of tree hollow microhabitats?

Methods

Study site and sampling

The study was conducted in Cabañeros National Park (39º 23’ 47’’ N; 4º 29’ 14’’ W; altitude varies between 560 and 1448 m), a natural area of 40856 ha located in central Spain. The climate is Mediterranean, the annual average temperature fluctuates from 12.9 to 15.6 ºC and the annual precipitation averages between 500 and 750 mm [27]. The park is constituted by extensive areas of well-preserved Mediterranean landscape, with various woodland types [27]. Field work was carried out in the most representative Mediterranean forests of the National Park: sclerophyllous forest of holm-oak *Quercus rotundifolia* Lam., mixed deciduous forest dominated by Pyrenean oak *Quercus pyrenaica* Willd. and the native oak *Quercus faginea* Lam., and riparian forest of narrow-leafed ash *Fraxinus angustifolia* Vahl. To capture saproxylic insects breeding and inhabiting tree hollows we used emergence traps specially modified from Colas [28]. Every tree hollow was covered with acrylic mesh and sealed up with staples. Specimens emerged and come into a white collecting pot containing ethylene glycol as preservative [21,28]. In every forest type we selected 30, 30 and 27 hollow trees, respectively. The first indispensable necessity for study basic specialized patterns occurring on saproxylic communities inhabiting this ecological niche was to represent the real heterogeneity and abundance of tree hollows in each woodland type, always having account the high degree of protection of this National Park and the inherent need to protect and conserve this important and limited microhabitat. We considered a maximum of 30 tree hollows representing the natural proportion per woodland type, including multiple ecological variables able to model saproxylic communities at microhabitat scale in the studied area, as hollow size, hollow position, tree diameter, etc. [30,18,19]. This passive method of capture allows recording saproxylic species shortly after their emergence from immature stages, offering a representative outline of the linkage of any recorded species to this microhabitat, being the interaction strength a good surrogate of this linkage. Collecting tubes were replaced every month throughout a year (February 2009 - March 2010).

Identification of selected taxa

We selected Coleoptera and Diptera as study groups at the hollow level, because they are the best known and represented groups in forests [30-32], allowing us to study the network properties from a quantitative point of view. We considered the Syrphidae as a bioindicator of species and interaction richness among the Diptera, because i) they have been traditionally used next to beetles in studies concerning saproxylic insects [e.g. 33,34], and present a high number of saproxylic species around Europe [33], using a wide range of microhabitats [35], what has led them to be used as indicators of woodland quality [24,34], to be flagships for the conservation of the wider community of saproxylic organisms [35] or to be included in national red lists [e.g. 36], and ii) they represent the best studied family (or just the unique) of Diptera in the study site, presenting high number and abundance of mainly exclusive saproxylic species highly strengthened with tree hollow microhabitats [20].

Identification of Coleoptera families was done using Delvare and Aberlenc keys [37], and for species identification of many families we also counted with the help of invited specialists (see Acknowledgments). Syrphids were identified using the van Veen [38] and Speight keys [39].

Classification into levels of interaction

Saproxylic communities are complex networks involving different types of interactions that depend on different trophic resources available inside tree hollow microhabitats. Because of the large number of both tree hollows and species nodes, we began breaking down the crude network into smaller sub-networks, recording biological/ecological information available for this saproxylic functional group, using the bibliography, the 'Frisbee' data base [40] and expert's information (see Acknowledgements). Clear facultative associations and species with unknown biology were removed for the analyses. For this objective, we classified the saproxylic entomofauna according to the main ecological guilds described by Speight [24] and Bouget et al. [41]: xylophagous, xylomycetophagous, saprophagous, predators and commensals (Table S1). Finally, based on the use of trophic resources on hollow trees, we classified the whole saproxylic community in two basic levels: 1) according to the type of interaction, a) direct saproxylic insects (wood-dependent), feeding on woody resources, as dead or dying wood, sap run or wood-inhabiting fungi, and b) insect-dependent sub-networks (insect-dependent), inhabiting tree hollows but mainly depending on the activity or presence of other saproxylic insects for their development: predators and commensals., and 2) according to trophic guilds: i) xylophagous, ii) saprophagous, iii) xylomycetophagous (wood-dependent sub-networks), and iv) predators and v) commensals (insect-dependent sub-networks).

Network analysis and statistics

Modularity

We used Aninhado [3] to analyse the existence of nestedness patterns (nestedness as NODF estimator), generating 1000 replicates for each saproxylic sub-network with a CE null model. CE considers that the probability of an interaction is proportional to the generalisation level of both species, so allowing evaluating the influence of abundances to nestedness pattern.

To study modularity we used 'netcarto' [5] and Pajek [42]. For a given partition of the nodes of a network into modules, the modularity *M* of this partition is [43-45]:

$$M \equiv \sum_{s=1}^{N_M} \left[\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right] \qquad (1)$$

where N_M is the number of modules, L is the number of links in the network, l_s is the number of links between nodes in module s, and d_s is the sum of the degrees of the nodes in module s. This heuristic module identification algorithm finds the minimum partition into modules. A good partition of a network must comprise many within-module links and as few as possible between-module links. Equation (1) does that by imposing that $M = 0$ if nodes are placed at random into modules or if all nodes are in the same cluster [5,43-45]. We assessed the simulated annealing procedure to find the optimal partition with largest modularity of the network into modules [46]. This stochastic optimization technique enables to find 'low-cost' configuration without getting trapped in 'high-cost' local minima, by means of the introduction of computational temperature T. When T is high, the system can explore configurations of high cost whereas at low T the system only explores low-cost regions. By starting at high T and slowly decreasing T, the system descends gradually towards deep minima, eventually overcoming small cost barriers. When identifying modules, the objective is to maximize the modularity, and thus the cost is $C = –M$, where M is the modularity as defined in equation (1). At each temperature, we perform a number of random updates (1000, f (iteration factor) = 0.1, c (cooling factor) = 0.995) and accept them with probability p [47]:

$$p = \left\{ \begin{matrix} 1 & \text{if } C_f \le C_i \\ \exp\left(-\frac{C_f - C_i}{T}\right) & \text{if } C_f > C_i \end{matrix} \right\} \qquad (2)$$

where C_f is the cost after the update and C_i is the cost before the update.

We also used 'netcarto' to heuristically describe the differences on the composition and interrelations among modules along 25 randomisations maximizing modularity (subjective benchmark). We considered that the partition with a lesser number of modules could be used as the 'minimum partition with largest optimisation of modularity' for each randomised sub-network, from we can know the main minimal subsets of interacting nodes or sub-modules of any modular network. Based on the connectivity in these resultant sub-modules, we yielded and studied the cartographic representation of the complex network [43]. We obtained the within-module degree for each node. If K_i is the number of links of node i to other nodes in its module s_i, $\overline{K}_{S_i}$ is the average of K over all the nodes in s_i, and σk_{S_i} is the standard deviation of K in s_i, then:

$$Z_i = \frac{K_i - \overline{K}_{S_i}}{\sigma k_{S_i}} \quad (3)$$

is so-called *Z-score* ($Z \geq 2.5$ determines hub nodes, and $Z < 2.5$ non-hubs nodes), which measures how well-connected node i is to other nodes in the module. To assess the connection of a node to modules other than its own, we obtained the *P-score* or participation coefficient P_i of each node i as:

$$P_i = 1 - \sum_{s=1}^{N_M} \left(\frac{K_{is}}{k_i}\right)^2 \quad (4)$$

where K_{is} is the number of links of node i to nodes in module s, and k_i is the total degree of node i. The *P-score* of a node ranges between 0 if all the links are done within-module and 1 if the links are uniformly distributed along the set of sub-modules. According to these values, we then classified each node into *system independent* 'universal roles':

kinless hub (R7), *connector hub* (R6), *provincial hub* (R5), *non-hub kinless* (R4), *non-hub connector* (R3), *peripheral* (R2) and *ultra-peripheral* (R1), analysing their number and distribution along sub-modules and implications on modularity patterns.

Interacting patterns

We used 'R-bipartite' [48] to quantitatively assess interacting and distributional patterns between trophic levels of each sub-network and the set of tree hollows assessed. Network attributes analysed were links (mean number of links per species [defined as the sum of links divided by the number of species]), species degree (the sum of the diversity of links per species), interaction strength (sum of dependencies for each species), connectance (the proportion of realised links of the total possible in each network [defined as the sum of links divided by the number of cells in the matrix]), linkage density (a quantitative measure defined as the mean number of interactions per species), H2' (a measure of network specialisation [which ranges between 0: no specialisation, and 1: complete specialisation]), V-ratio (Variance-ratio of species numbers to individual numbers within species for the higher trophic level [values larger than 1 indicate positive aggregation or association, values between 0 and 1 indicate disaggregation of species]).

Robustness to microhabitat extinction

We assessed microhabitat relevance throughout the simulation of primary extinction (slope-estimation derived from randomly removing tree hollow nodes of the lower trophic level) and secondary extinctions approach [49] [slope of the secondary extinction sequence to species in the higher trophic level, following an extermination of the least interconnected tree hollows in the lower trophic level]). We only performed network robustness to species extinctions for insects (higher trophic level) because the set of tree hollows (lower trophic level) is not really affected by removing saproxylic insects. We also studied sub-network robustness [50] as a measure of the system to the random and directed lost of tree hollows (the area below a extinction curve, where R = 1 correspond to a curve that decreases very mildly up to the point at which almost all animal species are eliminated, whereas with R = 0 the curve decreases abruptly as soon as any species is lost). The analyses were carried out separately for each sub-network.

Results

Characterisation of saproxylic sub-networks

We recorded 3680 individuals of Coleoptera belonging to 135 species and 41 families, and 462 individuals of Syrphidae: Diptera belonging to 22 species (Table S1). The complete network was constituted by 244 nodes, corresponding with 157 insect species nodes and 87 tree hollow nodes. The number of saproxylic insect and tree hollow nodes for the rest of the saproxylic sub-networks is reflected in Table 2.

Modularity and sub-modularity

The results showed a lack of nested patterns in the studied sub-networks, implying low nestedness values (less than 25% in all cases, P > 0.05) (Table 2). Quite the opposite, in all the levels of interaction evaluated we found a modular structure of interactions, which were characterised by the presence of a unique module in the largest sub-networks evaluated at global scale: 1) complete network, 2) direct saproxylic network, indirect saproxylic network, and 3) xylophagous, saprophagous, xylomycetophagous sub-networks. Furthermore, in predator and commensal sub-networks we found two and three modules, respectively, which were characterised by a main module housing the majority of interactions, and few isolated modules constituted by pairs of interacting species.

Table 2. Ecological and network attributes modelling saproxylic sub-networks. SP: number of interacting insect species nodes (higher trophic level); TH: number of interacting tree hollow nodes (lower trophic level); NODF: nestedness as NODF estimator; M: number of isolated modules; L/S: links per species; C: connectance; LD: linkage density; H2’: specialisation; V-ratio: variance ratio; PE: extinction slope of higher trophic level for a random extinction (100 replicates); RPE: robustness for a random extinction; SE: secondary extinction slope of the higher trophic level for a selective extinction of the least interconnected nodes (100 replicates); RSE: robustness for a directed extinction. * Values impossible to obtain because the matrix size blocks the running of the programme.

	Network metrics												
Network	**SP**	**TH**	**NODF**	**M**	**L/S**	**C**	**LD**	**H2**	**V-ratio**	**PE**	**RPE**	**SE**	**RSE**
Red	158	87	13.11	1	4.82	0.086	*	*	14.72	*	*	*	*
Direct	104	86	15.37	1	4.69	0.099	*	*	16.38	*	*	*	*
Indirect	54	73	11.76	1	2.284	0.074	6.618	0.55	8.97	2.72	0.72	7.48	0.87
Xylophagous	21	80	24.24	1	2.614	0.157	10.32	0.45	20.02	2.1	0.67	6.66	0.86
Saprophagous	45	81	13.93	1	2.575	0.089	7.562	0.54	10.87	2.73	0.72	8.43	0.88
Xylomycetophagous	38	82	17.57	1	2.525	0.097	11.3	0.36	19.27	2.57	0.71	7.88	0.87
Predators	26	66	12.38	2	1.576	0.086	5.568	0.6	6.65	1.5	0.59	4.6	0.79
Commensals	28	61	14.23	3	1.629	0.085	6.241	0.6	11.53	1.74	0.63	5.12	0.83

For the modularity comparison with randomised networks using simulated annealing procedure, all the sub-networks analysed were statistically significant: complete network (M = 0.255, p = 0.005), direct (M = 0.256, p = 0.006), indirect (M = 0.404, p = 0.009), xylophagous (M = 0.319, p = 0.009), saprophagous (M = 0.371, p = 0.009), xylomycetophagous (M = 0.35, p = 0.009), predator (M = 0.497, p = 0.012), and commensal network (M = 0.471, p = 0.012). The analyses of these sub-networks revealed the existence of a variable number of sub-modules in all the assessed sub-networks (Table 3). The complete network was composed of five to eight sub-modules, but seven sub-modules was the most supported result (48%). Direct sub-network was composed of six to eight sub-modules, but six and seven modules were the most supported (44% and 48%, respectively). Indirect sub-network was composed of six to eight sub-modules (seven and eight modules were the more supported 40% and 48% respectively). The xylophagous sub-network was composed of five to seven, being six sub-modules the most supported result (84%); saprophagous sub-network by five to nine sub-modules, being seven sub-modules the most frequent value (64%); xylomycetophagous sub-network of five to seven sub-modules (six sub-modules showed a support of 68%); predator sub-network of seven to 10 sub-modules (eight and nine sub-modules were the best supported 36% and 40%); commensal sub-network of seven to 10, being nine sub-modules, the most common configuration (50% of the results).

	Number of sub-modules					
Network	**5**	**6**	**7**	**8**	**9**	**10**
Complete network	4	28	48	20	-	-
Direct	-	44	48	8	-	-
Indirect	-	12	40	48	-	-
Xylophagous	12	84	4	-	-	-
Saprophagous	4	4	64	24	4	-
Xylomycetophagous	12	68	20	-	-	-
Predators	-	-	4	36	40	20
Commensals	-	-	4	16	52	28

Table 3. Variation of number of sub-modules. Number of sub-modules present in each sub-network, expressed as the percentage of times with the same number of sub-modules from the 25 randomisations arbitrarily considered.

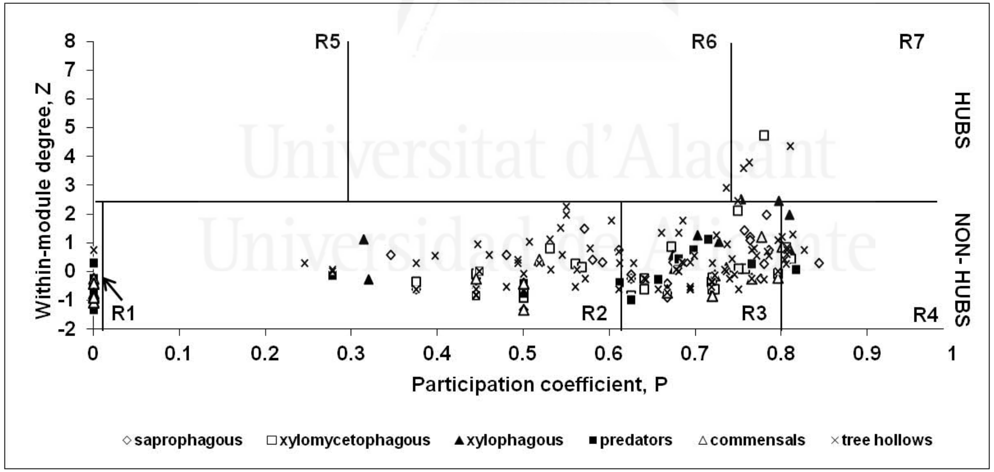
Analyses and characterisation of sub-modules and roles

The complete network was composed at least by five main interacting sub-modules, in which tree hollows, wood- and insect-dependent species comprised subsets of closely interacting nodes along randomisations. However, the node composition for each sub-module changed along the 25 randomisations considered for the whole network, being more or less variable depending on the sub-module considered. Sub-modules 2, 3, and 4 were the most cohesive sub-modules, and their constituting nodes appeared together in 76%, 88%, and 68% of the times, respectively; whereas sub-modules 1 and 5 were less cohesive, appearing together in 29.17% and 31.71% of the times, respectively.

Sub-module 2 was defined by the high number of saprophagous species interacting with a close subset of tree hollows of the three studied tree species, where Cetoniidae species were related with Tenebrionidae species and with uncommon Syrphidae species. The xylophagous guild was mainly represented by generalist Cryptophagidae species and the xylomycetophagous guild by Laemophloeidae, Latridiidae and Curculionidae species. Associated fauna was characterised of predator species belonging to Elateridae, Trogossitidae, Melyridae and Rhizophagidae. Sub-module 3 was mainly constituted of xylomycetophagous species interacting with holm-oak and ash tree hollows, where generalist species of Scolytiidae and Biphylidae coexisting with specialist Latridiidae, Endomychidae and Silvanidae species. The saprophagous guild was composed of hoverfly species commonly present in thermophylous forests. Sub-module 4 was characterised by a high number of both saprophagous and xylomycetophagous species interacting in tree hollows in deciduous forests. Saprophagous guild was composed by Cryptophagidae, Curculionidae and Syrphidae Diptera species. The xylomycetophagous guild was represented by Anobiidae, Cryptophagidae, Cerylonidae, Latridiidae, Mycetophagidae, Silvanidae, Tenebrionidae and Zopheridae species. Indirect fauna was characterised by predator species belonging to Elateridae and Cryptophagidae families, and by commensal species belonging to Nitidulidae. See Table S2 for know in detail the node composition of these five main sub-modules.

Complete network was composed by six ecological roles (Figure 1), corresponding with 6 *hub nodes*: one *connector hub* (R6), and five *kinless hub* (R7); and 238 *non-hub nodes*: 59 *ultra-peripheral* (R1), 72 *peripheral* (R2), 91 *non-hub connector* (R3) and 15 *non-hub kinless* (R4). No *provincial hub* nodes (R5) were present in this ecological network. The distribution of roles was similar among sub-modules. The higher proportion of nodes belonged to non-hubs with ecological roles R1 (24.18%), R2 (29.91%) and R3 (37.3%), comprising the 91.39% of the nodes, and thereby the ‘density landscape’ was displaced towards non-hub region, indicating the high proportion of weakly connected nodes throughout sub-networks. See Table S2 for Z-score, P-score and role for each node.

Figure 1. Ecological role diagram. Ecological role diagram for the saproxylic guilds and tree hollows, showing their role distribution along ecological regions in the *z-P* parameter space. This representation showed that the higher proportion of nodes belonged to non-hubs R1 (24.18%), R2 (29.91%), and R3 (37.3%), corresponding with the 91.39% of the nodes, what implicates a constant predominance of weak connections and a similar role composition along sub-modules and saproxylic trophic guilds. The number of hub nodes was low, and they normally corresponded with *kinless hub* (R7) tree hollow nodes heterogeneously connected along sub-modules. So role-to-role connectivity often happened among R1-R2-R3 and in less extent among R7-R1/R2/R3.



Interacting and distributional patterns

We observed a high variability in the distribution of interactions among the analysed sub-networks. Nodes in the direct sub-network usually presented a higher number of links, connectance, species degree, and interaction strength than indirect sub-networks. Moreover, the three feeding guilds depending on woody resources: xylophagous, saprophagous, xylomycetophagous, also presented higher values in these network metrics than indirect feeding guilds depending on the presence or activity of other saproxylic insects: predators and commensals. These woody-linked trophic levels showed a higher linkage density, because the abundances of both tree hollows and species in these sub-networks were two to three times higher than in saproxylic insect-dependent sub-networks.

All the wood-dependent sub-networks were composed by a higher number of generalist species than saproxylic insect-dependent sub-networks, and these generalist species usually presented higher interaction strength. The xylomycetophagous species *Xyleborus monographus* was the most generalist species, interacting with 61 tree hollows (> 70% of possible interactions). The xylophagous guild had the highest number of generalist species, and jointly with saprophagous guild held the highest heterogeneity of associations. The indirect, predator, and commensal trophic levels were composed by a relative lesser number of interactions, and also showed a lower number of generalist species. The commensal guild was more generalist than predators, and presented higher interaction strength in their connexions, as *Prionocyphon serricornis* (Helodidae), *Epuraea fuscicollis* and *Soronia oblonga* (Nitidulidae). As a common pattern, all the trophic levels were constituted by a high proportion of low-linked insects species (1-3 links), ranging from 40 to 48% in woody-linked sub-networks, and from 57 to 68% in saproxylic insect-linked sub-networks. These set of interactions were heterogeneously distributed along the tree hollows.

On the other hand, the most interconnected tree hollow nodes corresponded with large tree hollows, which commonly housed a higher diversity and amount of trophic resources, microhabitats or hosts/preys, and where a diverse 'team' of generalist insect species coexist and interacts, being less than the 36% specialist insect species (1 to 3 interactions). The level of specialisation (H2') differed among guilds (Table 2), being insect-dependent sub-networks (H2' = 0.545) and overall predator and commensal guilds the most specialised sub-networks (H2' = 0.601 in both cases). Among wood-dependent sub-networks, xylomycetophagous guild was the less selective in their distributional pattern (H2' = 0.364). Variance-ratio values were larger than 1 in all cases, indicating positive aggregation of species or competence among species belonging to same trophic guild, being predators the least aggregated guild (V-ratio = 6.65), and xylophagous and xylomycetophagous the most aggregated guilds (V-ratio > 19).

Robustness to species extinctions

Saproxylic sub-networks were moderately robust to tree hollow nodes extermination in both random and directed extinction simulations (see robustness values in Table 2), and most of the insect species survived even if 50% of the tree hollows were eliminated (Figure 2). Both wood- and insect-dependent sub-networks were more vulnerable to a random sequence of losses of tree hollows, presenting lower robustness values than a direct extermination of the least interconnected tree hollows. The wood-dependent sub-network and the feeding guilds constituting them: xylophagous, saprophagous and xylomycetophagous sub-networks, were more robust than insect-dependent sub-networks and their trophic guilds: predators and commensals sub-networks, in both random and directed cascading extinctions.

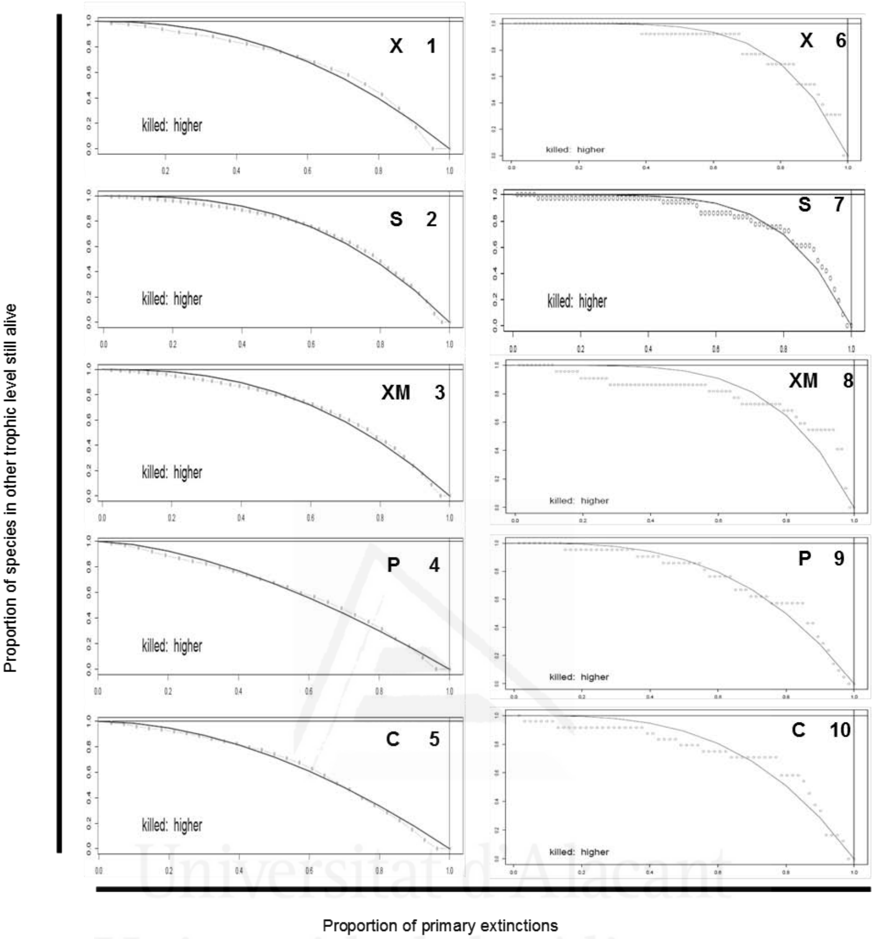


Figure 2. Sub-networks robustness. Random (1-5) and directed (6-10) extinction curve obtained for each feeding guild: xylophagous (X), saprophagous (SX), xylomycetophagous (XM), predators (P), and commensals (C), showing a relative high network robustness to both random and directed extinction simulations in all the trophic levels considered, being wood-dependent guilds more robust than insect-dependent guilds.

Discussion

Results show for first time how a quantitative complex network such as saproxylic community with different types of interaction are organised in interacting food webs , and represent a step forward to understand how sub-networks conforming complex networks may be related. All the saproxylic sub-networks assessed presented a modular pattern of interactions, determining at global scale one large module and a low number of small isolated modules in some of them. Depending on the sub-network, these large modules comprised different numbers of constituent sub-modules, appearing higher number of sub-modules in insect-dependent sub-networks. Wood-dependent sub-networks were more heterogeneously connected: more links, higher species degree, connectance and linkage density, and presented higher interaction strength than insect-dependent sub-networks. Moreover, insect-dependent sub-network and overall their constitutive feeding guilds: predators and commensals, were the most specialised and least aggregated sub-networks. As a consequence, wood-dependent sub-networks (including xylophagous, saprophagous and xylomycetophagous) presented higher network robustness in both random and directed extinction simulations.

Specialised interacting patterns

The majority of the nodes in all the saproxylic sub-networks were within a large and densely interconnected module at global scale, indicating that insect species of a functional module were usually coexisting in a similar subset of tree hollows. Moreover, the number of small modules of a sub-network was related with the number of participating nodes, and insect-dependent sub-networks (with lesser numbers of nodes) presented higher numbers of small isolated modules than wood-dependent sub-networks. This architecture of one large and few isolated modules also occurs in other ecological networks presenting two interaction types [13].

Modularity analysis revealed the existence of closely interacting sub-modules, shaping thereby the main interacting food webs for this saproxylic community. The study of modularity values and number of sub-modules for each sub-network along randomisations, showed a slight variation for modularity values, number of sub-modules and node associations among partitions, indicating the predominance of this specialised pattern along saproxylic sub-networks, and therefore, concluding that the number of randomisations considered using simulating annealing seemed to be a suitable procedure to assess the variation of modularity in complex networks. In the complete network, not all the resulting sub-modules were equally conclusive and solid, but modularity analyses pointed out at least three cohesive sub-modules for this ecological community. This relative high proportion of within-module links also occurs in other modular complex networks [51], showing the number of modules of a networks [5] and determining the ecological niche of their constituent species [11] and therefore preferential interrelations for this saproxylic network, as for instance the high species richness of saprophagous species inhabiting deciduous tree hollows in the sub-module 2, the high species number of saprophagous and xylomycetophagous coexisting and interacting with deciduous tree hollows in sub-module 4, or generalist xylomycetophagous species interacting with saprophagous hoverflies in ash and holm-oak tree hollows in sub-module 3.

The connectivity of the nodes of a complex network enables to classify nodes into universal roles according to their pattern of intra- and inter-module connections [5,43]. Ecological role distribution was characterised of a variable high proportion of non-hubs nodes, depending on the sub-module size or number of nodes, which entailed a general composition of weak but heterogeneously connected nodes. By this reason, a similar composition of non-hubs nodes occurred among sub-modules, and nodes of the same feeding guild tended to have similar ecological roles [see 52], therefore presenting similar topological properties [5]. The role composition obtained for this modular network could be associated with the high abundance and heterogeneity of tree hollows characteristic of Mediterranean forests [20], providing a diverse range of microhabitats and availability of trophic resources that allow to establish at least several weak interconnections for each insect species conforming this saproxylic community. In fact, the most interconnected nodes of the whole network mainly corresponded with a limited proportion of big tree hollows (corresponding with the highest internal volumes along the matrix of tree hollows studied, ranging from 0.1 to 0.28 m^3), which in general housed high amount of trophic resources/microhabitats as dead and decay wood, and therefore hosts/preys for indirect fauna. That big tree hollows are commonly associated with aged trees, which hold the highest numbers of saproxylic species inhabiting Mediterranean forests [53,22]. The role composition was determinant in supporting associations between pairs of sub-modules along randomisations, implying the relevance of weak connections in maintaining the modular structure and their constant role composition. The heterogeneity inherent to this microhabitat suggests the existence of other fundamental ecological patterns determining the species distribution and modelling interacting patterns, such as the influence of microenvironmental variables associated to tree hollow. Because we have a solid database recording the variation of a large set of ecological variables, our next step would be to conscientiously examine this topic elsewhere.

Interacting patterns conditioning modularity

The wood-dependent sub-network (including xylophagous, saprophagous and xylomycetophagous) presented higher species degree, connectance, links, linkage density, interaction strength than the insect-dependent sub-network (predators and commensals), comprising a higher heterogeneity of interactions. The resemblances among related sub-networks may be explained not only by the bound of the interaction, but by the similar abundances of weakly connected nodes (corresponding with the high amount of non-hub nodes) among guilds and throughout the matrix of tree hollow and insect species nodes, constituting a high diversity of interactions among nodes and sub-modules. Both wood- and insect-dependent interactions are coexisting in space and time in tree hollows, but they differ in the dependence on microhabitats for their development or establishment of the interaction. These biological and ecological aspects resulted in great differences in the species composition and interacting patterns of each sub-network and sub-module, driving the differences observed in modular patterns (as modularity values or number of sub-modules) of the resulting food webs involving different types of interaction. Antagonistic interactions tend to be organised in modules even when they are densely connected [16]. The xylophagous sub-network presented lower modularity values and number of sub-modules, and were more densely connected among them than the predator sub-network, emphasising clear differences in modularity patterns according to the boundary of the antagonistic interaction. The architecture and interacting patterns between commensal and predator guilds were similar, indicating that their shared dependence on wood-dependent sub-networks determines analogous network properties. In any case, weakly connected and highly modular antagonistic and mutualistic networks are related with a high interaction intimacy [54], which effect on network architecture depends on the interaction type (mutualistic vs. antagonistic) [11], and as our results highlight also on other types of interactions.

By other side, the specialisation index (H2') showed that insect-dependent sub-networks were more specialised in the distribution of their connections, what can be heavily determined by their dependence on the distribution and abundance of wood-dependent species. Variance-ratio showed the existence of competence patterns among species of the same feeding guild, so we can expect a stronger competence among ecologically related species coexisting in the same sub-module, as showed by Rezende et al. [52] for phylogenetically and ecologically related species among predators. Sirami et al. [18] suggested that saproxylic assemblages in Mediterranean forests are especially dependent on the availability of trophic resources at local habitat. Here, we also suggested that the distributional patterns structuring saproxylic communities were also influenced by the boundary of the interaction and interrelations occurring along functional modules housed in tree hollow microhabitats.

Implications to robustness in saproxylic networks

Saproxylic trophic levels were moderately robust to species extinction in both random and directed cascading extinction of tree hollows, being slightly more vulnerable to a random sequence of losses. In a random simulation, the high amounts of weak and heterogeneously connected insect nodes determined lower network robustness, being more sensitive to disappear with the removal of tree hollow nodes. Otherwise a directed removal of nodes gradually affected the dense distribution of these weak nodes. The high proportion of non-hubs connecting the most of nodes among sub-modules and sub-networks seemed to be conditioning relative good robustness to species extinctions, highlighting the importance of 'effective communication' [55] between insect species and tree hollows in the network of interactions. Stability and species coexistence of trophic networks is enhanced in modular and weakly connected architectures [4] retaining the impacts of a perturbation within a single module and minimising impacts on other modules [56]. On the contrary, food webs with a low level of modularity (densely connected species connected to each other) may confer higher robustness [57]. Accordingly, we found that sub-networks with a lower number of sub-modules, corresponding to wood-dependent sub-networks, presented higher network robustness. Finally, we observed a strong association among connectance, robustness and type of interaction. Wood-dependent feeding guilds with quite different species richness always presented higher connectance and higher robustness values than insect-dependent sub-networks of predators and commensals, for instance Dunne et al. [58] concluded that food-web robustness does not relate to species richness, but increases significantly with greater connectance. Therefore, robustness in saproxylic sub-networks seems to be conditioned by the presence of effective nodes, weak connections, a suitable number of sub-modules and the network connectance.

Usually if a portion of an ecosystem loses biodiversity as a result of some catastrophic event or severe anthropogenic modification, it will eventually regain species through linkage with adjacent ecosystems [59]. Our results highlight that saproxylic biodiversity is more dependent and specialised in trees with large holes, as in Ranius and Jansson [60], Micó et al. [29] and Gouix [53], where a higher richness and abundance of trophic resources, microhabitats or host/preys are available. These results are only focussed on the robustness according to the analysed network of interactions, and do not consider other critical characteristics characteristic to this Mediterranean forests, as isolation and low area of mature forests, or the limited proportions of tree hollows in them. Impoverishment linked to traditional habitat management based on removing old trees, dead or fallen wood, abruptly limits the microhabitat variability, and leads to habitat lost and isolation [61], affecting tree hollow-insect species interaction. Microhabitat impoverishment could also lead to an ecological disruption because of their important ecological role in forest ecosystems, i.e. fragmentation and nutrient recycling of wood decay [62] and performing in the maintenance of the trophic chains [31].

Our results emphasise the importance of the study of interrelations in understanding the distributional and interacting patterns modelling saproxylic communities in tree hollow microhabitats in Mediterranean forests. Conservation of one of the most complex and diverse terrestrial communities, such as saproxylic assemblages, needs a much better knowledge of species, processes and interactions.

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Supplementary material

Table S1. Species list, abundance and labels. Species list and abundance only considering saproxylic species. Saproxylic trophic guild of each species and their labels: xylophagous (C), saprophagous (A), xylomycetophagous (B), predator (E), and commensal (D).

	Abundance	Trophic guild label
DIPTERA		
Syrphidae		
Brachyopa insensilis Collin, 1939	10	A1
Brachypalpoides lentus (Meigen, 1822)	2	A2
Brachypalpus valgus (Panzer, 1798)	4	A3
Callicera aurata (Rossi, 1790)	2	A4
Callicera spinolae Rondani, 1844	29	A5
Ceriana vespiformis (Latreille, 1804)	9	A6
Criorhina floccosa (Meigen, 1822)	8	A7
Criorhina pachymera Egger, 1858	4	A8
Ferdinandea aurea Rondani, 1844	24	A9
Ferdinandea cuprea (Scopoli, 1763)	3	A10
Ferdinandea fumipennis Kassebeer, 1999	1	A11
Ferdinandea ruficornis (Fabricius, 1775)	6	A12

Mallota cimbiciformis (Fallen, 1817)	33	A13
Mallota dusmeti Andréu, 1926	97	A14
Mallota fuciformis (Fabricius, 1794)	3	A15
Milesia cabroniformis (Fabricius, 1795)	1	A16
Myathropa florea (Linnaeus, 1758)	203	A17
Myolepta difformis Strobl in Czerny & Strobl, 1909	10	A18
Myolepta dubia (Fabricius, 1805)	1	A19
Myolepta obscura Becher, 1882	4	A20
Sphiximorpha subsessilis (Illiger in Rossi, 1807)	1	A21
Spilomyia digitata (Rondani, 1865)	6	A22
COLEOPTERA		
Aderidae		
Aderus populneus (Panzer, 1796)	38	C1
Cnopus minor (Baudi, 1877)	1	C2
Otolelus neglectus (Jacquelin du Duval, 1863)	48	C3
Anobiidae		
Dorcatoma vaulogeri agenjoi Español, 1978	17	B1
Oligomerus brunneus (Olivier, 1790)	28	C4
Rhamna semen Peyerimhoff de Fontenelle, 1913	27	B2
Biphyllidae		
Diplocoelus fagi Guérin-Méneville, 1838	33	B3

Buprestidae		
Acmaeodera degener 14-punctata (Scopoli, 1763)	2	C5
Eurythyrea quercus (Herbst, 1780)	1	C6
Cerambycidae		
Alocerus moesiacus (Frivaldsky, 1838)	15	C7
Cerambyx welensii (Küster, 1846)	3	C8
Prinobius myardi Mulsant, 1851	12	C9
Stictoleptura trisignata (Fairmaire, 1852)	38	C10
Trichoferus fasciculatus (Faldermann, 1837)	1	C11
Cerylonidae		
Cerylon histeroides Fabricius, 1792	1	B4
Cetoniidae		
Cetonia aurataeformis Curti, 1913	245	A23
Potosia cuprea (Fabricius, 1775)	34	A24
Potosia opaca (Fabricius, 1787)	14	A25
Ciidae		
Cis striatulus Mellie 1848	1	B5
Cis villosulus Marsham, 1802	1	B6
Clambidae		
Calyptomerus sp	1	B7
Clambus sp	4	B8

Cleridae		
Opilo domesticus (Sturm, 1837)	7	E1
Cryptophagidae		
Atomaria (Anchicera) pusilla (Paykull, 1798),	2	B9
Cryptophagus cylindrus Kiesenwetter, 1858	4	A26
Cryptophagus dentatus (Herbst, 1793)	23	A27
Cryptophagus distinguendus Sturm, 1845	2	A28
Cryptophagus fallax Balfour-Browne 1953	1	A29
Cryptophagus micaceus Rey, 1889	142	E2
Cryptophagus punctipennis Brisout de Barneville, 1863	54	C12
Cryptophagus reflexus Rey, 1889	268	C13
Cryptophagus saginatus Sturm, 1845	36	B10
Cryptophagus scanicus (Linnaeus, 1758)	119	B11
Curculionidae		
Camptorhinus simplex Seidlitz, 1867	1	A30
Camptorhinus statua (Rossi, 1790)	82	A31
Gasterocercus hispanicus Alonso-Zarazaga, Jover y Micó, 2009	1	B12
Curculionidae (Scolytiinae)		
Xyleborinus saxesenii (Ratzeburg, 1837)	37	B13
Xyleborus dryographus (Ratzeburg, 1837)	9	B14
Xyleborus monographus (Fabricius, 1792)	321	B15

Dasytidae		
Aplocnemus brevis (Rosenhauer, 1856).	1	E3
Aplocnemus consobrinus (Rosenhauer, 1856)	1	E4
Aplocnemus limbipennis Kiesenwetter, 1865	1	E5
Mauroania bourgeoisi (Pic, 1894)	3	E6
Dermestidae		
Anthrenus (Anthrenus) angustefasciatus Ganglbauer, 1904	3	D1
Anthrenus (Anthrenus) festivus Erichson, 1846	8	D2
Anthrenus (Florilinus) minutus Erichson, 1846	40	D3
Anthrenus (Florilinus) verbasci (Linnaeus, 1767)	5	D4
Attagenus incognitus Hava, 2003	5	D5
Attagenus schaefferi (Herbst, 1792)	1	D6
Attagenus trifasciatus (Fabricius, 1787)	17	D7
Dermestes (Dermestes) bicolor Fabricius, 1781	1	D8
Dermestes (Dermestinus) erichsonii Ganglbauer, 1904	1	D9
Dermestes (Dermestinus) frischii Kugelann, 1792	1	D10
Dermestes (Dermestes) hispanicus Kalik, 1952	4	D11
Dermestes (Dermestinus) undulatus Brahm, 1790	22	D12
Orphilus niger (Rossi, 1790)	2	D13
Dynastidae		
Oryctes nasicornis (Linnaeus, 1758)	7	A32

Elateridae		
Ampedus aurilegulus (Schaufuss, 1862)	35	E7
Ectamenogonus montandoni Buysson, 1888	7	E8
Elater ferrugineus Linnaeus, 1758	33	E9
Elathous platiai Zapata & Sánchez-Ruiz 2007	1	E10
Ischnodes sanguinicollis (Panzer, 1793)	63	E11
Lacon punctatus (Herbst, 1779)	11	E12
Limoniscus violaceus (Müller, 1821)	2	A33
Megapenthes lugens (Redtenbacher, 1842)	20	E13
Procraerus tibilais (Boisduval & Lacordaire, 1835)	12	E14
Endomychidae		
Mycetaea hirta (Marsham, 1802)	7	B16
Symbiotes gibberosus (Lucas, 1849)	6	B17
Eucinetidae		
Nycteus meridionalis Laporte de Castelnau, 1836	1	B18
Helodidae (Scirtidae)		
Prionocyphon serricornis (Müller, 1821)	203	D14
Laemophloeidae		
Cryptolestes ferrugineus (Stephens, 1831)	7	B19
Laemophloeus nigricollis Lucas, 1849	2	B20
Placonotus testaceus (Fabricius, 1787)	2	B21

Latridiidae		
Corticaria obscura Brisout, 1863	2	D15
Dianerella ruficollis (Marsham, 1802)	1	B22
Enicmus brevicornis (Mannerheim, 1844)	4	B23
Enicmus rugosus (Herbst, 1793)	4	B24
Lathridius assimilis (Mannerheim, 1844)	25	B25
Leiodidae		
Agathidium (Neoceble) nigriceps Brisout, 1872	2	B26
Lucanidae		
Dorcus parallelepipedus (Linnaeus, 1785)	43	C14
Malachiidae		
Anthocomus fenestratus Linder, 1864	16	E15
Axinotarsus marginalis (Laporte de Castelnau, 1840)	6	E16
Hypebaeus albifrons (Fabricius, 1775)	3	E17
Troglops furcatus Abeille de Perrin, 1885	52	E18
Melandryidae		
Orchesia micans (Panzer, 1794)	8	B27
Melyridae		
Falsomelyris granulata (Fabricius, 1792)	2	E19
Mycetophagidae		
Litargus balteatus Le Conte, 1856	1	B28

	Litargus connexus (Geoffroy, 1785)	11	B29
	Mycetophagus quadriguttatus Müller, 1821	73	B30
Nitidulidae			
	Amphotis marginata (Fabricius, 1781)	2	D16
	Carpophilus sp	1	D17
	Epuraea fuscicollis (Stephens, 1832)	137	D18
	Epuraea ocularis Fairmaire, 1849	2	D19
	Soronia oblonga C.Brisout de Barneville, 1863	141	D20
Oedemeridae			
	Ischnomera xanthoderes (Mulsant, 1858)	113	C16
Platypodidae			
	Platypus cylindrus (Fabricius, 1792)	1	C17
Pselaphidae			
	Euplectus sp	1	D21
	Geopsephalus	1	D22
	tribu Goniaceritae	1	E20
Ptiliidae			
	sp 1	46	B31
Ptinidae			
	Dignomus irroratus (Kiesenwetter, 1851)	4	A34
	Ptinus (Cyphoderes) bidens Olivier, 1790	13	A35

Ptinus (Cyphoderes) hirticornis Kiesenwetter, 1867	3	A36
Ptinus (Ptinus) spitzyi Villa & Villa, 1838	1	A37
Ptinus (Ptinus) timidus Brisout de Barneville, 1866	274	C15
Rhizophagidae		
Rhizophagus unicolor Lucas, 1846	1	E21
Scraptiidae		
Anaspis regimbarti Schilsky, 1895	11	C18
Pentaria defarguesi Abeille de Perrin, 1885	1	C19
Scraptia schotti Leblanc, 2010	2	C20
Scraptia testacea Allen, 1940	80	C21
Scydmaenidae		
Cephenium (Cephenium) sp.	1	D23
Palaeostigus palpalis (Latreille, 1804)	5	D24
Scydmaenus (Cholerus) cornutus Motschulsky, 1845	3	D25
Stenichnus (Cyrtoscydmus) godarti (Latreille, 1806)	5	D26
Silvanidae		
Ahasverus advena (Waltl, 1834)	2	B32
Airaphilus sp	1	B33
Oryzaephilus surinamensis (Linnaeus, 1758)	1	B34
Silvanus bidentatus Fabricius, 1792	2	B35
Uleiota planata (Linnaeus, 1761)	7	B36

Tenebrionidae		
Corticeus fasciatus (Fabricius, 1790)	1	D27
Eledonoprius armatus (Panzer, 1799)	7	B37
Probaticus anthracinus (Germar, 1813)	37	A38
Probaticus granulatus (Allard, 1876)	1	A39
Stenohelops sublinearis (Kraatz, 1870)	4	A40
Tenebrio punctipennis Seidlitz, 1896	33	D28
Tenebrionidae (Alleculinae)		
Isomira hispanica Kiesenwetter, 1870	11	A41
Mycetochara linearis (Illiger, 1794)	20	A42
Mycetochara quadrimaculata (Latreille, 1804)	110	A43
Prionychus fairmairei (Reiche, 1860)	17	A44
Pseudocistela ceramboides (Linnaeus, 1761)	43	A45
Trogossitidae		
Tenebroides marrocanus Reitter, 1884	3	E23
Temnochila caerulea (Olivier, 1790)	3	E24
Zopheridae		
Colobicus hirtus (Rossi, 1790)	2	E25
Colydium elongatum (Fabricius, 1787)	6	E26
Endophloeus marcovichianus (Piller & Mitterpacher, 1783)	22	B38

Table S4. Node composition. Node composition for the five main sub-modules present at the complete network, with node names and their respective labels in the diagrams. k: number of links of a node; Z-score: within-module degree of a node; P-score: Participation coefficient (between-module degree); role: ecological region.

Sub-module	Node name	Label	k	*Z-score*	*P-score*	Role
	Fr2	5	29	1.284666	0.813317	R4
	Fr9b	13	22	2.893541	0.735537	R6
	Fr19	17	20	0.732798	0.765	R3
	Fr8	18	20	1.758715	0.685	R3
	Fr25	21	17	1.758715	0.602076	R2
	Qi17	36	13	0.292384	0.686391	R3
	VBQp8b	38	13	0.048853	0.733728	R3
	Fr9a	45	11	0.048853	0.677686	R3
	Qi23	47	11	0.292384	0.61157	R2
	Fr16	56	9	0.390826	0.493827	R2
	Fr26	57	9	-0.293119	0.641975	R3
	Fr9c	64	8	0.048853	0.53125	R2
	Fr21	69	7	0.732798	0	R1
	Qi20a	70	7	-0.536036	0.693878	R3
	Fr3	80	4	-0.635092	0.375	R2
	Qi18	85	3	-0.737034	0.666667	R3
	Qi19b	86	3	-0.812176	0.444444	R2
	C15	91	35	2.44266	0.796735	R3
	C16	92	35	2.501504	0.752653	R7
	C21	98	26	0.732798	0.810651	R4
	A43	100	23	1.07477	0.763705	R3
	E11	105	19	0.732798	0.698061	R3
	A42	121	12	0.732798	0.611111	R2
	A25	126	10	0.390826	0.58	R2
	D3	132	9	0.390826	0.518519	R2
	D7	133	9	-0.251577	0.765432	R3
	B27	141	6	-0.631579	0.722222	R3
	A41	143	6	-0.259896	0.5	R2
1	C9	145	5	-0.293119	0.32	R2

	A6	157	4	-0.635092	0.375	R2
	A8	158	4	-0.977064	0.625	R3
	E6	168	3	0.300273	0	R1
	E23	170	3	-0.812176	0.444444	R2
	D26	174	3	-0.737034	0.666667	R3
	C3	175	2	-0.737034	0.5	R2
	B32	181	2	-0.894737	0.5	R2
	C19	203	1	-1.319036	0	R1
	C20	204	1	-0.737034	0	R1
	A16	218	1	-0.428222	0	R1
	A21	220	1	-1.319036	0	R1
	E4	227	1	-0.737034	0	R1
	E20	231	1	-1.319036	0	R1
	D22	242	1	-0.428222	0	R1

Sub-module	**Node name**	**Label**	**k**	***Z-score***	***P-score***	**Role**
	Fr10	4	30	3.77366	0.762222	R7
	Fr23	6	28	1.07477	0.795918	R3
	Fr29	12	22	0.5581	0.785124	R3
	VSQp7	14	22	1.968036	0.549587	R2
	VSQp14	20	19	1.498057	0.542936	R2
	VSQp4	23	17	0.5581	0.698962	R3
	Qi2	26	15	0.292384	0.72	R3
	VBQp15	27	15	0.32311	0.684444	R3
	VBQp6	28	15	1.028079	0.506667	R2
	Qi1	31	14	0.754732	0.806122	R4
	VBQp2	34	14	0.32311	0.693878	R3
	Qi8	41	12	0.016244	0.680556	R3
	VSQf16	50	11	0.5581	0.396694	R2
	VSQp2	55	10	-0.368421	0.72	R3
	Fr17	74	6	-0.635092	0.611111	R2
	Qi12a	78	5	-0.251577	0.64	R3
	C13	89	51	1.968036	0.80892	R4
	A23	90	39	1.968036	0.78238	R3
	C12	102	22	1.028079	0.727273	R3
	B25	110	16	0.088121	0.757813	R3
	B10	115	14	0.793089	0.530612	R2
2	A24	116	14	0.754732	0.785714	R3

	A45	117	14	0.32311	0.673469	R3
	A44	119	13	0.32311	0.591716	R2
	E7	139	7	-0.381858	0.612245	R2
	D24	152	5	-0.851837	0.72	R3
	B23	154	4	-0.851837	0.625	R3
	A34	160	4	-0.851837	0.625	R3
	A40	167	3	-0.894737	0.666667	R3
	D4	172	3	-0.251577	0.444444	R2
	C5	176	2	-0.812176	0	R1
	B20	178	2	-0.754732	0.5	R2
	B21	179	2	-0.894737	0.5	R2
	A2	183	2	-0.851837	0	R1
	A7	185	2	-0.851837	0	R1
	A9	186	2	-0.851837	0	R1
	A28	189	2	-1.319036	0.5	R2
	E24	192	2	-0.251577	0	R1
	C2	198	1	-0.754732	0	R1
	C6	199	1	-1.086826	0	R1
	C11	201	1	-1.086826	0	R1
	C17	202	1	-1.088316	0	R1
	B12	208	1	-1.086826	0	R1
	B34	214	1	-0.754732	0	R1
	A32	223	1	-1.086826	0	R1
	A37	224	1	-1.086826	0	R1
	E10	229	1	-1.088316	0	R1
	E19	230	1	-0.754732	0	R1
	E21	232	1	-1.086826	0	R1
	D11	237	1	-1.088316	0	R1
	D13	238	1	-0.894737	0	R1
	D21	241	1	-0.754732	0	R1

Sub-module	**Node name**	**Label**	**k**	***Z-score***	***P-score***	**Role**
	VSQf12	8	27	1.263068	0.72428	R3
	Fr12	29	14	0.818927	0.806122	R4
	Qi15	32	14	1.120804	0.530612	R2
	Fr24	39	12	0.251577	0.805556	R4
	Qi4a	40	12	0.016244	0.736111	R3
3	Qi19a	46	11	0.292384	0.628099	R3

Qi4b	48	11	0.568524	0.545455	R2
Fr6	51	10	-0.293119	0.78	R3
Qi25	52	10	0.568524	0.46	R2
Qi3	53	10	-0.259896	0.74	R3
Qi13	58	9	0.292384	0.518519	R2
Qi5a	59	9	0.292384	0.493827	R2
Fr28	61	8	0.292384	0.375	R2
Fr5	62	8	0.048853	0.5625	R2
Fr7	63	8	-0.635092	0.75	R3
Fr11	67	7	-0.616847	0.693878	R3
Fr20	68	7	-0.635092	0.693878	R3
Qi24	71	7	0.292384	0.244898	R2
Qi26	72	7	0.016244	0.44898	R2
Qi7	73	7	-0.259896	0.571429	R2
Fr27	75	6	0.048853	0.277778	R2
Qi22	76	6	0.016244	0.277778	R2
Qi11	77	5	-0.536036	0.56	R2
Qi14	79	5	-0.536036	0.48	R2
Qi5b	81	4	-0.085644	0.5	R2
Qi6	82	4	-0.251577	0.625	R3
Qi21	87	3	-0.812176	0.444444	R2
B15	88	61	4.710623	0.779898	R7
D14	95	28	0.844664	0.80102	R4
B3	96	27	2.100687	0.748971	R3
A17	99	24	1.416743	0.756944	R3
B13	103	22	0.818927	0.805785	R4
B2	109	16	0.844664	0.671875	R3
C10	114	14	0.568524	0.673469	R3
C7	124	11	1.120804	0.31405	R2
A5	125	10	0.568524	0.48	R2
A14	130	9	0.568524	0.345679	R2
A18	137	7	-0.251577	0.77551	R3
E1	138	7	0.016244	0.44898	R2
A13	142	6	-0.259896	0.444444	R2
D2	151	5	-0.851837	0.72	R3
B8	153	4	-0.259896	0	R1
B6	163	1	-0.737034	0	R1

	A36	166	3	-0.737034	0.666667	R3
	E16	169	3	-0.812176	0.444444	R2
	B5	206	1	-1.088316	0	R1
	B7	207	1	-1.319036	0	R1
	B16	209	1	-0.085644	0.444444	R2
	B22	211	1	-1.088316	0	R1
	B35	215	1	-1.319036	0	R1
	A39	225	1	-1.088316	0	R1
	E3	226	1	-1.088316	0	R1
	D9	235	1	-1.086826	0	R1

Sub-module	**Node name**	**Label**	**k**	***Z-score***	***P-score***	**Role**
	VBQp3	2	43	3.578947	0.756084	R7
	VSQf15	7	28	1.210526	0.80102	R4
	VBQp14	10	25	0.684211	0.784	R3
	VBQp1	15	21	0.5581	0.770975	R3
	VSQf13	16	20	2.263158	0.55	R2
	VSQp10	19	19	0.390826	0.803324	R4
	VSQf9	22	17	0.016244	0.795848	R3
	VSQp1	24	16	0.421053	0.742188	R3
	Fr22	30	14	0.754732	0.826531	R4
	VSQf6	35	14	0.599511	0.806122	R4
	VBQp5	37	13	-0.105263	0.745562	R3
	VBQp17	42	12	0.684211	0.611111	R2
	VBQp7	43	12	1.33758	0.680556	R3
	VBQp16	49	11	0.947368	0.446281	R2
	VSQf5	54	10	1.33758	0.66	R3
	Qi20b	65	8	-0.536036	0.71875	R3
	VBQp12	66	8	-0.368421	0.71875	R3
	Qi12b	83	3	-0.631579	0.444444	R2
	A31	93	29	1.210526	0.763377	R3
	B11	94	28	0.421053	0.811224	R4
	D20	97	27	1.210526	0.776406	R3
	E9	107	17	0.048853	0.816609	R4
	D18	108	17	-0.21838	0.795848	R3
	B30	111	16	0.088121	0.75	R3
	A27	112	16	0.300273	0.84375	R4
4	A38	113	16	1.473684	0.570313	R2

	C4	120	12	0.157895	0.736111	R3
	E15	122	12	0.421053	0.680556	R3
	A35	127	10	0.256933	0.78	R3
	E2	128	10	0.157895	0.68	R3
	B38	129	9	0.157895	0.567901	R2
	E12	131	9	0.251577	0.765432	R3
	A1	135	8	-0.105263	0.625	R3
	B1	146	5	-0.631579	0.72	R3
	B19	148	5	-0.631579	0.64	R3
	B29	149	5	-0.21838	0.72	R3
	B36	150	5	-0.251577	0.64	R3
	B24	155	4	-0.368421	0.375	R2
	A3	156	4	-0.977064	0.625	R3
	A22	159	4	-0.251577	0.625	R3
	D5	162	4	-0.259896	0	R1
	B37	182	2	-0.631579	0	R1
	A4	184	2	-0.631579	0	R1
	A20	187	2	-0.737034	0.5	R2
	A26	188	2	-0.737034	0.5	R2
	D15	196	2	-0.428222	0.5	R2
	B4	205	1	-0.894737	0	R1
	B33	213	1	-1.088316	0	R1
	A12	217	1	-0.894737	0	R1
	A29	221	1	-0.894737	0	R1
	A30	222	1	-0.894737	0	R1
	D17	239	1	-0.894737	0	R1
	D19	240	1	-0.428222	0	R1
	D23	243	1	-0.754732	0	R1
	D27	244	1	-0.894737	0	R1

Sub-module	**Node name**	**Label**	**k**	***Z-score***	***P-score***	**Role**
	VSQp8	1	46	4.367864	0.810019	R7
	VBQp10	3	37	2.438015	0.749452	R3
	Qi9	9	25	0.793089	0.768	R3
	VSQf3	11	23	0.947368	0.73724	R3
	Fr18	25	15	0.793089	0.577778	R2
	VBQp13	33	14	-0.259896	0.765306	R3
5	VBQp8a	44	12	-0.146868	0.722222	R3

Fr1	60	8	-0.635092	0.65625	R3
Qi16	84	3	-0.812176	0.444444	R2
C1	101	22	1.263068	0.702479	R3
E18	104	20	1.120804	0.715	R3
B31	106	17	-0.085644	0.795848	R3
C14	118	13	0.088121	0.674556	R3
D28	123	12	-0.146868	0.722222	R3
B14	134	8	-0.368421	0.71875	R3
E14	136	8	-0.293119	0.65625	R3
C18	140	6	-0.616847	0.666667	R3
E13	144	6	-0.146868	0.277778	R2
B17	147	5	0.256933	0.56	R2
E8	161	4	-0.977064	0.625	R3
A10	164	3	-0.428222	0.666667	R3
A15	165	3	-0.631579	0.444444	R2
E26	171	3	-0.634787	0.666667	R3
D25	173	3	-0.851837	0.444444	R2
B9	177	2	-0.851837	0	R1
B26	180	2	-0.428222	0.5	R2
A33	190	2	-0.737034	0.5	R2
E17	191	2	-0.428222	0.5	R2
E25	193	2	-0.428222	0.5	R2
D1	194	2	-1.319036	0.5	R2
D12	195	2	-0.428222	0.5	R2
D16	197	2	-0.428222	0.5	R2
C8	200	1	-0.428222	0	R1
B18	210	1	-1.086826	0	R1
B28	212	1	-0.428222	0	R1
A11	216	1	-0.428222	0	R1
A19	219	1	-0.894737	0	R1
E5	228	1	-1.086826	0	R1
D6	233	1	-0.428222	0	R1
D8	234	1	-0.428222	0	R1
D10	236	1	-1.086826	0	R1

CAPÍTULO 4

Influence of tree hollow microenvironmental variables on saproxylic guild diversity in Mediterranean woodlands

Influencia de las variables microambientales sobre la diversidad de los gremios saproxílicos en bosques mediterráneos

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Abstract

Saproxylic diversity assessment is a major goal for conservation strategies in woodlands. This assessment should consider historical woodland management and environmental factors that structure ecological communities, with particular emphasis on those linked to microhabitats. We assessed the diversity of six saproxylic guilds, which included: i) saprophagous (SA) Syrphidae (Diptera), and ii) xylophagous (X), saproxylophagous (SX), saprophagous (SA), xylomycetophagous (XM), predators (P) and commensals (C) Coleoptera, co-occurring in tree hollows located in three different types of Mediterranean woodlands, in Cabañeros National Park (Spain). We also evaluated the influence of hollow microenvironmental variables (understood as the physical and biotic characteristics of a hollow and tree individual) on saproxylic guild distribution. We found that the type of Mediterranean woodland highly influenced the diversity and composition of hollow saproxylic guilds, and those woodlands that provided greater heterogeneity of hollow microhabitats determined higher guild diversity, which was found in historically less managed woodlands (with no current management). Nevertheless, the population of certain species or even the diversity of complete guilds was enhanced in woodlands that were still managed. On the other hand, hollow volume was the main determining factor for saproxylic guild richness and abundance in general, and large hollow volume was related to higher diversity (except for saprophagous richness and abundance, and commensal richness), which highlights the importance of multi-habitat hollow trees. Moreover, saproxylic guilds also responded to other different microenvironmental variables, indicating different ecological preferences among guilds. Finally, we discussed the possible implications on conservation and management strategies in Mediterranean woodlands.

Keywords

Woodland management, functional guilds, Coleoptera, Syrphidae, *Quercus*, *Fraxinus*

Introduction

Factors influencing saproxylic insect community structures represent a significant topic for conservation programmes in the world. Many studies have related saproxylic insect assemblages to local vegetation structure and composition, altitude and landscape composition or woodland management (Økland et al. 1996; Grove, 2002; Saint-Germain et al. 2007; Fayt et al. 2006; Ulyshen and Hanula, 2009). However, saproxylics are closely tied to tree microhabitats, such as hollows, bark, fungi, sap runs, insect workings, etc. (Warren and Key, 1991; Jonsell et al. 1998; Speight et al. 2010; Gouix, et al. 2012), and few studies have determined the influence of microhabitat variability within and among woodlands (Winter and Möller, 2008; Saint-Germain et al. 2010; Gouix and Brustel, 2011).

Tree hollows in standing living trees are relevant microhabitats for saproxylics (Alexander, 2008; Müller and Bütler, 2010), and are one of the most important within Mediterranean woodlands (Sirami et al. 2008; Marcos-García et al. 2010). Tree hollows are mainly formed after the colonisation of heart-rot fungi (Stokland et al. 2012); then processes of rot penetrate the bark and heartwood of a tree (Kitching, 2000) with decomposition breakdown occurring at different rates (Irmler et al. 1996). Other important factors for tree hollow formation are physical damage to the trunk or branches caused by natural causes (e.g. branches broken by the weight of snow, wind action, lightning, fire or the actions of nesting vertebrates) or more commonly due to anthropogenic action (high variation of pruning types according to traditional uses of tree species) (Kitching, 2000; Stokland et al. 2012). Therefore, hollows can occur in different parts of the tree, and present an exclusive formation processes conjunction that is influenced to a high extent by the traditional management performed on each woodland type. Regardless of their origin, tree hollows offer temperature and humidity regimes characterised by stability (personal data) and high diversity of trophic resources (Marcos-García et al. 2010; Micó et al. 2011; Quinto et al. 2012), which determine a rich saproxylic fauna of tree hollow specialist species (Jonsell et al. 1998; Ulyshen and Hanula, 2009, Gouix and Brustel, 2011; Quinto et al. ‘unpub. res.’). Studies concerning microhabitat heterogeneity are necessary to attain a better understanding of the diversity and distribution of the whole saproxylic assemblage in different Mediterranean woodlands, hence optimising conservation strategies for saproxylics at local scale.

It is well known that different saproxylic feeding guilds can be identified according to their use of trophic resources: xylophagous, saproxylophagous, saprophagous, xylomycetophagous, predators and commensals (Speight, 1989; Bouget et al. 2005). A key point is that in each tree hollow many representatives of each guild interact among themselves as well as with tree hollow trophic resources, in a different way and to a different degree (Quinto et al. 2012). So, the diversity of different feeding guilds is expected to be affected in a different way by the microenvironmental characteristics of the hollow. However, the way in which these guilds interact (among themselves and with the hollow) and how this interaction affects their diversity are still scarcely understood. In this study we focused on the tree hollow microenvironmental variables (understood as physical and biotic characteristics of the hollow and the tree individual) in order to understand how these parameters contribute to community structure at local scale, by analysing tree hollow diversity patterns among different guilds in Mediterranean woodlands in Cabañeros National Park (Spain).

We addressed the following questions: How do tree hollow guild richness and ecological diversity change among types of Mediterranean woodlands (different tree species and management)? We expected to find that woodland type was highly relevant in Mediterranean saproxylic assemblages, where different trophic guilds are not affected equally by woodland type. Secondly, do microenvironmental factors determine tree hollow guild distribution? We hypothesised that guilds were dependent on different microenvironmental variables and that consequently some kinds of tree hollows would also benefit different trophic guilds.

Methods

Study area

This study took place in the Cabañeros National Park (Spain), a large natural area of 40,856 ha constituted by Mediterranean ecosystems, where various woodland types are located inside a predominantly grassland and scrubland matrix (Vaquero de la Cruz, 1997). We selected three of the most representative Mediterranean woodlands of the Park for our study: a sclerophyllous woodland of holm-oak *Quercus rotundifolia* Lam. (N39 26.758 W4 31.865), where altitude ranged between 665 and 689 m; one riparian woodland of narrow-leafed ash *Fraxinus angustifolia* Vahl. (N39 26.839 W4 33.822), with altitude ranging between 574 and 506 m; and finally, one mixed acidophilus deciduous woodland of Pyrenean oak *Quercus pyrenaica* Willd. and the native oak *Quercus faginea* Lam. (N39 21.336 W4 23.697), where altitude ranged between 747 and 771 m.

Cabañeros National Park is a fairly recently protected area (since 1995) with ancient management history over hundreds of years, and where different tree species have received different traditional uses (Figure 1). The selected sclerophyllous oak woodland is located in a buffer area of the park, where lateral branch clear-cuttings are still allowed for collecting firewood, constituting an evergreen but moderately open stand with trees that mainly house rounded tree hollows with small openings. Although no management activity is currently permitted in the riparian ash woodland, main axis cuttings at the first crosstree occurred until 1995, which has derived in trees with large diameters, fine branches and many hollows in upper parts that extend from the top to the base of the trunk. Finally, only collection of naturally produced firewood took place in the deciduous oak woodland before 1995 and nowadays, all anthropogenic activities are forbidden, so that this constitutes the most natural woodland. Therefore, historical woodland management/tree species may determine differences in microhabitat configuration in different woodland types.

Figure 1. Woodland types: DO: deciduous oak, RA: riparian ash, SO: sclerophyllous oak. Picture authorship: E. Micó.

Selection of tree hollows took place taking hollow availability for each woodland type into account, and a reasonable number of tree hollows were chosen, given that the study was to take place in a protected area. This choice was intended to represent the real variability and abundance of microhabitats in each woodland type, and finally, 30 tree hollows in the sclerophyllous oak and in the deciduous oak woodland were selected, as well as 27 in the riparian ash woodland.

Sampling method

We used emergence traps: covered and sealed the tree hollows with black acrylic mesh and attached a collecting pot containing ethylene glycol to the exterior of the mesh (Quinto et al. ‘unpub. res.’). This passive method allowed saproxylic species to be recorded shortly after their emergence from immature stages, and has been used effectively to characterise whole saproxylic beetle communities (Quinto et al. ‘unpub. res.’), as well as particular beetle species linked to tree hollows (Gouix and Brustel, 2011). Pots were replaced every month for a year (February 2009 - March 2010).

Study groups and classification into trophic guilds

We surveyed the saproxylic Syrphidae (Diptera) and 42 Coleoptera families, and external taxonomists collaborated in the identification of species and immature stages (see Acknowledgments). We only considered Syrphidae from the Diptera for the following reasons: i) they use a wide range of woody microhabitats (Speight et al.

2010) and present high numbers of saproxylic species in Europe (Thompson and Rotheray, 1998), and ii) they represent the best studied family of Diptera in Cabañeros National Park (Ricarte and Marcos-García, 2008; Ricarte et al. 2009; Marcos-García et al. 2010; Quinto et al. 2012), with high numbers and abundance of mainly exclusive saproxylic species, highly associated with tree hollow microhabitats (Speight et al. 2010).

Each species was classified into trophic guilds according to biological/ecological information in the available bibliography, the 'Frisbee' data base (Bouget et al. 2008) and information from taxonomists (pers. com.). We considered the classification of five trophic guilds described by Bouget et al. (2005) and Speight (1989): xylophagous (X), saproxylophagous (SX), xylomycetophagous (XM), predators (P) and commensals (C). Saproxylophagous beetles mainly benefit from woody substrates such as wood or litter in their early decaying stages (Micó et al. 2011; Stokland et al. 2012). Syrphidae was considered separately from saproxylophagous guilds; its saproxylic species are aquatic or semi-aquatic, only suited to processing liquids, and clearly exploit different breeding sites in tree hollows, such as soft decayed heartwood, tree exudates, or water bodies with many types of compost wherever rich organic mud has accumulated (Rotheray and Gilbert, 2011). For this reason, Syrphidae constituted an independent guild called saprophagous (S).

Microenvironmental variables

We assessed a diverse range of qualitative and quantitative ecological and biological variables able to model saproxylic communities at microhabitat scale, following the bibliography and our empirical knowledge on Mediterranean woodlands. The variables evaluated were:

- Tree diameter (*Diam*): quantitative ecological. Tree diameter is one of the most reported variables that affect saproxylic species diversity in many woodland types with different woodland management (Økland et al. 1996; Grove 2002; Ranius, 2002a; Sirami et al. 2008) and is even related to the presence of certain beetle (Buse et al. 2008) or hoverfly species (Rotheray and MacGowan, 2000). We measured the tree perimeter at 0.30 and 1.30 cm, and applied the equation $diam = \frac{P}{\pi}$ (cm), where P is the mean perimeter of the two considered heights.
- Hollow volume (*Volth*): quantitative ecological. It is expected that large hollows can house greater heterogeneity of microsites and/or diversity and amount of trophic resources required by each (Marcos-García et al. 2010; Micó et al. 2011; Quinto et al. 2012). We homogenised the volume of each hollow as a cylinder with a circular base, and then $Volth = \pi r^2 h$ (cm^3), where r is the radius at hollow opening level (the unique measurable radius in many cases) and h the total height of the tree hollow.
- Wood mould volume inside the hollow (*Volom*): quantitative ecological. Wood mould is the principal substrate in tree hollows, whose quality mainly depends on the type of fungal decomposition process and what kind of microclimatic conditions prevail, determining a rich wood mould fauna that is taxonomically very diverse (Stokland et al. 2012). High amounts of wood mould are related to higher frequency of wood mould fauna (Ranius and Nilsson, 1997). We estimated the volume of

organic matter contained in each hollow when we installed traps. We considered the volume of organic matter as a semi-sphere, and then $Volom = \frac{2}{3}\pi r^3$ (cm^3), where r is the radius of the upper level of organic matter.

- Height hollow-ground (*Height*): quantitative ecological. Height (cm) was measured from the lower hollow opening point to the ground. There are some studies that have addressed vertical stratification of saproxylic beetles (Ranius, 2002a; Gibb et al. 2006; Hjältén et al. 2007; Ulyshen and Hanula, 2007; Vodka et al. 2009) and hoverfly species (Birtele and Hardersen, 2012) in temperate woodlands, and generally, it has been found that the adult fauna of the canopy is distinct from that from the understory. Nevertheless, few studies have focused on vertical aspects in the selection of breeding substrates in tree hollows (Ranius and Nilsson, 1997; Ranius, 2002a), or the distribution of the immature stages of different species.
- Hollow opening area (*Area*): quantitative ecological. This value was calculated considering the opening area as an ellipse, with $Area = \pi ab$ (cm^2), where a and b are one-half of the ellipse's major and minor axes respectively (height and width of the hollow opening or vice versa). Hollows with small openings can buffer relative humidity and temperature better (personal measurements with data loggers located outside and inside tree hollows), perhaps determining differences in the saproxylic assemblage.
- Hollow orientation (*Orient*): qualitative ecological. Sun-exposure conditions favour the presence of saproxylic beetle species

specifically linked to open or shaded substrates (Kappes and Topp, 2004; Lindhe et al. 2005; Sverdrup-Thygeson and Birkemoe, 2009), even determining different species assemblages (Hjältén et al. 2007). It is known that in temperate forests the abundance of hollow specialist species is higher in hollows with openings facing the sun (Ranius and Nilsson, 1997). As the Mediterranean climate has long periods of droughts, it is expected that hollow orientation also has a determining effect on the structure of Mediterranean saproxylic assemblages. We measured the orientation of each tree hollow using an orienteering compass, and considered the eight cardinal and intermediate directions (from north to northwest) and a ninth factor of variation reflecting horizontal hollows (with no orientation).

- Accumulated water (*Water*): qualitative ecological. Water-filled tree hollows are important aquatic environments for insects reported from most parts of the world (Kitching, 2000). The internal hollow shape determines the accumulation of variable water volumes and their permanence in time. This favours the appearance of the immature stages of strictly aquatic saproxylic beetles and flies, strongly linked to different water environments occurring in different tree hollows, such as the beetle *Prionocyphon serricornis,* which is linked to large and deep hollows with high leaf litter content, or the hoverfly *Myathropa florea,* linked to shallow open hollows with low litter content (Schmidl et al. 2008). We searched for the presence or not of accumulated water in each selected tree hollow.

- Beetle gallery presence (*Scolyt*): qualitative biological. We observed that many tree hollows either had high numbers of beetle galleries, or none at all, especially those produced by scolytids. Scolytid species present necessary ectosymbiotic connections with the specific ambrosia fungi group, which is highly sensitive to drought. They only develop in moist living wood and fresh timber, which is only located in colonised galleries or the body of xylobiont (Krivosheina, 1991). Moreover, many Curculionidae Scolytinae species and their associated fauna are naturally attracted to volatiles emitted by stressed, dead or dying host trees in high densities (Schlyter, 2007). In adition, several saproxylic species are associated to different insect workings (from scolytids or other insect groups), such as several hoverfly species (Reemer, 2005; Speight et al. 2010). As fungi colonisation of new dying tree species occurs fairly quickly (Krivosheina, 1991), the presence of many scolytid galleries may be an indicator of a different fauna favoured by woody substrates derived from the action of ambrosia fungi. We recorded the number of hollows that had or did not have these galleries in each selected tree hollow.
- Cetoniidae faeces presence *(Ceton*): qualitative biological. The presence of high amounts of cetonid faeces inside tree hollows has commonly been observed in Mediterranean woodlands (Micó et al. 2011). The action of cetonid larvae on woody substrates produces a richer substrate that is easier to assimilate, which determines high saproxylic insect diversity (Ranius, 2002b; Jönsson et al. 2004; Micó et al. 2011, Sánchez-Galván et al.

‘unpub. res.’). We recorded the number of hollows that presented cetonid faeces for each woodland type.

- Presence or activity of vertebrates (*Verteb*): qualitative biological. Many vertebrate groups create or use tree hollows to nest and constitute an important 'microhabitat group' for many beetle species (Gärdenfors, 2000; Ranius and Jansson, 2002). On the contrary, vertebrate presence/activity can also act decreasing the frequency of some key species (e.g. the ecosystem engineer *Osmoderma eremita* in Ranius and Nilsson, 1997). Before trap installation, we recorded tree hollows that presented vertebrate activity (hairs, feathers, nests, etc.) in each woodland type.

The variation of these parameters in each woodland type is reflected in Table 1.

Table 1. Variation of tree hollow microenvironmental variables per woodland type. Mean number and standard error for each quantitative ecological variable is provided. For qualitative biological variables we show the number and percentage of tree hollows in which they were present. DO: deciduous oak woodland, RA: riparian ash woodland, SO: sclerophyllous oak woodland. *Volth and Volom values are transformed to m^3 **Area values to m^2. ***Orientation types, corresponding with 1: north, 2: northeast, 3: east, 4: southeast, 5: south, 6: southwest, 7: west, 8: northwest, and 9: horizontal tree hollow.

		DO	RA	SO
Diam (cm)	Mean ± SE	66.37 ± 2.34	69 ± 2.61	49.35 ± 1.58
Volth (m^3)*	Mean ± SE	0.207 ± 0.027	0.228 ± 0.034	0.072 ± 0.011
Volom (m^3)*	Mean ± SE	0.085 ± 0.009	0.096 ± 0.010	0.034 ± 0.004
Height (cm)	Mean ± SE	120 ± 21.36	149 ± 13.36	138.5 ± 11.63
Area (m^2)**	Mean ± SE	0.106 ± 0.023	0.100 ± 0.019	0.030 ± 0.004
Orient	Types***	1 (23.3%), 4 (23.3%), 7 (13.33%), 9 (13.33%)	3 (25.93%), 5 (25.93%), 6 (11.11%), 9 (11.11%)	4 (23.33%), 3 (16.67%) 1 (13.33%), 6 (13.33%), 8 (13.33%)
Scolyt	n (%)	9 (30)	14 (51.85)	2 (6.67)
Ceton	n (%)	8 (26.67)	14 (51.85)	4 (13.33)
Water	n (%)	10 (33.33)	4 (14.85)	21 (70)
Verteb	n (%)	2 (66.67)	5 (18.52)	1 (3.33)

Data analysis

To evaluate intrinsic differences in tree hollow parameters among the selected woodlands, the variation of quantitative variables and total saproxylic species richness and abundance were tested with one-way ANOVA with Bonferroni post hoc tests, using Statistica 8.0 (StatSoft, 2007).

The completeness of guilds in each woodland type was obtained by using ACE and Chao1 estimators, using EstimateS 8.0 (Colwell, 2005). Rarefaction curves for guild richness with 95% confidence intervals were created for each guild. Minimum abundance value was considered as standard sampling size, using Species Diversity and Richness 3.02 software (Henderson and Seaby, 2002). The number of effective species for guild diversity was calculated using the formula for true diversity order 1 (Jost, 2006), which equals the exponential of the Shannon entropy index:

$$^{1}D = \exp - \left(\sum_{i=1}^{S} p_i \ln p_i \right)$$

where ^{1}D is diversity of order 1, p_i is the proportional abundance of the i species in the community, and S is species richness. This measure of diversity weights each species exactly according to its frequency in the community (without favouring rare or common species). Diversity was estimated using the Chao and Shen estimator (Chao and Shen, 2003), with the program SPADE (Chao and Shen, 2010). To evaluate differences in species composition among woodlands, we calculated the incidence-based Sorensen similarity index for each saproxylic guild, and ANOSIM similarity analysis was performed to test the significance of these differences using Primer v.6 software (Clarke and Gorley, 2006).

Canonical correspondence analysis (CCA) was used to examine relationships between species richness and abundance of guilds and environmental variables using Canoco, version 4.5 (ter Braak and Šmilauer, 2002). We used the option for downweighting rare species and Hill's scaling. Global permutation tests (carried out by Monte Carlo permutation tests with 199 permutations under the full model) were performed to judge the statistical significance of the relationship between guilds and microenvironmental variables.

Linear multiple regression (Kleinbaum et al. 1998) was also used to analyse the relationship between guild species richness, abundance and explanatory variables. We checked for normality of the variables by means of a Kolmogorov-Smirnov test. Data were logarithmically transformed (ln) only for overall data that did not pass normality in each guild. Our main objective was to identify the subset of explanatory variables that accounted for a biologically important proportion of variation in guild abundance parameters. Explanatory variables were found to be statistically significant for explaining the variation in a specific Y variable when $P<0.05$. The residuals of the final models obtained with linear multiple regressions revealed no obvious suggestions of non-normality or colinearity (Kleinbaum et al. 1998). Statistical analysis was performed using SigmaStat, version 3.5 (Systat software, 2006).

Results

Saproxylic guild characterisation

We identified 152 species and 3877 individuals belonging to Coleoptera and 23 species and 464 individuals belonging to Syrphidae (Diptera) (Table 2). Saproxylic guilds were composed of xylophagous: 21 species and 1030 individuals; saproxylophagous: 24 species and 724 individuals; saprophagous: 23 species and 464 individuals; xylomycetophagous: 40 species and 863 individuals; predators: 39 species and 611 individuals; and commensals: 28 species and 649 individuals. The classification of each species into guilds can also be seen in Table 2.

Differences among woodland types

We found statistical differences in all tree hollow quantitative variables among woodland types (*Diam*: F = 23.87, df = 2, $p < 0.005$; *Volth*: F = 11.65, df = 2, $p < 0.005$; *Volmo*: F = 17.81, df = 2, $p < 0.005$; *Area*: F = 6.14, df = 2, $p < 0.005$). The deciduous oak and riparian ash woodlands were similar in *Diam*, *Volth*, *Volmo* and *Area*, whereas the sclerophyllous oak woodland presented significantly lower values ($p < 0.05$ in all cases). *Height* was the unique parameter that did not present differences among woodland types (F = 0.778, df = 2, p = 0.463).

We also found statistical differences in total saproxylic richness (F = 14.16, df = 2, $p < 0.005$) and abundance (F = 14.84, df = 2, $p < 0.005$) among woodland types. As for species richness, deciduous oak woodland presented significantly higher species richness than riparian ash (p =

0.017) and sclerophyllous oak woodlands ($p < 0.005$), whereas riparian ash and sclerophyllous oak woodlands were similar ($p = 0.066$). The same pattern was seen in species abundance, where deciduous oak woodland presented significantly higher species abundance than riparian ash ($p = 0.014$) and sclerophyllous oak woodlands ($p < 0.005$), and the riparian ash and sclerophyllous oak woodlands were again similar ($p = 0.059$).

Guild ecological diversity and composition among woodland types

Richness estimators showed completeness to be higher than 60% for almost all guilds and woodland types (Table 3). Only the X guild in the sclerophyllous oak woodland obtained lower completeness for both ACE and Chao 1. Broadly speaking, saproxylic guilds were better represented in the deciduous oak woodland.

Table 2. Species list, guild classification and abundance among woodland types.

Family	Species	Guild	D	R	S	Total
DIPTERA						
Syrphidae	*Brachyopa grunewaldensis*	SA	8	1	0	9
	Brachyopa insensilis	SA	1	1	0	2
	Brachypalpoides lentus	SA	2	0	0	2
	Brachypalpus valgus	SA	2	2	0	4
	Callicera aurata	SA	2	0	0	2
	Callicera spinolae	SA	3	10	17	30
	Ceriana vespiformis	SA	0	8	1	9
	Criorhina floccosa	SA	8	0	0	8
	Criorhina pachymera	SA	2	1	1	4
	Ferdinandea aurea	SA	24	0	0	24
	Ferdinandea cuprea	SA	3	0	0	3
	Ferdinandea fumipennis	SA	1	0	0	1
	Ferdinandea ruficornis	SA	6	0	0	6
	Mallota cimbiciformis	SA	17	3	13	33
	Mallota dusmeti	SA	18	2	77	97
	Mallota fuciformis	SA	2	0	1	3
	Milesia crabroniformis	SA	0	1	0	1

	Myathropa florea	SA	46	129	29	204
	Myolepta difformis	SA	4	3	3	10
	Myolepta dubia	SA	1	0	0	1
	Myolepta obscura	SA	4	0	0	4
	Sphiximorpha subsessilis	SA	0	1	0	1
	Spilomyia digitata	SA	3	1	2	6
COLEOPTERA						
Aderidae	*Aderus populneus*	X	26	9	4	39
	Cnopus minor	X	0	0	1	1
	Otolelus neglectus	X	0	46	1	47
Anobiidae	*Dorcatoma vaulogeri agenjoi*	XM	8	3	6	17
	Oligomerus brunneus	X	20	2	0	22
	Rhamna semen	XM	13	3	11	27
	Stagetus elongatus	XM	1	6	1	8
	Stagetus micoae	XM	0	2	0	2
Biphyllidae	*Diplocoelus fagi*	XM	8	19	6	33
Buprestidae	*Acmaeodera degener*	X	0	0	2	2
	Eurythyrea quercus	X	1	0	0	1
Cerambycidae	*Alocerus moesiacus*	X	2	0	13	15
	Cerambyx welensii	X	3	0	0	3
	Prinobius myardi	X	0	11	1	12

	Stictoleptura trisignata	X	20	1	17	38
	Trichoferus fasciculatus	X	1	0	0	1
Cerylonidae	*Cerylon histeroides*	XM	1	0	0	1
Cetoniidae	*Cetonia aurataeformis*	SX	144	78	22	244
	Potosia cuprea	SX	6	11	17	34
	Potosia opaca	SX	1	6	7	14
Ciidae	*Cis striatulus*	XM	0	0	1	1
	Cis villosulus	XM	0	1	0	1
Clambidae	*Calyptomerus* sp	XM	0	1	0	1
	Clambus sp	XM	0	0	4	4
Cleridae	*Opilo domesticus*	P	1	1	5	7
Cryptophagidae	*Atomaria pusilla*	XM	1	1	0	2
	Cryptophagus aurelioi	SX	14	4	3	21
	Cryptophagus cylindrellus	SX	4	0	0	4
	Cryptophagus dentatus	SX	11	10	2	23
	Cryptophagus distinguendus	SX	0	1	1	2
	Cryptophagus fallax	SX	1	0	0	1
	Cryptophagus micaceus	P	73	54	15	142
	Cryptophagus punctipennis	X	22	18	14	54
	Cryptophagus reflexus	X	96	70	103	269
	Cryptophagus saginatus	XM	24	2	10	36

	Cryptophagus scanicus	XM	88	14	17	119
Curculionidae	*Camptorhinus simplex*	SX	2	0	0	2
	Camptorhinus statua	SX	89	3	11	103
	Gasterocercus hispanicus	XM	2	0	0	2
Curculionidae Scolytinae	*Xyleborinus saxesenii*	XM	11	20	6	37
	Xyleborus dryographus	XM	6	3	0	9
	Xyleborus monographus	XM	165	74	82	321
Dasytidae	*Aplocnemus brevis*	P	0	0	1	1
	Aplocnemus consobrinus	P	0	1	0	1
	Aplocnemus limbipennis	P	0	1	0	1
	Mauroania bourgeoisi	P	1	1	1	3
Dermestidae	*Anthrenus angustefasciatus*	C	0	2	1	3
	Anthrenus festivus	C	1	7	0	8
	Anthrenus minutus	C	0	39	1	40
	Anthrenus verbasci	C	0	3	2	5
	Attagenus incognitus	C	1	0	4	5
	Attagenus schaefferi	C	1	0	0	1
	Attagenus trifasciatus	C	1	13	3	17
	Dermestes bicolor	C	1	0	0	1
	Dermestes erichsonii	C	1	0	0	1
	Dermestes frischii	C	0	0	1	1

	Dermestes hispanicus	C	0	0	4	4
	Dermestes undulatus	C	5	0	17	22
	Orphilus niger	C	2	0	0	2
Dynastidae	*Oryctes nasicornis*	SX	7	0	0	7
Elateridae	*Ampedus aurilegulus*	P	28	35	0	63
	Ectamenogonus montandoni	P	2	5	0	7
	Elater ferrugineus	P	25	8	0	33
	Elathous platiai	P	0	0	1	1
	Ischnodes sanguinicollis	P	21	13	1	35
	Lacon punctatus	P	4	7	0	11
	Limoniscus violaceus	SX	0	2	0	2
	Megapenthes lugens	P	15	8	1	24
	Procraerus tibilais	P	2	10	3	15
Endomychidae	*Mycetaea hirta*	XM	2	2	3	7
	Symbiotes gibberosus	XM	2	2	2	6
Eucinetidae	*Nycteus meridionalis*	XM	1	0	0	1
Helodidae	*Prionocyphon serricornis*	C	122	58	23	203
Histeridae	*Abraeus perpusillus*	P	24	8	0	32
	Aeletes atomarius	P	0	6	0	6
	Atholus duodecimstriatus	P	0	1	0	1
	Gnathoncus communis	P	34	13	0	47

	Gnathoncus nannetensis	P	10	4	0	14
	Hetaerius ferrugineus	P	1	0	0	1
	Margarinotus brunneus	P	1	0	0	1
	Margarinotus merdarius	P	12	2	8	22
	Margarinotus uncostriatus	P	2	0	0	2
	Merohister ariasi	P	2	1	11	14
	Paromalus flavicornis	P	23	4	1	28
	Platylomalus complanatus	P	0	1	0	1
	Platylomalus gardineri	P	1	0	0	1
	Platysoma filiforme	P	1	1	0	2
Laemophloeidae	*Cryptolestes ferrugineus*	XM	5	0	2	7
	Laemophloeus nigricollis	XM	1	1	0	2
	Placonotus testaceus	XM	1	1	0	2
Latridiidae	*Corticaria obscura*	C	2	0	0	2
	Dianerella ruficollis	XM	0	0	1	1
	Enicmus brevicornis	XM	3	1	0	4
	Enicmus rugosus	XM	4	0	0	4
	Latridius assimilis	XM	14	9	2	25
Leiodidae	*Agathidium nigriceps*	XM	1	1	0	2
Lucanidae	*Dorcus parallelepipedus*	X	34	9	0	43
Malachiidae	*Anthocomus fenestratus*	P	11	1	4	16

	Axinotarsus marginalis	P	0	0	6	6
	Hypebaeus albifrons	P	3	0	0	3
	Troglops furcatus	P	25	5	22	52
Melandryiidae	*Orchesia micans*	XM	4	2	2	8
Melyridae	*Falsomelyris granulata*	P	0	2	0	2
Mycetophagidae	*Litargus balteatus*	XM	1	0	0	1
	Litargus connexus	XM	9	2	0	11
	Mycetophagus quadriguttatus	XM	51	5	17	73
Nitidulidae	*Amphotis marginata*	C	2	0	0	2
	Carpophilus sp	C	1	0	0	1
	Epuraea fuscicollis	C	127	0	10	137
	Epuraea ocularis	C	2	0	0	2
	Soronia oblonga	C	136	3	2	141
Oedemeridae	*Ischnomera xanthoderes*	X	49	24	41	114
Platypodidae	*Platypus cylindrus*	X	0	0	1	1
Pselaphidae	*Euplectus* sp	C	0	1	0	1
	Geopsephalus sp	C	0	1	0	1
	sp1 (Goniaceritae tribe)	P	0	1	0	1
Ptiliidae	sp2	XM	36	10	0	46
Ptinidae	*Dignomus irroratus*	SX	3	1	0	4
	Ptinus bidens	SX	10	2	1	13

	Ptinus hirticornis	SX	1	1	1	3
	Ptinus spitzyi	SX	1	0	0	1
	Ptinus timidus	X	174	91	9	274
Rhizophagidae	*Rhizophagus unicolor*	P	1	0	0	1
Scraptiidae	*Anaspis regimbarti*	X	10	1	0	11
	Pentaria defarguesi	X	0	1	0	1
	Scraptia ophthalmica	X	0	2	0	2
	Scraptia testacea	X	25	41	14	80
Scydmaenidae	*Cephenium* sp	C	0	1	0	1
	Palaeostigus palpalis	C	3	1	1	5
	Scydmaenus cornutus	C	2	1	0	3
	Stenichnus godarti	C	0	5	0	5
Silvanidae	*Ahasverus advena*	XM	1	1	0	2
	Airaphilus sp	XM	1	0	0	1
	Oryzaephilus surinamensis	XM	0	0	1	1
	Silvanus bidentatus	XM	0	2	0	2
	Uleiota planata	XM	5	2	0	7
Tenebrionidae	*Corticeus fasciatus*	C	1	0	0	1
	Eledonoprius armatus	XM	7	0	0	7
	Isomira hispanica	SX	0	1	10	11
	Mycetochara linearis	SX	4	16	0	20

	Mycetochara quadrimaculata	SX	21	43	46	110
	Prionychus fairmairei	SX	8	9	0	17
	Probaticus anthracinus	SX	34	4	2	40
	Probaticus granulatus	SX	0	0	1	1
	Pseudocistela ceramboides	SX	36	7	0	43
	Stenohelops sublinearis	SX	3	1	0	4
	Tenebrio sp	C	29	4	1	34
Trogossitidae	*Tenebroides marrocanus*	P	0	1	2	3
	Temnochila caerulea	P	0	1	2	3
Zopheridae	*Colobicus hirtus*	P	1	1	0	2
	Colydium elongatum	P	5	1	0	6
	Endophloeus marcovichianus	XM	22	0	0	22
TOTAL			2308	1216	817	4341

Guilds	F	R^2	P	Model
X richness	4.23	0.4	<0.001	1.42 +0.00Volth
X abundance	4.95	0.4	<0.001	1.12 -2.15Diam +0.93Volth
SX richness	6.67	0.4	<0.001	1.13 +0.00Volth
SX abundance	5.57	0.4	<0.001	-0.33 +0.61Volth -0.21Height
XM richness	9.39	0.6	<0.001	4.05 +0.00Volth +0.00Area
XM abundance	17.9	0.2	<0.001	-0.05 +0.34Area
P richness	7.37	0.5	<0.001	0.55 +0.00Volth -1.13Ceton -1.42Water
P abundance	2.36	0.3	0.002	-0.72 +0.44Volth -0.62Ceton
C abundance	6.65	0.2	0.003	-0.68 +0.35Scolyt

Table 3. Richness estimators values for each saproxylic guild per woodland type. DO: deciduous oak woodland, RA: riparian ash woodland, SO: sclerophyllous oak woodland. X: xylophagous, SX: saproxylophagous, SA: saprophagous, XM: xylomycetophagous, P: predators, C: commensals. *Guilds with completeness lower than 60%.

Xylophagous

When we standardised at the minimum abundance value (221 individuals), the three woodlands types presented similar xylophagous species richness (Figure 2a). The Chao and Shen estimator showed differences in the number of effective species among woodland types. The deciduous oak and riparian ash woodlands presented similar effective xylophagous species (7.38 ± 0.33, CI: 6.74, 8.03, and 7.66 ± 0.38, CI: 6.92, 8.39, respectively), whereas sclerophyllous oak woodland had lower xylophagous diversity (5.92 ± 0.52, CI: 4.89, 6.94). No significant differences in guild composition among woodland types were found (R =

0.018, p = 0.235), although the similarity percentage varied among woodland types: deciduous oak and riparian ash woodland (71.43%), riparian ash-sclerophyllous oak (66.67%) and deciduous oak-sclerophyllous oak (59.26%).

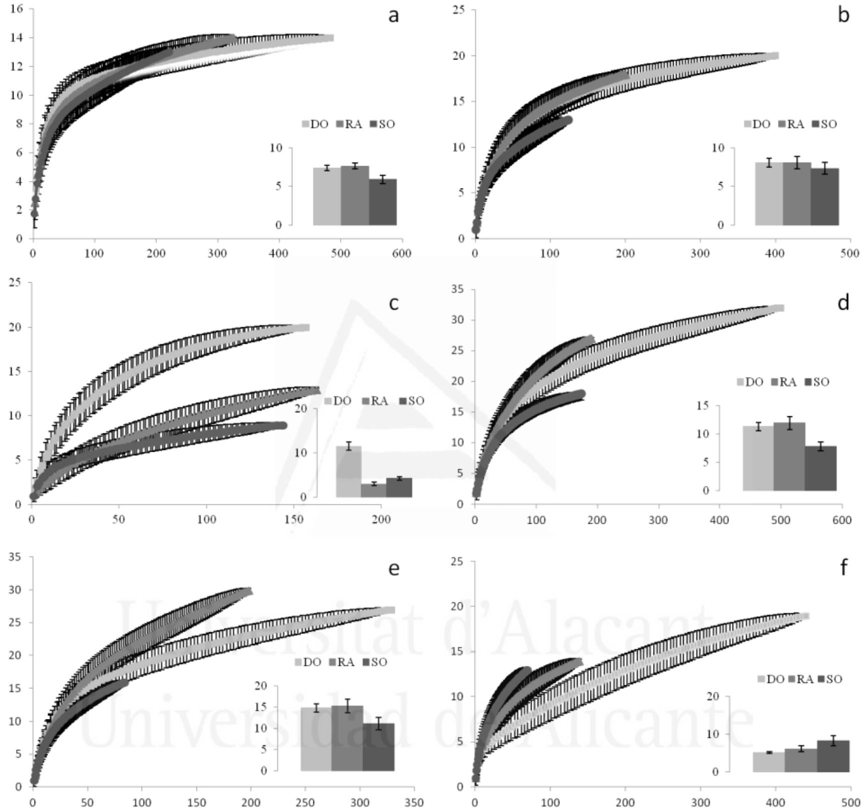

Figure 2. Rarefaction curves for guild richness and ecological guild diversity. a: xylophagous; b: saproxylophagous; c: saprophagous; d: xylomycetophagous; e: predators; f: commensals.

Saproxylophagous

At the minimum abundance value (124 individuals), the deciduous oak and riparian ash woodlands were similar in saproxylophagous species richness, and both were significantly different from the sclerophyllous oak woodland (Figure 2b). The Chao and Shen estimator did not show differences in the effective number of saproxylophagous species among woodland types (deciduous oak: 8.09 ± 0.56, CI: 6.98, 9.19; riparian ash: 8.08 ± 0.79, CI: 6.54, 9.62; sclerophyllous oak: 7.35 ± 0.77, CI: 5.85, 8.86). Although there were no significant differences in the saproxylophagous species composition among woodlands (R = 0.032, p = 0.184), the similarity percentage varied among woodland pairs: deciduous oak-riparian ash 78.95%, deciduous oak-sclerophyllous oak 60.61%, and riparian ash-sclerophyllous oak 77.42%.

Saprophagous

The three woodland types presented significantly different saprophagous species richness at the minimum abundance value (144 individuals). Deciduous oak woodland presented higher numbers of species, in a decreasing order, followed by riparian ash and sclerophyllous oak woodlands (Figure 2c). The Chao and Shen estimator revealed clear differences in the effective number of saprophagous species among the three woodland types. Deciduous oak was the woodland that presented higher effective species (11.51 ± 0.96, CI: 9.62, 13.40), followed by sclerophyllous oak (4.21 ± 0.41, CI: 3.41, 5.01), and riparian ash (2.96 ± 0.40, CI: 2.18, 3.75). Regarding saprophagous species composition, all three woodland types were similar (R = 0.039, p = 0.106) (deciduous oak-riparian ash: 60.61%, deciduous oak-sclerophyllous oak: 55.17%, riparian ash-sclerophyllous oak: 72.73%).

Xylomycetophagous

At the standardised value (174 individuals), all three woodland types presented significantly different xylomycetophagous species richness. Riparian ash was the woodland that was richest in xylomycetophagous species, followed by deciduous oak and sclerophyllous oak in decreasing order (Figure 2d). The Chao and Shen estimator did not show differences in effective xylomycetophagous species between deciduous oak (11.33 ± 0.77, CI: 9.82, 12.85) and riparian ash woodlands (11.97 ± 1.18, CI: 9.67, 14.28), whereas sclerophyllous oak woodland presented the lowest number of effective species of xylomycetophagous (7.87 ± 0.79, CI: 6.32, 9.42). The ANOSIM showed statistical differences in species composition among woodland types (R = 0.112, p = 0.014), with deciduous oak-riparian ash as the most similar woodlands (77.97%), followed distantly by both deciduous oak-sclerophyllous oak and riparian ash-sclerophyllous oak (56% and 57.78%, respectively).

Predators

At the minimum abundance value (84 individuals), statistical differences in predator species richness between riparian ash and sclerophyllous oak woodlands were found, whereas deciduous oak-riparian ash and deciduous oak-sclerophyllous oak were similar (Figure 2e). No differences in the effective number of predator species were found between deciduous oak and riparian ash woodlands (14.83 ± 0.95, CI: 12.96, 16.69 and 15.30 ± 1.56, CI: 12.25, 18.36, respectively), and sclerophyllous oak woodland presented the lowest diversity of predator species (11.10 ± 1.48, CI: 8.20, 14.00). The predator species composition was significantly different among woodland types (R = 0.088, p = 0.015), deciduous oak-riparian ash were the most similar woodlands (73.68%), followed by riparian ash-sclerophyllous oak woodlands (56.52%) and deciduous oak-sclerophyllous oak woodlands (51.16%).

Commensals

The three woodland types presented significantly different commensal species richness at minimum abundance value (70 individuals) (Figure 2f). Sclerophyllous oak woodland presented higher effective species of commensals (8.33 ± 1.31, CI: 5.76, 10.91) than the riparian ash (6.18 ± 0.77, CI: 4.67, 7.68) and deciduous oak woodlands (5.21 ± 0.28, CI: 4.66, 5.76). The ANOSIM showed strong differences in the commensal species composition among woodland types (R = 0.168, p = 0.001), with riparian ash-sclerophyllous oak being the most similar woodlands (59.26%), followed by deciduous oak-sclerophyllous oak (50%), whereas deciduous oak-riparian ash were the least similar woodlands (42.42%).

Influence of microenvironmental variables on guild distribution

The assessed microenvironmental variables explained up to 75% of the cumulative percentage of variance for guild richness (Monte Carlo test, eigenvalues = 0.065, F-ratio = 1.48, p-value = 0.014) and 70.6% for guild abundance (Monte Carlo test, eigenvalues = 0.296, F-ratio = 3.01, p-value = 0.002) (Figure 3). As regards guild richness, the xylomycetophagous guild was associated with *Area*, the saprophagous guild with *Water* and *Orient*, the saproxylophagous guild with *Volth* and *Ceton*, and the xylophagous, commensal and predator guilds with *Height* and *Ceton*. For guild abundance, the xylomycetophagous guild was associated with *Area*, the saprophagous guild with *Water*, the saproxylophagous and predator guilds with *Ceton* and *Volth*, the xylophagous guild with *Scolyt* and *Area*, and the commensal guild with *Orient* and *Height*.

We found a significant and positive relationship between overall guild species richness and abundance and the *Volth* variable, except for saprophagous richness and abundance, and commensal richness. Other important variables for each dependent variable are presented in Table 4. The main patterns were as follows, for xylophagous abundance, *Diam*, *Height* and *Area* have a negative relationship with this dependent variable. For saproxylophagous abundance, *Height* was of negative importance in the model. For xylomycetophagous richness and abundance, another significant variable was *Area* in a positive relationship. In predator richness, *Ceton* and *Water* were important variables too but with a negative relationship, and in predator abundance *Ceton* also had a relationship in a negative form. Finally, commensal guild abundance presented a negative relationship with the

Scolyt variable. No significant models were found for saprophagous data (richness and abundance) or for commensal richness.

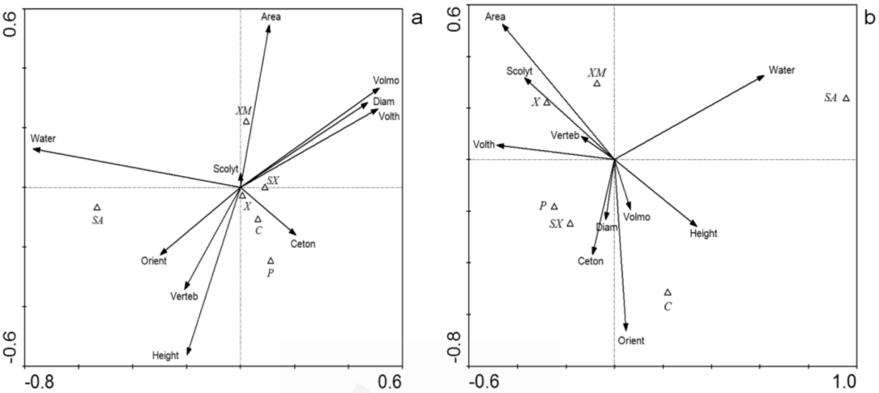

Figure 3. CCA analysis for total guild richness (a), and total guild abundance (b).

Discussion

Tree hollow guild diversity among woodland types

We demonstrated that all the saproxylic guilds linked to hollows were generally better represented in species richness and diversity in the deciduous oak and riparian ash woodlands (except for the commensal guild), and that they were also the most similar in species composition (even when no significant differences were found), and corresponded to historically less managed woodlands. Woodland management is a key factor for the species diversity of saproxylic insect assemblages both within (Johansson et al. 2006; Sirami et al. 2008) and among tree species (Buse et al. 2008). Different types of management cause significant differences in woodland and tree characteristics such as trunk diameter, stem density, dead wood diversity and amount, and types of tree hollows (Buse et al. 2008; Sirami et al. 2008). These differences determine substrate availability and supply of microhabitats for certain functional groups, and in general, lower richness and abundance is shown in intensively managed woodlands (Gibb et al. 2006; Sirami et al. 2008; Ulyshen and Hanula, 2009). In contrast, natural-unmanaged mature woodlands usually present higher diversity of hollow microhabitat types in living trees (Winter and Möller, 2008).

As an example, many xylomycetophagous beetles are closely associated to mature standing trees that present fruiting bodies or inconspicuous mycelia of specific saproxylic fungus species (Wallace, 1954; Jonsell et al. 2001), such as the polypore species (Kalia et al. 1994; Jonsell et al. 2001; Jonsell and Weslien, 2003). In addition, distinct beetle assemblages are associated with different polypore species (Kalia et al. 1994; Jonsell et al. 1998) or to their frequency (Økland et al. 1996; Müller et al. 2008), reaching species richness peak in unmanaged woodlands and in woodlands under low-intensity management (Müller et al. 2008). Diversity of saprophagous hoverflies also increases with substrate age (Reemer, 2005), when dead wood becomes a more rewarding food resource in the course of decomposition, as it reaches adequate values of C:N ratio and the availability of water or bark cover microsites increases (Hövemeyer and Schauermann, 2003). Our results suggest that higher guild diversity is associated with woodlands that provide higher heterogeneity of tree hollows, favouring the establishment of different fauna of each guild, which happens in the less managed woodlands (Winter and Möller, 2008, Ulyshen and Hanula, 2009).

On the contrary, the clear-cuttings determine a subsequent increase in the temperature fluctuation of a tree that is reflected in a decay progress (Wallace, 1954), and at least in temperate woodlands this has had a negative influence on species diversity (Økland et al. 1996; Kouki et al. 2001; Hjältén et al. 2007; Johansson et al. 2006), which favoured the predominance of certain species groups such as bark beetles Curculionidae Scolytinae (Jonsell and Weslien, 2003), or xylophagous larvae (Müller et al. 2008). Our results also show that in Mediterranean woodlands these practices favour other saproxylic guilds such as the Vulnerable *Mallota dusmeti* (a thermophilic Syrphidae species) (Marcos-García and Quinto, 2011) and other saprophagous hoverflies such as *M. cimbiciformis* or *Callicera spinolae*, or the whole commensal guild. The clear-cuttings of lateral branches sporadically performed in the sclerophyllous oak Mediterranean woodland could therefore be acting as a homogenising factor of guild diversity, by determining many but similar hollow microhabitats. This, in general, results in lower saproxylic guild richness by reducing microclimatic differences between the hollows and the area outside the evergreen canopy typical of this woodland type. However, the xylophagous guild diversity was similarly high in all the assessed woodland types, which indicates that they are less dependent on types of management practices (also seen in Müller et al. 2008; Vodka et al. 2009). Therefore, historical woodland management acts as a driving force for the differences in microhabitat configuration among types of Mediterranean woodlands in Cabañeros National Park, and also establishes strong differences in saproxylic guild diversity and composition.

Determining variables for saproxylic guild diversity

Generally, we found that both guild richness and abundance were related to higher hollow volumes. Higher occurrences of many taxonomic groups are associated with large hollow volumes, such as, for instance, some Cerambycidae species (Fayt et al. 2006), *Limoniscus violaceus* (Elateridae) and its co-occurring beetle species (Gouix et al. 2012), or the aquatic fauna adapted to water-filled tree hollows (Schmidl et al. 2008). Tree hollows are per se heterogeneous multi-habitats (simultaneously housing several microhabitat types) (Winter and Möller, 2008), and their hollow configuration is unique and highly complex to standardise. In fact, the use of suitable sampling methods revealed that many species that are known to depend on specific microhabitats are recorded in these multi-habitat hollows, even when no microsite evidence had been found (Quinto et al. 'unpub. res.'). Therefore, large tree hollow volumes may be related to the availability and variability of the microhabitat types they contained.

Richness and abundance of the xylophagous guild was influenced by many ecological and biological variables, which suggested the coexistence of species with notable differences in their life cycles. A high number of scolytid galleries reflected current/recent scolytid overpopulation due to their aggregation tendency (Schlyter, 2007), which results in a decrease of saproxylic diversity (Kappes and Topp, 2004). The presence of cetonid faeces could be indicating another negative effect on xylophagous richness, with a dominance of the fauna typical of more advanced decay stages linked with cetonids (Ranius and Nilsson, 1997). The tree diameter, height hollow-ground and opening area also negatively influenced xylophagous abundance, and in general the total xylophagous richness was not high in tree hollow microhabitats, which suggested higher preferences for other woodland environments (Quinto et al. 'unpub. res.').

All our results indicated that xylomycetophagous guild richness and abundance were related to large hollow openings and as we have already indicated, also to larger sized hollows. How large openings influence xylomycetophagous distribution is still poorly understood. To examine this correlation it would be appropriate to assess whether the diversity of saproxylic fungi is affected by this variable. Unfortunately, it was not possible to take any fungi variables due to limited knowledge about wood-inhabiting fungi in Mediterranean woodlands and the great complexity found in temperate woodlands (Nordén et al. 2004; Ódor et al. 2006).

Higher numbers of species and individuals of the saproxylophagous guild were associated with hollows higher from the ground and with presence of cetonid faeces. Cetonid larvae are able to digest polysaccharides and lignin, and produce large quantities of faeces that are rich in nutrients (Micó et al. 2011), which probably facilitates the establishment of other saproxylic insects (Ranius 2002b; Jönsson et al. 2004; Sánchez-Galván et al. 'unpub. res.'). Saproxylic cetonids are species that are highly dependent on tree hollows, and their frequency is higher in hollows with large quantities of wood mould (Ranius and Nilsson, 1997; Micó and Galante, 2003), which varied widely between tree hollows (Ranius, 2007). Moreover, saproxylophagous larvae were found more frequently in specific decay types. This highlights the importance of substrate quality (Saint-Germain et al. 2010). The importance of vertical stratification of saproxylophagous beetles has rarely been studied (Ranius and Nilsson, 1997; Ulyshen and Hanula, 2007), although several saproxylophagous species are significantly related to hollow openings distant from (Ranius 2002a) or near to the ground (Gouix et al. 2012).

Many saprophagous hoverflies are linked to different aquatic/humid microsites that occur in tree hollows (Rotheray and MacGowan, 2000; Fayt et al. 2006; Speight et al. 2010), often presenting different nutrient requirements (Schmidl et al. 2008; Sánchez-Galván et al. 'unpub. res.') or even vertical stratification (Birtele and Hardersen, 2012 based on adults activity). The quantity and quality of breeding microsites are relevant limiting factors for the saprophagous because there are usually few trees that are able to provide suitable habitats (as seen in Rotheray and MacGowan, 2000; Reemer, 2005). Accordingly, our results demonstrated that the saprophagous guild occupied a low proportion of tree hollows (less than 70% in all woodlands) and that hoverfly species commonly coexisted (with up to six species belonging to five different genera) in tree hollows containing water and that faced north-east to south-east (higher species abundance). Several authors have shown that numerous saproxylic assemblages are specifically adapted to exposed woody substrates (south to west) within temperate woodlands (Ranius and Nilsson, 1997; Jonsell et al. 1998; Ranius and Jansson, 2000; Kappes and Topp, 2004; Lindhe et al. 2005), even among aquatic communities of Syrphidae inhabiting water-filled tree hollows (Fayt et al. 2006; Schmidl et al. 2008). However, in Mediterranean areas, water content is one of the most important limiting factors due to the Mediterranean climate (with long periods of drought), and therefore tree hollows with a more predictable aquatic environment, less exposed and containing higher water volume, also tended to have higher saprophagous richness and abundance.

The predator and commensal guilds were negatively influenced by biological variables. These guilds are composed of species that depend on other invertebrate presence or activities (not only the concerned insect groups) as trophic resources. The incidence of hollows with 'water presence', 'cetonid faeces' or 'scolytid presence' may indicate particular hollow environments that benefit certain groups that become more abundant (Schlyter, 2007; Schmidl et al. 2008, Speight et al. 2010; Sánchez-Galván et al. 'unpub. res.'), which can lead to more homogeneous diversity of their associated fauna of predators and commensals. Nevertheless, specific research focused on their markedly different trophic requirements is necessary to understand these results better.

Transcendence for saproxylic diversity conservation

Iberian Mediterranean woodlands are characterised by a significant number of Central European and North African species (Ricarte et al. 2009), and their hollow microhabitats contain species-rich assemblages composed of high proportions of hollow specialist species (Quinto et al. 'unpub. res.'). Tree hollows can be considered to be one of the most important Mediterranean microhabitats within woodland ecosystems in terms of species diversity (Sirami et al. 2008). They act as 'isolated islands' where different colonising species of each feeding guild are the result of interacting patterns (Quinto et al. 2012), limited dispersive behaviour (Ranius and Hedin, 2001; Buse et al. 2008; Irmler et al. 2010), or as we show in this paper, availability and variability of hollow microhabitats.

Our results suggest that the type of management carried out in these Mediterranean woodlands, as well as whether this continued after

1995, when the zone was declared a National Park, have both influenced the diversity and composition of the hollow guilds to a great extent by conferring different availability of types and numbers of hollow microhabitats. Old-unmanaged woodlands with multi-habitat hollow trees reflect the ecological continuity of woodlands and hold higher saproxylic guild diversity. Nevertheless, the population of certain protected species, such as the Vulnerable hoverfly *Mallota dusmeti,* can be enhanced by continuous traditional management of trees. Therefore, tree hollow heterogeneity, within and between woodlands, is highly relevant for the conservation of saproxylic communities in the most mature Mediterranean woodlands in Cabañeros National Park (deciduous oak and riparian ash), and it provides abundant and diverse trophic resources for a long-time. For these reasons, more efforts should be directed towards ensuring not only microhabitat availability but also heterogeneity among woodlands, increasing the level of protection of mature woodlands with large hollows located within buffer areas, or considering criteria of woodland structure and microhabitat supply in future expansions of the park. This growing empirical knowledge on hollow saproxylic communities provides an integrative understanding of their local structure and dynamics.

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DISCUSIÓN GENERAL

Discusión general

El desarrollo de esta tesis ha permitido conocer qué especies de insectos - Coleoptera y Diptera: Syrphidae - componen el ensamble saproxílico ligado a las oquedades de los árboles, uno de los microhábitats más importantes en términos de biodiversidad de los bosques mediterráneos (Sirami et al. 2008). Se trata de la primera vez que se realizan estudios sistemáticos en oquedades de bosques mediterráneos de la Península Ibérica, y en particular, en el Parque Nacional de Cabañeros (España), considerando simultáneamente estos dos órdenes de insectos bioindicadores de la calidad de los bosques. Dentro de las comunidades de insectos saproxílicos encontramos una gran diversidad de especies que pueden ser agrupadas de acuerdo a regímenes tróficos o gremios ecológicos, principalmente xilófagos, saprófagos, saproxilófagos, xilomicetófagos, depredadores y comensales. Los grupos taxonómicos y ecológicos utilizados en este estudio han resultado ser muy diversos y abundantes, presentando una alta variabilidad a lo largo de las oquedades seleccionadas, lo que indica la idoneidad de este microhábitat para la evaluación patrones ecológicos y de diversidad saproxílica en bosques mediterráneos ibéricos.

Los resultados derivados de este estudio taxonómico han permitido detectar la presencia de numerosas especies de las que no se tenía constancia en el Parque Nacional de Cabañeros (en algunos casos incluso en la Península Ibérica), o evaluar el estado de las poblaciones de las distintas especies que componen la comunidad de insectos saproxílicos asociada a las oquedades. Este microhábitat presenta un alto componente de especies endémicas (en concordancia con Ricarte *et al.*, 2009) o raras dentro del contexto europeo, ya sea porque tienen baja capacidad dispersiva, o debido a que son exclusivas del microhábitat oquedad o los recursos tróficos que allí se encuentran, como es el caso de la especie *Limoniscus violaceus* (Elateridae), principalmente asociado con oquedades basales (Apéndice 3). Además, las oquedades son el abrigo de múltiples especies contempladas por la Directiva Habitat o en el Libro Rojo de Invertebrados de España (Tabla general, Apéndice 2, 3 y 4), lo que evidencia la importancia de este microhábitat para la conservación de los insectos saproxílicos en los bosques mediterráneos ibéricos, con especial énfasis en sus especies amenazadas. De igual manera, se amplía el rango de distribución de numerosas especies, en algunos casos siendo las citas más meridionales del continente europeo (Tabla general), y quedan reflejadas nuevas asociaciones de los insectos con la especie arbórea, la preferencia por las oquedades o la coexistencia entre especies (Apéndice 1 y 2).

Uno de los principales hándicaps del estudio de las comunidades de insectos saproxílicos es el bajo número de métodos de muestreo capaces de caracterizar la alta diversidad taxonómica y biológica asociada a los distintos sustratos y microhábitats presentes en los ecosistemas forestales. Los resultados obtenidos ponen de manifiesto la mayor eficacia de la trampa de emergencia para caracterizar la diversidad de especies y familias así como la diversidad funcional de gremios ecológicos saproxílicos en las oquedades, capturando una mayor proporción de especies fuertemente vinculadas a este microhábitat (capítulo 2). A lo largo de un año de estudio se registró un total de 22 especies y 464 individuos de Diptera: Syrphidae, y 150 especies y 3873 individuos pertenecientes a 41 familias de Coleoptera (Tabla general). De forma paralela, el uso de la trampa de emergencia aporta una valiosa información sobre ciclos biológicos, fenología, periodo de actividad de los adultos, comportamiento o coexistencia de especies, así como la preferencia de las especies por el microhábitat de oquedad frente al resto de sustratos/ambientes presentes en el bosque, por lo que nuestros resultados amplían en gran medida el conocimiento que se tenía para muchas especies.

Por otra parte, aunque las trampas de ventana proporcionaron una diversidad de especies y familias similar a las trampas de emergencia, la composición de especies varió en gran medida entre estos tipos de trampa. Estos resultados reflejan una mayor afinidad de la trampa de ventana para inventariar la porción del ensamble de coleópteros saproxílicos con capacidad de vuelo, y por tanto provenientes no sólo de las oquedades sino también de los distintos hábitats, sustratos o microhábitats presentes en la matriz de bosque objeto de estudio. Por estos motivos, las trampas de ventana y de emergencia son métodos altamente complementarios, y su uso combinado proporciona inventarios más completos del ensamble de coleópteros asociado a las oquedades, registrando una mayor diversidad de especies y familias saproxílicas con distintas biologías o preferencias de hábitat. Ambos métodos permiten una fácil estandarización de los protocolos de muestreo, por lo que resultan excelentes candidatos para realizar distintos tipos de estudios comparativos entre tipos de bosques mediterráneos, escogiendo qué método/s utilizar de acuerdo a la porción del ensamble saproxílico que se desea estudiar.

Aunque las trampas de tubo presentaron una baja eficiencia para el estudio de la fauna saproxílica del bosque, cabe destacar que su uso puede ser de gran utilidad cuando se realizan estudios dirigidos a familias de coleópteros tales como Bostrichiidae, Biphyllidae, Melyridae, Mycetophagidae o Curculionidae Scolytinae, ya que presentan una gran afinidad por los principios activos químicos y/o visuales que comprende este trampa: cebo, color y silueta.

Debido a que las trampas de emergencia permiten obtener un perfil certero de la diversidad saproxílica ligada a los microhábitats de oquedad, su uso permite evaluar las interacciones especie-sustrato y especie-especie. El análisis de redes ecológicas con múltiples tipos de interacción permite conocer qué patrones determinan la estructura, dinámica y estabilidad de las interacciones de una comunidad (Fontaine *et al.*, 2011). Los resultados obtenidos revelaron que la interacción oquedad-insecto saproxílico presenta un patrón modular, lo que indica la existencia de subgrupos de especies de insectos saproxílicos interactuando con subgrupos de oquedades (capítulo 3). De acuerdo con Lewinshon et al. (2006) un patrón modular puede ser el resultado de la heterogeneidad del hábitat, divergencias en los regímenes de selección, o agrupaciones filogenéticas de especies estrechamente relacionadas. En este sentido, los módulos obtenidos para la red global representan las principales agrupaciones tróficas entre especies de insectos pertenecientes a los distintos gremios ecológicos, las cuales se establecen en torno a oquedades de distinta especie arbórea o que presentan determinadas características microambientales. Sin embargo, algunos módulos resultaron muy cohesivos, lo que es indicativo de una mayor probabilidad de interacción entre sus especies-oquedades constituyentes. Otros por el contrario, presentaron una mayor variabilidad, lo que viene determinado por la existencia de una gran proporción de nodos heterogéneamente conectados con los distintos módulos. Los resultados obtenidos reflejan además agrupaciones que no son evidentes a primera vista, por lo que la realización de un estudio heurístico de los módulos permite conocer la robustez y tamaño de los principales módulos, identificar asociaciones entre módulos o detectar subgrupos cohesivos de menor tamaño (Donatti *et al.*, 2011).

De manera general, las subredes que dependen de la madera como recurso trófico presentaron una mayor diversidad de especies e interacciones, fueron menos especializadas y obtuvieron una menor competencia interespecífica que las subredes que dependen de la presencia de otros insectos saproxílicos como recurso trófico. Estas subredes se establecen de acuerdo al recurso trófico que explotan o al gremio ecológico al que pertenecen, por lo que dependen de manera distinta de la disponibilidad de microhábitats para su desarrollo biológico y para el establecimiento de la interacción, determinando notorias diferencias en sus patrones de interacción.

La naturaleza de la interacción también tiene implicaciones en la estabilidad de las subredes saproxílicas, y las subredes dependientes de la madera como recurso trófico fueron más estables frente a la extinción aleatoria y dirigida de sus microhábitats. No obstante, cabe resaltar que el conjunto de las subredes saproxílicas presentó una elevada robustez ante ambos tipos de extinciones. De acuerdo con Thébault & Fontaine (2010), la estabilidad y estructura de las redes ecológicas dependen en gran medida del tipo de interacción, de la diversidad de especies o de las diferencias en los atributos de interacción. Por tanto, la estructura de módulos interconectados encontrada en la interacción oquedad-insecto saproxílico refleja capacidad para amortiguar las perturbaciones ambientales.

La heterogeneidad de las oquedades actúa como un importante agente modelador de la riqueza de especies y diversidad funcional de los gremios saproxílicos en los bosques mediterráneos estudiados (capítulo 4). Cada oquedad es una unidad de estudio única e independiente, resultante de un proceso inicial de formación natural o artificial y de la conjunción de distintos procesos de descomposición posteriores. Por tanto, es comprensible que los bosques menos manejados (o al menos actualmente no manejados): los robledales mixtos de *Quercus pyrenaica* y *Q. faginea*, y las fresnedas de *Fraxinus angustifolia* presenten una configuración de microhábitats más heterogénea debido a que albergan una mayor variabilidad de procesos de formación y de descomposición de los que dependen las distintas especies/gremios saproxílicos, alojando así una mayor diversidad taxonómica y funcional. Por el contrario, las actividades tradicionales de manejo como las podas de ramas laterales que se practican en el encinar de *Q. rotundifolia* actúan como un factor homogeneizador de las características de las oquedades, y por ende, de la diversidad de los gremios tróficos, por lo que algunas especies/grupos se ven beneficiados por este manejo. Dada la alta variabilidad de tipos de bosque y de manejos que ocurren a lo largo de la Península Ibérica, esta tesis sienta las bases y da paso a estudios comparativos que permitan realizar asociaciones entre patrones de diversidad saproxílica y su relación con el tipo de bosque mediterráneo.

En esta misma línea, un mayor volumen de las oquedades conlleva una mayor riqueza y abundancia de los gremios saproxílicos, destacando la existencia de oquedades clave o ‘multihábitat’ donde tienen lugar múltiples recursos tróficos o micrositios (Winter & Möller, 2008) y que determinan comunidades saproxílicas más complejas. Adicionalmente, nuestros resultados muestran que los distintos gremios responden positiva o negativamente a diferentes variables ecológicas o biológicas microambientales, de acuerdo a los requerimientos particulares de las especies que albergan, existiendo por tanto un entramado de interacciones especie-oquedad y especie-especie que denotan la complejidad del ensamble entomosaproxílico. Un claro ejemplo lo constituye el gremio de los sírfidos saprófagos, quienes dependen de oquedades capaces de contener o preservar un mayor volumen de agua, donde distintas especies de sírfidos compiten por ocupar este microhábitat acuático y explotar sus recursos. Una vez identificadas las principales variables que afectan a la distribución y diversidad de los gremios saproxílicos en las oquedades del bosque mediterráneo, resultaría conveniente realizar estudios futuros pormenorizados de esas variables con la finalidad de comprender cómo afectan a la distribución de las distintas especies constituyentes de los gremios saproxílicos en el microhábitat de oquedad.

Las oquedades de los bosques mediterráneos ibéricos atesoran una diversa e interesante fauna de insectos saproxílicos, con un alto componente de especies de Coleoptera protegidas a nivel europeo (Nieto & Alexander, 2010). En concordancia con estudios realizados en el sur de Francia (Sirami *et al*., 2008), las características particulares de la oquedad son determinantes de una mayor diversidad saproxílica. Frente al resto de sustratos o microhábitats presentes en el bosque, las oquedades de gran volumen favorecen las poblaciones de la especie 'En peligro' *Limoniscus violaceus* (apéndice), o de la especie 'Vulnerable' *Ischnodes sanguinicollis* (ambas Elateridae). Además, este microhábitat es muy estable en el tiempo, no depende de la heterogeneidad de la matriz ambiental, y no sufre alteraciones cuando se practica el manejo tradicional (Sirami *et al*., 2008). Bajo este contexto, la conservación de esta comunidad y de sus especies emblemáticas en los bosques mediterráneos está en gran medida vinculada con la conservación de bosques maduros con árboles viejos y oquedades de gran tamaño, ya que a lo largo de los años proporciona diversidad y cantidad recursos tróficos. No obstante, las poblaciones de otras especies, o incluso la diversidad de gremios saproxílicos completos, pueden ser potenciadas por el manejo tradicional. Tal es el caso del díptero *Mallota dusmeti* (Syrphidae), catalogado como especie 'Vulnerable' en el Libro Rojo de los Invertebrados de España (apéndice), que obtuvo una mejor representación en el encinar de Garbanzuelo (la mayor población conocida para esta especie protegida), donde las podas generan con el tiempo numerosas oquedades que permiten la acumulación de agua y el desarrollo de las condiciones microclimáticas de las que depende esta especie para su desarrollo. Siendo así, las estrategias para conservar el ensamble saproxílico y sus especies protegidas en la Península Ibérica deben contemplar no sólo la heterogeneidad de oquedades de los bosques mediterráneos y su estrecha vinculación con los tipos de manejo tradicional, sino que también deben implementarse con determinadas medidas de manejo dirigidas a potenciar sus poblaciones o diversificar esta comunidad.

Al integrar el conjunto de resultados derivados de esta tesis es fácil apercibirse de la complejidad biológica que encierra el sistema oquedad-insecto saproxílico, suscitando asimismo nuevas preguntas a resolver, como qué ocurre con los patrones especializados en distintos tipos de bosque mediterráneo. La red saproxílica es una red compleja (alto número de especies participantes) y ecológicamente heterogénea, aspectos que favorecen la presencia de un patrón modular. Como observamos en el capítulo 3, estos módulos están formados por subgrupos de insectos que interactúan preferentemente con subgrupos de oquedades de distintas especies arbóreas o con distintas características ecológicas. Por otra parte, en el capítulo 4 hallamos grandes diferencias en la diversidad y distribución de los gremios saproxílicos de acuerdo a la configuración de oquedades por tipo de bosque. Dados estos antecedentes, cabe esperar una gran variabilidad en los patrones de redes cuando descendemos el foco de estudio a la escala de bosque. Un patrón modular es más probable en redes de mayor tamaño (Olesen *et al*., 2007), sin embargo, aun cuando una red compleja es manifiestamente modular, otros patrones especializados como el anidamiento pueden ocurrir dentro de los módulos más grandes (Lewinsohn *et al*., 2006). Por otra parte, el avance continuado de las metodologías empleadas en el análisis de redes permite realizar deducciones cada vez más precisas, siendo posible evaluar la influencia que las abundancias relativas tienen sobre los patrones de redes resultantes. Esta primera exploración de los patrones de redes ecológicos que modelan la interacción oquedad-insecto saproxílico representa el primer paso para entender cómo se organizan y relacionan los distintos tipos de interacción en el microhábitat de oquedad, siendo el siguiente paso poder responder a la pregunta: ¿Cómo se organizan los patrones de interacción cuando se evalúan por separado distintos tipos de bosque mediterráneo?

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Tabla general. Listado de Coleoptera y Diptera (Syrphidae) en las oquedades presentes en los bosques mediterráneos estudiados. Fr: *Fraxinus angustifolia*; Qf: *Quercus faginea*; Qp: *Quercus pyrenaica*; Qr: *Quercus rotundifolia*.

		Abundancia	Especie vegetal
DIPTERA			
Syrphidae	*Brachyopa grunewaldensis* Kassebeer, 2000	11	Fr, Qf, Qp
	Brachypalpoides lentus (Meigen, 1822)	2	Qf, Qp
	Brachypalpus valgus (Panzer, 1798)	4	Fr, Qp
	Callicera aurata (Rossi, 1790)	2	Qp
	Callicera spinolae Rondani, 1844	30	Fr, Qf, Qp, Qr
	Ceriana vespiformis (Latreille, 1804)	9	Fr, Qr
	Criorhina floccosa (Meigen, 1822)	8	Qf, Qp
	Criorhina pachymera Egger, 1858	4	Fr, Qf, Qp, Qr
	Ferdinandea aurea Rondani, 1844	24	Qf, Qp
	Ferdinandea cuprea (Scopoli, 1763)	3	Qp
	Ferdinandea fumipennis Kassebeer, 1999	1	Qp
	Ferdinandea ruficornis (Fabricius, 1775)	6	Qp
	Mallota cimbiciformis (Fallen, 1817)	33	Fr, Qf, Qr
	Mallota dusmeti Andréu, 1926	97	Fr, Qf, Qr
	Mallota fuciformis (Fabricius, 1794)	3	Qf, Qp, Qr
	Milesia cabroniformis (Fabricius, 1795)	1	Fr

	Myathropa florea (Linnaeus, 1758)	204	Fr, Qf, Qp, Qr
	Myolepta difformis Strobl in Czerny & Strobl, 1909	10	Fr, Qf, Qp, Qr
	Myolepta dubia (Fabricius, 1805)	1	Qf
	Myolepta obscura Becher, 1882	4	Qf, Qp
	Sphiximorpha subsessilis (Illiger in Rossi, 1807)	1	Fr
	Spilomyia digitata (Rondani, 1865)	6	Fr, Qp, Qr
COLEOPTERA			
Aderidae	*Aderus populneus* (Panzer, 1796)	39	Fr, Qf, Qp, Qr
	Cnopus minor (Baudi, 1877)	1	Qr
	Otolelus neglectus (Jacquelin du Duval, 1863)	47	Fr, Qr
Anobiidae	*Dorcatoma vaulogeri agenjoi* Español, 1978	17	Fr, Qf, Qp, Qr
	Oligomerus brunneus (Olivier, 1790)	22	Fr, Qf, Qp
	Rhamna semen Peyerimhoff de Fontenelle, 1913	27	Fr, Qf, Qp, Qr
	Stagetus elongatus (Mulsant & Rey, 1861)	8	Fr, Qp, Qr
	Stagetus micoae Viñolas, 2011	2	Fr
Biphyllidae	*Diplocoelus fagi* Guérin-Ménéville, 1838	33	Fr, Qf, Qp, Qr
Buprestidae	*Acmaeodera degener 14-punctata* (Scopoli, 1763)	2	Qr
	Eurythyrea quercus (Herbst, 1780)	1	Qp
Cerambycidae	*Alocerus moesiacus* (Frivaldsky, 1838)	15	Qp, Qr
	Cerambyx welensii (Küster, 1846)	3	Qp
	Prinobius myardi Mulsant, 1851	12	Fr, Qr

	Stictoleptura trisignata (Fairmaire, 1852)	38	Fr, Qf, Qp, Qr
	Trichoferus fasciculatus (Faldermann, 1837)	1	Qp
Cerylonidae	*Cerylon histeroides* Fabricius, 1792	1	Qf
Cetoniidae	*Cetonia aurataeformis* Curti, 1913	244	Fr, Qf, Qp, Qr
	Potosia cuprea (Fabricius, 1775)	34	Fr, Qf, Qp, Qr
	Potosia opaca (Fabricius, 1787)	14	Fr, Qp, Qr
Ciidae	*Cis striatulus* Mellie, 1848	1	Qr
	Cis villosulus Marsham, 1802	1	Fr
Clambidae	*Calyptomerus* sp	1	Fr
	Clambus sp	4	Qr
Cleridae	*Opilo domesticus* (Sturm, 1837)	7	Fr, Qp, Qr
Cryptophagidae	*Cryptophagus aurelioi* Otero, 2009	21	Fr, Qf, Qp, Qr
	Cryptophagus cylindrellus Johnson, 2007	4	Qp
	Cryptophagus dentatus (Herbst, 1793)	23	Fr, Qf, Qp, Qr
	Cryptophagus distinguendus Sturm, 1845	2	Fr, Qr
	Cryptophagus fallax Balfour-Browne 1953	1	Qp
	Cryptophagus micaceus Rey, 1889	142	Fr, Qf, Qp, Qr
	Cryptophagus punctipennis Brisout de Barneville, 1863	54	Fr, Qf, Qp, Qr
	Cryptophagus reflexus Rey, 1889	269	Fr, Qf, Qp, Qr
	Cryptophagus saginatus Sturm, 1845	36	Fr, Qf, Qp, Qr
	Cryptophagus scanicus (Linnaeus, 1758)	119	Fr, Qf, Qp, Qr

Curculionidae	*Camptorhinus simplex* Seidlitz, 1867	2	Qf
	Camptorhinus statua (Rossi, 1790)	103	Fr, Qf, Qp, Qr
	Gasterocercus hispanicus Alonso-Zarazaga, Jover & Micó, 2009	2	Qp
Curculionidae Scolytinae	*Xyleborinus saxesenii* (Ratzeburg, 1837)	37	Fr, Qf, Qp, Qr
	Xyleborus dryographus (Ratzeburg, 1837)	9	Fr, Qf, Qp
	Xyleborus monographus (Fabricius, 1792)	321	Fr, Qf, Qp, Qr
Dasytidae	*Aplocnemus brevis* (Rosenhauer, 1856).	1	Qr
	Aplocnemus consobrinus (Rosenhauer, 1856)	1	Fr
	Aplocnemus limbipennis Kiesenwetter, 1865	1	Fr
	Mauroania bourgeoisi (Pic, 1894)	3	Fr, Qp, Qr
Dermestidae	*Anthrenus (Anthrenus) angustefasciatus* Ganglbauer, 1904	3	Fr, Qr
	Anthrenus (Anthrenus) festivus Erichson, 1846	8	Fr, Qp
	Anthrenus (Florilinus) minutus Erichson, 1846	40	Fr, Qr
	Anthrenus (Florilinus) verbasci (Linnaeus, 1767)	5	Fr, Qr
	Attagenus incognitus Hava, 2003	5	Qf, Qr
	Attagenus schaefferi (Herbst, 1792)	1	Qp
	Attagenus trifasciatus (Fabricius, 1787)	17	Fr, Qp, Qr
	Dermestes (Dermestes) bicolor Fabricius, 1781	1	Qp
	Dermestes (Dermestinus) erichsonii Ganglbauer, 1904	1	Qf
	Dermestes (Dermestinus) frischii Kugelann, 1792	1	Qr
	Dermestes (Dermestes) hispanicus Kalik, 1952	4	Qr

	Dermestes (Dermestinus) undulatus Brahm, 1790	22	Qf, Qr
	Orphilus niger (Rossi, 1790)	2	Qp
Dynastidae	*Oryctes nasicornis* (Linnaeus, 1758)	7	Qp
Elateridae	*Ampedus aurilegulus* (Schaufuss, 1862)	63	Fr, Qf, Qp
	Ectamenogonus montandoni Buysson, 1888	7	Fr, Qp
	Elater ferrugineus Linnaeus, 1758	33	Fr, Qf, Qp
	Elathous platiai Zapata & Sánchez-Ruiz, 2007	1	Qr
	Ischnodes sanguinicollis (Panzer, 1793)	35	Fr, Qf, Qp, Qr
	Lacon punctatus (Herbst, 1779)	11	Fr, Qf, Qp
	Limoniscus violaceus (Müller, 1821)	2	Fr
	Megapenthes lugens (Redtenbacher, 1842)	24	Fr, Qf, Qp, Qr
	Procraerus tibilais (Boisduval & Lacordaire, 1835)	15	Fr, Qp
Endomychidae	*Mycetaea hirta* (Marsham, 1802)	7	Fr, Qp, Qr
	Symbiotes gibberosus (Lucas, 1849)	6	Fr, Qp, Qr
Eucinetidae	*Nycteus meridionalis* Laporte de Castelnau, 1836	1	Qp
Helodidae	*Prionocyphon serricornis* (Müller, 1821)	203	Fr, Qf, Qp, Qr
Histeridae	*Abraeus perpusillus* (Marsham, 1802)	32	Fr, Qf, Qp
	Aeletes atomarius (Aubé, 1843)	6	Fr
	Atholus duodecimstriatus (Schrank, 1781)	1	Fr
	Gnathoncus communis (Marseul, 1862)	47	Fr, Qf, Qp
	Gnathoncus nannetensis (Marseul, 1862)	14	Fr, Qf, Qp

	Hetaerius ferrugineus (Olivier, 1789)	1	Qp
	Margarinotus brunneus (Fabricius, 1775)	1	Qf
	Margarinotus uncostriatus (Marseul, 1854)	2	Qf
	Merohister ariasi (Marseul, 1864)	14	Fr, Qf, Qp, Qr
	Paromalus flavicornis (Herbst, 1792)	28	Fr, Qf, Qp, Qr
	Platylomalus complanatus (Panzer, 1796)	1	Fr
	Platylomalus gardineri (Scott, 1913)	1	Qp
	Platysoma filiforme (Erichson, 1834)	2	Fr, Qp
Laemophloeidae	*Cryptolestes ferrugineus* (Stephens, 1831)	7	Qf, Qp, Qr
	Laemophloeus nigricollis Lucas, 1849	2	Fr, Qf
	Placonotus testaceus (Fabricius, 1787)	2	Fr, Qp
Latridiidae	*Corticaria obscura* Brisout, 1863	2	Qf
	Dianerella ruficollis (Marsham, 1802)	1	Qr
	Enicmus brevicornis (Mannerheim, 1844)	4	Fr, Qp
	Enicmus rugosus (Herbst, 1793)	4	Qf, Qp
	Latridius assimilis (Mannerheim, 1844)	25	Fr, Qf, Qp, Qr
Leiodidae	*Agathidium nigriceps* Brisout, 1872	2	Fr, Qp
Lucanidae	*Dorcus parallelepipedus* (Linnaeus, 1785)	43	Fr, Qf, Qp
Malachiidae	*Anthocomus fenestratus* Linder, 1864	16	Fr, Qp, Qr
	Axinotarsus marginalis (Laporte de Castelnau, 1840)	6	Qr
	Hypebaeus albifrons (Fabricius, 1775)	3	Qp

	Troglops furcatus Abeille de Perrin, 1885	52	Fr, Qf, Qp, Qr
Melandryidae	*Orchesia micans* (Panzer, 1794)	8	Fr, Qf, Qp, Qr
Melyridae	Falsomelyris granulata (Fabricius, 1792)	2	Fr
Mycetophagidae	*Litargus balteatus* Le Conte, 1856	1	Qp
	Litargus connexus (Geoffroy, 1785)	11	Fr, Qf, Qp
	Mycetophagus quadriguttatus Müller, 1821	73	Fr, Qf, Qp, Qr
Nitidulidae	*Amphotis marginata* (Fabricius, 1781)	2	Qp
	Carpophilus sp	1	Qf
	Epuraea fuscicollis (Stephens, 1832)	137	Qf, Qp, Qr
	Epuraea (Haptoncus) ocularis Fairmaire, 1849	2	Qf
	Soronia oblonga C. Brisout de Barneville, 1863	141	Fr, Qf, Qp, Qr
Oedemeridae	*Ischnomera xanthoderes* (Mulsant, 1858)	114	Fr, Qf, Qp, Qr
Platypodidae	*Platypus cylindrus* (Fabricius, 1792)	1	Qr
Pselaphidae	*Euplectus* sp	1	Fr
	Geopsephalus sp	1	Fr
	sp 1 (tribu Goniaceritae)	1	Fr
Ptiliidae	sp 2	46	Fr, Qf, Qp
Ptinidae	*Dignomus irroratus* (Kiesenwetter, 1851)	4	Fr, Qf, Qp
	Ptinus (Cyphoderes) bidens Olivier, 1790	13	Fr, Qf, Qp, Qr
	Ptinus (Cyphoderes) hirticornis Kiesenwetter, 1867	3	Qp, Qr
	Ptinus (Ptinus) spitzyi Villa & Villa, 1838	1	Qp

	Ptinus (Ptinus) timidus Brisout de Barneville, 1866	274	Fr, Qf, Qp, Qr
Rhizophagidae	*Rhizophagus unicolor* Lucas, 1846	1	Qp
Scraptiidae	*Anaspis regimbarti* Schilsky, 1895	11	Fr, Qp
	Pentaria defarguesi Abeille de Perrin, 1885	1	Fr
	Scraptia ophthalmica Mulsant, 1856	2	Fr
	Scraptia testacea Allen, 1940	80	Fr, Qf, Qp, Qr
Scydmaenidae	Cephenium (Cephenium) sp	1	Fr
	Palaeostigus palpalis (Latreille, 1804)	5	Qp, Qr
	Scydmaenus (Cholerus) cornutus Motschulsky, 1845	3	Fr, Qp
	Stenichnus (Cyrtoscydmus) godarti (Latreille, 1806)	5	Fr
Silvanidae	*Ahasverus advena* (Waltl, 1834)	2	Fr, Qp
	Airaphilus sp	1	Qf
	Oryzaephilus surinamensis (Linnaeus, 1758)	1	Fr
	Silvanus bidentatus Fabricius, 1792	2	Qr
	Uleiota planata (Linnaeus, 1761)	7	Fr, Qp
Tenebrionidae	*Corticeus fasciatus* (Fabricius, 1790)	1	Qp
	Eledonoprius armatus (Panzer, 1799)	7	Qp
	Isomira hispanica Kiesenwetter, 1870	11	Fr, Qr
	Mycetochara linearis (Illiger, 1794)	20	Fr, Qf, Qp
	Mycetochara quadrimaculata (Latreille, 1804)	110	Fr, Qf, Qp, Qr
	Prionychus fairmairei (Reiche, 1860)	17	Fr, Qp

	Probaticus anthracinus (Germar, 1813)	40	Fr, Qf, Qp, Qr
	Probaticus granulatus (Allard, 1876)	1	Qr
	Pseudocistela ceramboides (Linnaeus, 1761)	43	Fr, Qf, Qp
	Stenohelops sublinearis (Kraatz, 1870)	4	Fr, Qp
	Tenebrio sp	34	Fr, Qp, Qr
Trogossitidae	*Tenebroides marrocanus* Reitter, 1884	3	Fr, Qr
	Temnochila caerulea (Olivier, 1790)	3	Fr, Qr
Zopheridae	*Colobicus hirtus* (Rossi, 1790)	2	Fr, Qp
	Colydium elongatum (Fabricius, 1787)	6	Fr, Qp
	Endophloeus marcovichianus (Piller & Mitterpacher, 1783)	22	Qf, Qp

CONCLUSIONES GENERALES

Conclusiones generales

1. El estudio de las oquedades seleccionadas para la realización de esta tesis pone en relieve la elevada biodiversidad saproxílica asociada con este microhábitat en los bosques mediterráneos ibéricos, contribuyendo en gran medida a la biodiversidad total de los ecosistemas forestales a escala local.
2. Los métodos evaluados son eficaces para muestrear distintas porciones del ensamble saproxílico en los bosques mediterráneos.
3. La trampa de emergencia es un método efectivo para caracterizar la diversidad taxonómica y ecológica del ensamble saproxílico asociado a las oquedades, y su uso permite conocer aspectos clave de la biología de las especies o estudiar las interacciones saproxílicas.
4. La combinación de las trampas de emergencia y las trampas de ventana permite realizar inventarios más completos de la fauna saproxílica de los bosques mediterráneos, ya que permiten la captura de especies con distintas biologías y requerimientos tróficos. El sencillo diseño de estas trampas, la gran diversidad de insectos que proporcionan, y las facilidades que brindan a la hora de estandarizar los protocolos de muestreo, las convierte en excelentes candidatos para realizar estudios comparativos faunísticos, ecológicos o de seguimiento de especies saproxílicas.
5. La interacción oquedad-insecto saproxílico presenta un patrón modular a lo largo de los distintos niveles considerados, caracterizado por la presencia de módulos grandes y cohesivos. Este patrón modular delimita las principales agrupaciones

tróficas oquedad-insecto, las cuales se conforman en torno a distintas especies arbóreas o características ecológicas de las oquedades.

6. Las subredes saproxílicas dependientes de la madera como recurso trófico presentan a) una mayor diversidad de especies, b) un menor número de módulos, c) una mayor diversidad y heterogeneidad de interacciones, d) una menor especialización, y d) una menor competencia interespecífica que las subredes que dependen de la presencia de otros insectos saproxílicos.
7. Las diferencias en los patrones de redes entre tipos de interacción tiene implicaciones en la estabilidad frente a las perturbaciones, de modo que las subredes con mayor diversidad de especies e interacciones fueron también las más robustas. No obstante, los gremios tróficos fueron relativamente resistentes a la eliminación simulada de oquedades.
8. La diversidad taxonómica y ecológica de los gremios saproxílicos es mayor en los bosques con mayor heterogeneidad de oquedades: robledales y fresnedas, donde una mayor variabilidad y cantidad de recursos tróficos y micrositios está disponible para el desarrollo de distintas especies de cada gremio trófico, correspondiendo además con los bosques tradicionalmente menos manejados.
9. El tipo de manejo que aún se practica en el bosque esclerófilo determina una alta homogeneidad de microhábitats y de su fauna asociada, aunque potencia las poblaciones de algunas especies o gremios, como la especie de sírfido *Mallota dusmeti* (Diptera), endemismo Iberomagrebí catalogado como Vulnerable en España.

10. Los distintos gremios responden de forma diferente a las distintas variables microclimáticas estudiadas, siendo el volumen de la oquedad el factor más importante tanto para la riqueza como para la abundancia de los gremios saproxílicos.
11. La conservación de la comunidad saproxílica asociada a las oquedades discurre paralela a la conservación de los bosques mediterráneos más maduros: con árboles añosos y oquedades grandes, en ocasiones siendo oportuno aplicar estrategias de manejo que enriquezcan la composición de microhábitats para la comunidad saproxílica.

APÉNDICE I

The Genus *Ferdinandea* Rondani, 1844 (Diptera, Syrphidae) in the Iberian Peninsula: First Records and New Breeding Sites

El género *Ferdinandea* Rondani, 1844 (Diptera, Syrphidae) en la Península Ibérica: Primeras citas y nuevos sitios de cría

Ricarte, A., Nedeljković, Z., **Quinto, J.**, Marcos-García, M.A., 2010. The Genus *Ferdinandea* Rondani, 1844 (Diptera, Syrphidae) in the Iberian Peninsula: First Records and New Breeding Sites. J. Entomol. Res. Soc., 12(3): 57-69.

Abstract

Following a review of all the available Iberian material belonging to the genus *Ferdinandea* Rondani, 1844, results show that the fauna of the Iberian Peninsula have all the four species recorded in the Palaearctic region: *F. aurea* Rondani 1844*, F. cuprea* (Scopoli, 1763)*, F. fumipennis* Kassebeer, 1999, and *F. ruficornis* (Fabricius, 1775). Examined material of *F. ruficornis* represents the first record from the Iberian Peninsula. A revised key to the Iberian *Ferdinandea* species is provided, as well as updated distribution maps for each of the species. Breeding sites for *F. aurea* and *F. ruficornis* are reported, in the case of *F. aurea* as the first known (in *Quercus faginea* and *Quercus pyrenaica*), and in the case of *F. ruficornis* as the first in *Q. pyrenaica*. Special attention should be paid to the conservation of *F. ruficornis*, highly restricted in its Iberian range and threatened with extinction in different European countries.

Key words

Ferdinandea ruficornis, key to species, life cycle, *Quercus*, conservation, species distribution, Iberian Peninsula

Introduction

The genus *Ferdinandea* Rondani, 1844 (Syrphidae: Eristalinae) comprises medium-sized hoverflies with strong black bristles on the thorax and scutellum, as well as dark spots on the wings (Thompson & Rotheray, 1998; Van Veen, 2004). Peck (1988) listed five *Ferdinandea* species from the Palaearctic region, *F. aurea* Rondani, 1844, *F. cuprea* (Scopoli, 1763), *F. ruficornis* (Fabricius, 1775), *F. nigrifrons* (Egger, 1860) and *F. sziladyi* Drensky, 1934, despite the taxonomic status of the latter two being unclear today (Speight, 2010). Marcos-García *et al*. (2002) and Ricarte & Marcos-García (2007) reported the occurrence of three *Ferdinandea* species in the Iberian Peninsula: *F. aurea*, *F. cuprea* and *F. fumipennis* Kassebeer 1999.

The preferred habitats of the *Ferdinandea* adults are deciduous forests, where their saproxylic larvae live in sap-runs of generally over-mature trees, mainly *Quercus*, but also in sap-runs associated with the tunnelling activity of the caterpillar of *Cossus cossus* (Linnaeus, 1758) (Rotheray, 1993). Early stages of *F. cuprea* and *F. fumipennis* are described (Hartley, 1961; Ricarte *et al*., 2007), and their breeding sites are reported (compilation of original references in Speight, 2010). *F. ruficornis* early stages are not described and breeding site data are poor and dispersed (Speight, 2010); no data for *F. aurea* are available in this respect. According to Speight (2010), *F. ruficornis* should be regarded as a threatened species at least over western Europe. The status of *F. ruficornis* in this European region seems to be related to the forestry practices that negatively influence the existence of *C. cossus* and the continuance of over-mature trees in forests (Speight, 2010). In The Danish Red Data Book *F. ruficornis* is catalogued as “Regionally Extinct” (Bygebjerg, 2007) and in countries such as Belgium, France and Germany is threatened with extinction (Speight *et al*., 2010). Taxonomy, biology, and distribution of *F. ruficornis* need to be ascertained in order to establish adequate conservation strategies.

In this study we update the knowledge of the genus *Ferdinandea* in the Iberian Peninsula by compiling all published data and examining all the available specimens from this geographic region. A taxonomic key to the Iberian *Ferdinandea* species, including the first-recorded *F. ruficornis*, is also provided, as well as other revised data on taxonomy, biology, distribution, and conservation of the species.

Material and methods

Examined specimens came from different localities and belonged to the collections referred to in the text with the following acronyms: CEUA = Colección Entomológica Universidad de Alicante, University of Alicante, Spain; MNCN = Museo Nacional de Ciencias Naturales, Madrid, Spain; NS = Department of Biology and Ecology, Entomological Collection, University of Novi Sad, Serbia; RBINS = Royal Belgian Institute of Natural Sciences, Brussels, Belgium. Most of the specimens examined are deposited in the CEUA. Thus, to avoid unnecessary repetition, the repository of specimens is only mentioned when the material studied does not belong to CEUA. All specimens from CEUA are bar-code labelled according to a GBIF protocol and are recorded in a data base available in the Centro Iberoamericano de la Biodiversidad (CIBIO), at the University of Alicante.

Examination of specimens was complemented with a review of published data and taxonomic information from correspondence with other specialists (see “acknowledgements”). Thus the examined material of each species is divided into published (Andorran/Portuguese/Spanish specimens), new (Spanish specimens) and additional (data on non-Andorran/Portuguese/Spanish specimens, published or not, useful to perform the taxonomic study). A detailed description of the examined material is provided for new data and for some additional data, as well as for the material of MNCN, which was published several decades ago. For specimens with detailed data, the catching method was hand net (specific date), Malaise trap (period of time), and emergence trap (when specified in the text).

Authors identified the specimens based on keys and descriptions in Kassebeer (1999), Van Veen (2004) and Speight & Sarthou (2010). As a result of the taxonomic study, a revised key to the Iberian species of *Ferdinandea* is provided. Terminology on adult morphology broadly follows Thompson (1999), except for genitalia characters, which follow Kassebeer (1999). Additionally, the following sections with updated data are presented for each species: taxonomic notes, biology, world distribution, and conservation (Europe and Iberian Peninsula). Species biology, distribution and conservation status in Europe follows Speight (2010) and Speight *et al*. (2010). Criteria followed by Speight *et al*. (2010) to establish the conservation status of the species are detailed in Speight & Castella (2010). Maps were made with the software ArcView GIS 3.3®.

Results

Key to adults of the Iberian species of the genus *Ferdinandea*

1. Face with a dark brown to black vitta..................................*F. aurea*

- Face pale-coloured overall, without vitta..2

2. Antennal arista orange; each of the 2nd and 3rd terga shiny except for some dull areas centrally and laterally, in both cases on the posterior part of the tergum, shiny along the full length of the posterior margin;

male genitalia: ventral lobe of distiphallus with a conspicuously-elongated pointing process (about 3× longer than basiphallus)..*F. ruficornis*

-Antennal arista dark brown to black; each of the 2nd and 3rd terga shiny anteriorly, dull along the full length of the posterior margin; male genitalia: ventral lobe of distiphallus with a moderately-elongated pointing process (about 1.5× longer than basiphallus)...3

3. Wing membrane hyaline in veins R2+3 and R4+5 distally; antennae orange (basoflagellomere may be black apically), with dark brown to black arista; scutum with a pair of medial grey-pollinose vittae reaching the posterior margin; scutellum yellow, with lateral angles black (the black areas together occupy about 1/4 of the scutellum width in dorsal view); male genitalia: ventral lobe of distiphallus flat; dorsal lobe of basiphallus diverging for a section of about half of its total length……..*F. cuprea*

- Wing membrane brown-pigmented in veins R2+3 and R4+5 distally; antennae black including arista; scutum with a pair of medial grey-pollinose vittae not reaching the posterior margin, or faintly reaching; scutellum yellow, with lateral angles black (the black areas together usually occupy about 1/3 of the scutellum width in dorsal view); male genitalia: ventral lobe of distiphallus conical; dorsal lobe of basiphallus diverging for a section of about 1/4 of its total length...*F. fumipennis*

F. aurea Rondani, 1844

F. aurea Rondani, 1844: 198

Distribution: Palaearctic species confined to southern Europe: central and southern Spain, including Balearic Islands (Fig. 1), southern France, Italy and Greece.

Material examined:

Published: SPAIN: from the provinces of Cáceres, Salamanca (Marcos-García, 1985), Ciudad Real (Ricarte & Marcos-García, 2008; Ricarte, 2008) and Mallorca (Gil Collado, 1930; Compte-Sart, 1958).

New: SPAIN: Alicante: Agres: 5♂♂, Caveta del Voltor (30SYH161937, 1200m), 11.IX.2001; 1♂, 11-25.IX.2001; 1♂, 10-24.IX.2002; 2♂♂, 24.IX-7.X.2002; 1♂, Foia Ampla (30SYH169931, 1060m), 11-25.IX.2001; 1♂, 10-24.IX.2002, leg. C. Pérez-Bañón, M.A. Marcos-García & S. Rojo; Alcoy: 1♀, Font Roja, 10-24.IX.1992; 2♂♂, 8-22.X.1992, leg. F. Luna; 25♂♂ and 4♀♀, 21.IX.1993; 1♂, 29.IX.1993, leg. P.M. Isidro; 1♀, El Menejador (30SYH143819, 1350m), 27.VIII-10.IX.2002; 1♂, 22.IX.2004, leg. A. Ricarte; Jijona: 1♂, Venta de la Carrasqueta (30SYH191770, 980m), 11-26.IX.2001; 4♂♂ and 1♀, 10/24-IX-2002; 1♂, 7-21.X.2002, leg. C. Pérez-Bañón, M.A. Marcos-García & S. Rojo; 1♂ and 1♀, Mas de Sant Ignaci (30SYH187766, 1020m), 17-31.VII.2001; 2♂♂, 11-26.IX.2001, leg. C. Pérez-Bañón, M.A. Marcos-García & S. Rojo; 1♂, Mas de Cano (30SYH201775, 940m), 10-24.IX.2002, leg. C. Pérez-Bañón, M.A. Marcos-García & S. Rojo; Ciudad Real: 1♀ from larva collected in a root hole of a *Q. faginea* tree in “P.N. de Cabañeros, valle de Canalejas, 1.V.2005 by T. Jover (puparium/30.V.2005, adult/¿?, puparium was not preserved)”; collected by emergence trap: 4♂♂, Valle Santiago, trap 7, 24.9.2009, in a hole of *Q. pyrenaica*; 4♂♂ and 1♀, Valle Santiago, trap 16, 26.10.2009, in a hole of *Q. pyrenaica*; 2♀♀, trap 16, 26.10.2009, in a hole of *Q. faginea*, leg.: Micó, Quinto & Briones, det. Z. Nedeljković; 11♀♀, trap 16, in a hole of *Q. faginea*, leg.: Micó, Quinto & Briones, det.: A. Ricarte. Salamanca: 1♂, Las Veguillas, 12.IX.1979, leg. M.A. Marcos-García; Valencia: Chelva: 2♂♂, Fuente de la Esparraguera (XJ6289, 990m), 6.X.1993; 10♂♂ and 1♀, Mas de Caballero (XJ6190, 1000m), 24.IX-8.X.1994; 12♂♂ and 5♀♀, 8-22.X.1994; 7♂♂ and 2♀♀, 22.X-5.XI.1994, leg. C. Pérez-Bañón; Utiel: 1♂ and 3♀♀, Casas Medina (XJ5787, 920m), 17.X.1993; 2♂♂, Atalaya del Remedio (XJ6088, 1310m), 24.IX.1994.

Taxonomic notes

The type material of *F. aurea* was collected in Italy and is deposited in the Museo di Storia Naturale, University of Florence, Sezione “La Specola”, Italy. Rondani did not designate a holotype, and described this species based on multiple specimens (Christian F. Thompson, pers. com.).

This species is unequivocally distinguished by the presence of a dark brown to black facial vitta extending from the mouth edge to the base of the antennae. The male genitalia are similar to *F. ruficornis* genitalia.

Biology (Table 1)

The preferred habitats of this species are over-mature forests of *Quercus pubescens* Willd, *Quercus ilex* L. or *Quercus suber* L. Despite larva not being described, T. Jover collected an early stage (larva or puparium) of this species in a root hole of an old *Q. faginea* Lam tree in Cabañeros National Park, Spain (puparium not preserved). Moreover, specimens collected by emergence trap in the same locality allowed an association between this *Ferdinandea* species and *Q. pyrenaica* to be established. These are the first known breeding site data on *F. aurea*. Flight period (Iberian Peninsula): mid July to beginning of December.

Conservation

Europe. Exhibiting a moderate decrease of populations. It is threatened with extinction in the Continental region *sensu* Romau (1996).

Iberian Peninsula. Although *F. aurea* populations seem to be decreasing in Europe, profuse samplings in some localities of the Iberian Peninsula have shown its high abundance; for instance, it is the most abundant saproxylic hoverfly in Cabañeros National Park (Ricarte *et al*., 2009) and, as shown by our results, it is widespread in some protected areas of south-eastern Spain (Caveta del Voltor, Foia Ampla, El Menejador, Venta de la Carrasqueta, Mas de Sant Ignaci, Mas de Cano; all these localities belong to the Sierra de Mariola and Font Roja natural parks). Despite abundant in some localities, further studies to assess the status of *F. aurea* populations in the rest of its Iberian range are in need. The provided data on breeding sites contribute in focusing on *Quercus* forests, if protection for this species was required.

F. cuprea (Scopoli, 1763)

Conops cupreus Scopoli, 1763: 355

Distribution: Palaearctic species distributed from Fennoscandia south to southern Spain (Fig. 2) and North Africa (Algeria) and round the Mediterranean through southern Europe to Turkey; from Ireland eastwards through central/northern parts of Eurasia to the Pacific coast of Siberia and Japan.

Material examined:

Published: ANDORRA: Carles-Tolrà (2006); PORTUGAL: from the former province of Minho (Corti, 1903); SPAIN: from the provinces of Vizcaya (Seebold, 1903), Asturias, Huesca, Madrid, Segovia (Arias, 1912; Gil Collado, 1930), Barcelona (Navás, 1901; Gil Collado, 1930), Cáceres, Salamaca (Marcos-García, 1985) [part as *F. nigrifrons* (Egger, 1860), except for the specimens re-identified as *F. fumipennis* in Ricarte & Marcos-García (2007)], León [Marcos-García (1990), as *F. nigrifrons*]; data on the specimens deposited in MNCN, all pre-identified as *F. cuprea*:

2♂♂, Panticosa, Escalera (MNCN_Ent Nº Cat. 41243 and 41207); 1♂ and 1♀, Escorial, Arias Encobet, Mercet, VII.1905 (MNCN_Ent Nº Cat. 41255 and 41214); 1♀, Paular (MNCN_Ent Nº Cat. 41236); 1♀, Covadonga, IIV 928 J. Dusmet (MNCN_Ent Nº Cat. 41208); 1♀, La Granja, Arias Encobet, *F. cuprea* Scop J. Gil det. (MNCN_Ent Nº Cat. 41220).

New: SPAIN: Ciudad Real: collected by emergence traps: 2♀♀, P.N. Cabañeros, El Brezoso, 23.4.2009, in a hole of *Q. pyrenaica*; 1♂, Valle Santiago, 8^2, 26.6.2009, in a hole of *Q. pyrenaica*, leg.: Micó, Quinto & Briones.

Additional: FRANCE: 1♂, Rambt, 30.5.04, “Coll. J. Villeneuve”, *F. ruficornis* F, R.M.H.N.Beig. 15.392; 1♀, Rambouillet, 24.V.10, “Coll. J. Villeneuve”, *F. ruficornis* F, R.M.H.N.Beig. 15.392; 1♀, Broût·Vernet, H. du Buysson, “Coll. J. Villeneuve”, *F. ruficornis* F, R.M.H.N.Beig. 15.392 [RBINS]. All specimens deposited in RBINS were re-identified by A. Ricarte. SERBIA: specimens published in Vujić et al. (1998) and Vujić & Šimić (1994) [NS]. NON-LOCATED: 1♂, Visf., juin 80, “Collection Maurissen”, Van der Wulp det.: *F. ruficornis* F.; 1♀, Aidderf, Aug 67, “Collection Maurissen”, Van der Wulp det.: *F. ruficornis* F. [RBINS].

Taxonomic notes

The type specimen of *F. cuprea* was collected in “Carniola”, the current province of Kranjska, Slovenia. This specimen is lost because Scopoli’s collection was destroyed (Christian F. Thompson, pers. com.).

Regarding its identification: in spite of the antenna being mostly orange (antennal arista is always dark brown to black), some specimens have the basoflagellomere black apically; the scutum has four silvery-pollinose vittae and the medial pair reaches the posterior margin of the scutum; the scutellum is yellow with black corners (up to 1/4 of the scutellum width in dorsal view is black); setae on scutellum are mostly black; both the 2nd and 3rd terga have a dull band reaching the posterior margin; some specimens show dull areas in the central and lateral parts of each of the 2nd and 3rd terga posteriorly, but in other specimens the dull areas only occur in the lateral parts posteriorly; pilosity on both posterior anepisternum and 4th sternum ranges from completely yellow to partly black.

Biology (Table 1)

The preferred habitats of this species are deciduous forests with over-mature trees, including alluvial forests of *Populus-Salix*, *Carpinus-Quercus*, acidophilous *Quercus* forests and *Q. pubescens* and *Betula* forests. Larvae are found in semi-aqueous material in *Populus* trees damaged by *C. cossus* L. They have also been collected in tree wounds and sap runs on the trunks of living deciduous trees (*Quercus, Acer, Aesculus, Betula, Malus, Populus, Salix and Ulmus*). We report a hole in *Q. pyrenaica* as a new breeding site for this species. Flight period (Iberian Peninsula): March-September, not found in June.

Conservation

Europe. Widespread and unthreatened.

Iberian Peninsula. Restricted exclusively to the northern half of the Peninsula (Fig. 2). It is not as locally-abundant as *F. aurea* or *F. fumipennis* (e.g., see Ricarte *et al*., 2009), even in northern localities (Marcos-García, 1985). There are no enough data to regard *F. cuprea* as threatened in the Iberian Peninsula but it appear to be rarer than *F. aurea* and *F. fumipennis*.

***F. fumipennis* Kassebeer, 1999**

F. fumipennis Kassebeer, 1999: 155

Distribution: Ibero-Maghreb endemic reported from Spain, including Balearic Islands (Fig. 3), Morocco and Tunisia.

Material examined:

Published: SPAIN: from the provinces of Alicante, Ciudad Real, Mallorca, Murcia, Salamanca and Valencia (Ricarte & Marcos-García, 2007; Ricarte *et al*., 2007; Carles-Tolrà & Lencina, 2010).

New: SPAIN: Alicante: Jijona: 1♂, Venta de la Carrasqueta, 10-23.IV.2002 [NS]; 1♂, 23.IV-15.V.2002, leg. C. Pérez-Bañón, M.A. Marcos-García & S. Rojo; 1♀, Alcoy, Font Roja, 15.III.1994, leg. P.M. Isidro; Ciudad Real: P.N. Cabañeros: 1♀, maJ2 (*Q. pyrenaica* forest, 30S371749-4359712), 5-29.X.2004; 1♂, 18.III-12.IV.2005; 1♂, maF1 (riparian forest of *Fraxinus angustifolia*, 30S365590-4367922), 26.II-19.III.2005; 1♂, maF2 (riparian formation of *F. angustifolia*, 30S365590-4367922), 28.X-18.XI.2004; 1♀, 19.III-13.IV.2005, leg. A. Ricarte; Salamanca: 2♀♀, Dehesa campanario de Azaba, 13.IV.2010, leg.: M.A. Marcos-García (1♀, "point 8, ovipositing in *Q. pyrenaica*"; 1♀, "encina E_19_1, white sap run").

Taxonomic notes

The holotype of *F. fumipennis* was collected in Morocco and, according to Kassebeer (1999), belongs to the collection abbreviated as "DID" (?). The holotype is lost, probably belonging to the private collection of Christian F. Kassebeer. Kassebeer (1999) states that there are several male and female paratypes from Morocco and Tunisia deposited in the Zoological Museum, Natural History Museum of Denmark, Copenhagen, but there is no record of this material in the checklist of the Syrphidae types from this museum (http://zoologi.snm.ku.dk/english/).

Regarding its identification: this species is very similar to *F. cuprea*; to separate the females of both species, the wing pigmentation is a key character, since in *F. fumipennis* the wing presents dark brown pigmentation on the membrane close to veins R2+3 and R4+5 distally; some body parts (antennae, scutellum, etc.) are darker in *F. fumipennis* males than in *F. cuprea* males, and the genitalia are the only distinctive character to separate the males of both species; *F. fumipennis* has black antenna, including arista, and the black areas of the scutellum are usually larger than in *F. cuprea*; additionally, the pair of medial silvery-pollinose vittae on the scutum does not reach, at least so conspicuously, the posterior margin. Kassebeer (1999) figured the male genitalia and he remarked that the main difference between these two closely-related species is the structure of the hypopygium, especially in the basiphallus and the distiphallus. In *F. fumipennis* the dorsal lobe of the basiphallus diverges along 1/4 of its total length, but in *F. cuprea* along 1/2 of its total length; in *F. fumipennis* the ventral lobe of the distiphallus is a rounded cone in shape, but in *F. cuprea* it is flat; in *F. fumipennis* the dorsal lobe of the distiphallus is a tapering pointing-at-the-apex process engrossed basally, but in *F. cuprea* it is either not engrossed or only gently engrossed.

Biology (Table 1)

The preferred habitats of this species are acidophilous oak forests of *Q. pyrenaica* Willd and riparian forests of *Fraxinus angustifolia* Vahl. Larvae have been found in material collected from a sap-run on the trunk of a live *Q. pyrenaica* (Ricarte *et al*., 2007). Flight period (Iberian Peninsula): late February to mid November, not found in June and August.

Conservation

Europe. Unthreatened species, despite being restricted to the Iberian Peninsula.

Iberian Peninsula. *F. fumipennis* is an Ibero-Maghreb endemic occurring in the southern half of the Iberian Peninsula and in the Balearic Islands (Fig. 3). It is locally more abundant than the closely related *F. cuprea* and appears to be the second most common species, after *F. aurea*. Despite abundant, the conservation of *F. fumipennis* in the Iberian Peninsula stays relevant because this region represents its only known European redoubt.

Table 1. New and reviewed data on associations *Ferdinandea*-tree. Bold lettering identifies new *Ferdinandea*-tree associations.

Ferdinandea species	**Breeding tree**
F. aurea	*Quercus pyrenaica, Q. faginea*
F. cuprea	*Acer*, *Aesculus*, *Betula*, *Malus*, *Populus*, *Quercus* (including *Q. pubescens* and *Q. pyrenaica*), *Salix*, *Ulmus*
F. fumipennis	*Q. pyrenaica*
F. ruficornis	reared from sappy material in the burrows of *Cossus cossus* caterpillars in *Quercus*; *Q. pyrenaica*

F. ruficornis (Fabricius, 1775)

Syrphus ruficornis Fabricius, 1775: 769

First record for the Iberian Peninsula

Distribution: From Denmark south to central Spain (Fig. 4); from Britain eastwards through central and southern Europe into European Russia and the Caucasus, and through Siberia and Uzbekistan to the Pacific; northern China.

Material examined:

New: SPAIN: Ciudad Real: P.N. Cabañeros: 1♀, maJ1 (*Q. pyrenaica* forest, 30S371749-4359712), 1-24.VIII.2004; 2♂♂ and 1♀, 18.III-12.IV.2005; 1♀, 30.V-10.VI.2004; 1♀, maJ2 (*Q. pyrenaica* forest, 30S371749-4359712), 24.VIII-12.IX.2004; 1♂, 18.III-12.IV.2005, leg.: A. Ricarte; xPa1, 1♀, 8.IV.2005 (30S379778-4357230, flying around a mature *Q. pyrenaica* tree), leg.: E. Galante [as *F. fumipennis* in Ricarte and Marcos-García (2007)]; collected by emergence trap: 2♂♂ and 4♀♀, El Brezoso (*Q. pyrenaica* forest, 30S383132-4357017, 750m), 26.X.2009, in a hole of *Q. pyrenaica* (this trunk hole contained a sap run exuding and flowing into the hole), leg.: Micó, Quinto & Briones.

Additional: FRANCE: 1♀, Rambouillet, 10.8.04, "Coll. J. Villeneuve": *F. ruficornis* F, R.M.H.N.Beig. 15.392 [RBINS]. All specimens deposited in RBINS were re-identified by A. Ricarte 2010. SERBIA: specimens published in Vujić & Šimić (1994) [NS]. NETHERLANDS: 1♀, Nedlth, 10/6 86, "Collection Maurissen", Van der Wulp det.: *F. ruficornis* F [RBINS]. NON-LOCATED: 1♀, *Chrys. ruficornis* Fbr., "Coll. J. Villeneuve": *F. ruficornis* F, R.M.H.N.Beig. 15.392 [RBINS].

Taxonomic notes

Fabricius did not designated a holotype nor indicate the number of specimens forming the type series (Christian F. Thompson, pers. com.). The only known type specimen of *F. ruficornis* is a female collected in Dania (Denmark), deposited in the collection of the Natural History Museum of Denmark, Zoological Museum, Copenhagen, Denmark. This specimen is in poor condition because it has been attacked by *Anthrenus* (Thomas Pape, pers. com.) and only wings plus head and a part of the thorax remain; antennae are partially missing and no arista is preserved.

Regarding its identification: *F. ruficornis* has the characteristically orange to light brown arista, but it is never as black as in *F. fumipennis* (sometimes in *F. cuprea*); scutellum has mostly yellow setae; both the 2nd and 3rd terga have shiny areas centrally and laterally, but also have dull areas centrally and postero-laterally; the posterior margin of each of the 2nd and 3rd terga is shiny.

The examined Iberian specimens have only yellow hairs on 2nd and 3rd terga, except for one specimen from Cabañeros that has a few black hairs on the 3rd tergum posteriorly. Some additional specimens from Great Britain and the Czech Republic presented black hairs on 2nd and 3rd terga, sometimes only on 3rd tergum. Also a specimen from Sweden with black hairs on 3rd tergum is known (Wouter van Steenis, in lit.). Specimens with black hairs at least on 3rd tergum also have black hairs on 3rd and 4th sterna. In specimens without black hairs on terga, there are no black hairs on sterna.

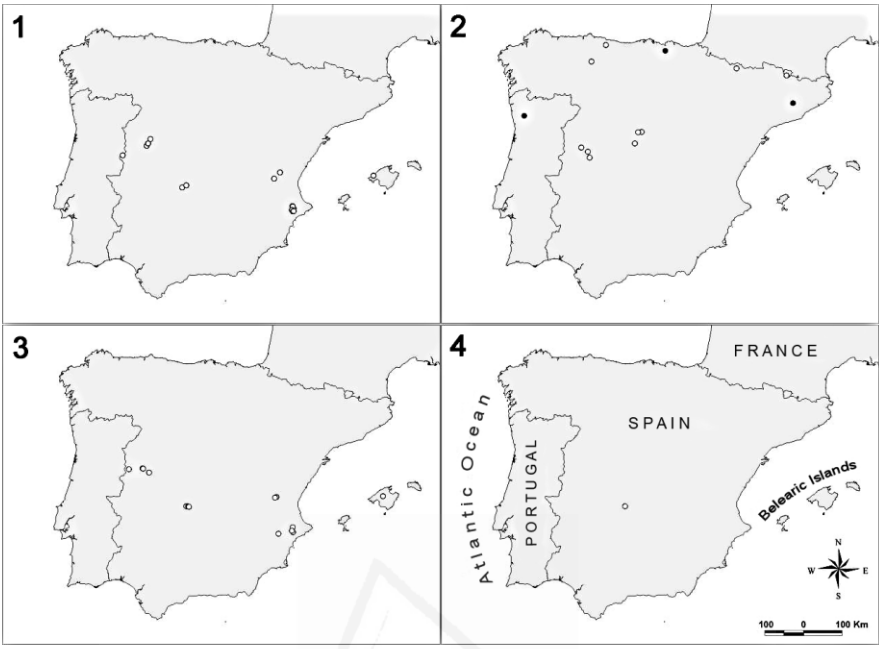
Biology (Table 1)

The preferred habitats of this species are *Quercus* forests and alluvial hardwood forests. The larva is not described, but has been reared from sappy material in the burrows of *C. cossus* caterpillars. We report *Q. pyrenaica* as a breeding site of this species. Flight period (Iberian Peninsula): mid March to October, not found in July.

Conservation

Europe. Threatened with extinction, but in a more alarming situation at regional level in different states of western Europe. The high dependence of *F. ruficornis* on the declining moth *C. cossus* and on over-mature trees ensures the hoverfly's scarcity.

Iberian Peninsula. Despite *Ferdinandea* hoverflies have been recorded throughout the Iberian Peninsula, *F. ruficornis* is only known from the locality provided in this study (Cabañeros National Park). It certainly is a rare species, probably threatened with extinction at Iberian level. According to our results, Iberian populations of *F. ruficornis* highly depend on over-mature forests of *Q. pyrenaica*.



Figs 1–4. Distribution of the *Ferdinandea* species in the Iberian Peninsula and Balearic Islands. 1. *F. aurea*; 2. *F. cuprea*; 3. *F. fumipennis*; 4. *F. ruficornis*. In Fig. 2 a black circle indicates the locality of a published *F. cuprea* specimen which was unavailable for the authors of this study.

Conclusions and Discussion

Following this study, the four species cited for the Palaearctic region result in forming the *Ferdinandea* fauna of the Iberian Peninsula: *F. aurea, F. cuprea, F. fumipennis* and *F. ruficornis*. The first record for the Iberian Peninsula of *F. ruficornis* is provided, as well as the first records of *F. aurea* for each of the Mediterranean Spanish provinces of Alicante and Valencia. Especially relevant are the records of *F. ruficornis*, threatened with extinction in different European areas (Speight *et al.*, 2010). *F. ruficornis* appears to be a species with a very restricted distribution in the Iberian Peninsula and certainly could be considered of special relevance at conservation level, since it has only been found in a protected area in central Spain (Cabañeros National Park). In Cabañeros, all the Iberian *Ferdinandea* species have been collected in different localities of several habitat types (Ricarte & Marcos-García, 2008), but *F. ruficornis* only was collected in a couple of *Q. pyrenaica* forests, which in some ways suggests a degree of association with this tree species in the Mediterranean region. The specimens of *F. ruficornis* collected by emergence trap in *Q. pyrenaica* trees indicate that larva lives in rot-holes of this tree species. These new data about *F. ruficornis* contribute to the conservation value of the *Q. pyrenaica* forests, which have been shown as one of the most species-rich habitats in Cabañeros (Ricarte & Marcos-García, 2008). Thus *Q. pyrenaica* forests are each time more and more consolidated as one of the priority habitats for conservation in central Spain.

At taxonomic level, *F. ruficornis* shows a marked intra-specific variability in some characters. For instance, there are specimens with black hairs, at least, on 3rd tergum, but other specimens have only yellow hairs on terga. This fact explains the non-adjustment of most of the Iberian specimens to the key in Speight & Sarthou (2010), which is based only on specimens with black hairs on 2nd and 3rd terga. The variability is not only in the tergal hairs but also in the sternal hairs, which are from all yellow to partly black. Differences in these characters suggest the possibility to test the unity of this taxon by future molecular analyses, and by assessing new characters studied in recent works such as that in Doczkal & Pape (2009). These analyses may show the presence of cryptic species within *F. ruficornis*, as has been reported in other Eristalinae hoverflies (e.g. Mengual *et al*., 2006; Ståhls *et al*., 2009).

The type of *F. cuprea* is apparently lost forever; then a neotype may be designated to fix the concept of *F. cuprea*, not so evident after the recent description of closely-related species such as *F. fumipennis*, and the high variability in colouration reported for *Ferdinandea* species (Kassebeer, 1999). In spite of *F. aurea* seems to be a distinctive species, a holotype should also be designated amongst the specimens that Rondani used to base the original description (Ricarte *et a*l., in prep).

Data on the breeding trees of *F. aurea* (rot-holes in *Q. faginea* and *Q. pyrenaica* trees; Table 1) are important because it is the first known information on the life cycle of this hoverfly species. Despite *Q. faginea* also being present in north-Africa, its European distribution is restricted to the south of the Iberian Peninsula, and also the south of France and Italy, in accordance with a similar distribution of *F. aurea*. *Q. pyrenaica* seem to be a broadly used tree species for breeding by *Ferdinandea* species, as the larvae of all the Iberian species live on it (Table 1).

According to the maps provided, the Mediterranean character is evident of both *F. aurea* and *F. fumipennis*, which are distributed in the southern half of the Iberian Peninsula. *F. cuprea* is distributed in the northern half of the Iberian Peninsula, but central Spain represents a connecting area between both faunas. We remark the high relevance of Cabañeros as a protected area in this connecting region of the Iberian Peninsula.

An extra effort should be made to find the early stages of *F. aurea* and *F. ruficornis*. This is to know their full life cycles and ecological requirements, and provide a more robust base to conserve a typically-Mediterranean species and an endangered species, respectively (Speight *et al*., 2010). In the same line, the taxonomy of *F. ruficornis* at Palaearctic level should be definitively clarified to assess its real conservation status. The present paper means a first approach to the taxonomy of the genus *Ferdinandea* by studying the Iberian material of this genus and remarking some of the taxonomic problems to be solved in the future (Ricarte *et al*., in prep).

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APÉNDICE 2

Lo que las oquedades esconden

Marcos-García, M.A., Micó. E., **Quinto, J.,** Briones, R. Galante, E., 2010. Lo que las oquedades esconden. Cuadernos de biodiversidad 34: 3-7.

Abstract

What the hollows hide? Saproxylic insects comprise the largest component of the biodiversity in terrestrial ecosystems. They are the responsible for the mechanical breakdown of woody material both directly, by tunnelling and feeding in living trees that are decaying, snags (standing dead trees) and logs (fallen trees, portions of trunk and large branches), or indirectly, through symbiotic relationships with fungi and other micro-organisms that humidify wood. In this paper we open a door to reflection about the importance of the tree holes for the saproxylic biodiversity in the Mediterranean forests.

" ….ustedes los ingleses con su fascinación por mirar bichos a través de microscopios y su amor por recolectar huesos, no ven lo minúsculas que resultan todas sus preocupaciones en el esquema general de las cosas...". Esta frase fue dirigida a Charles Darwin durante su viaje en el Beagle por mostrar con cierta frecuencia interés por las formas vivas poco conspicuas y principalmente por las de pequeño tamaño (DARNTON, 2006). Y en efecto, no es fácil mirar a través de un microscopio sin sentir fascinación por lo que se observa. Pero siendo esto verdad, se equivocaban en algo que vamos a intentar explicar a lo largo de estas líneas: sus preocupaciones no eran minúsculas, muy al contrario, estaban bien justificadas y por supuesto que resultan cruciales en el esquema general de las cosas, en este caso, en el funcionamiento integral de los ecosistemas.

Aunque por razones obvias, lo primero que acapara nuestra atención al observar la naturaleza es lo más llamativo por su tamaño, color, diseño, abundancia, etc., para entender bien los procesos naturales del funcionamiento de nuestros ecosistemas, la observación y el estudio debe hacerse en todas sus escalas y en toda su dimensión, incluyendo lo que permanece oculto a primera vista.

Existe una extensa literatura que nos facilita el conocimiento de la riqueza e importancia florística y faunística que caracteriza el bosque mediterráneo, principalmente en lo que se refiere al conocimiento de sus vertebrados, su vegetación y algunos pocos referidos a determinados grupos de artrópodos. Sin embargo, muy poco se conoce de sus insectos saproxílicos (GALANTE & MARCOS, 2004; MICÓ et al, 2005, 2008; RICARTE et al., 2007, 2009; MENDEZ et al., 2010), a pesar de que en este grupo de artrópodos, son muchas las especies que actúan como bioindicadoras del estado de conservación de nuestros bosques, constituyendo uno de los ensambles más interesantes en todos los ecosistemas donde se desarrollan. Vamos a explicar el porqué de esta fascinación y así entenderemos la importancia que tienen en el esquema general de las cosas.

Los bosques y, concretamente, los bosques maduros son un objetivo básico de conservación. Ellos albergan una gran cantidad de madera muerta (en pie y en suelo) que constituye una fuente de alimento y refugio para numerosas especies, de insectos, micromamíferos, aves, hongos, etc. Asimismo, en estos bosques maduros encontramos árboles viejos de gran diámetro que ofrecen a su vez numerosos microhábitat distintos tales como rugosidades de la corteza, lesiones, oquedades naturales de pequeño y gran tamaño etc. De entre todos ellos, las oquedades pueden considerarse auténticas cajas sorpresa (Fig. 1), formadas por muy diferentes motivos, algunos de ellos naturales como la caída de un rayo o la fragmentación de una rama por la acción del viento, y otros favorecidos por la acción humana como el manejo de la poda.

Figura 1: Oquedad en un tronco de fresno (Foto: E. Micó).

Si nos asomamos al interior de estas oquedades y analizamos su contenido, veremos que en ellas se almacena toda aquella materia orgánica vegetal que, por la propia gravedad o por la acción del viento, queda allí retenida (hojas, trozos de corteza, polen, resina, frutos, etc.). Este depósito natural, por sus propias características, mantiene elevada humedad en su interior y actúa además de contenedor del agua de lluvia durante variables periodos de tiempo a lo largo del año, pudiendo ser, en los largos periodos estivales del bosque mediterráneo, los únicos microhábitats donde hay agua acumulada. Y es en este hábitat tan particular, tan efímero y tan dependiente de otros factores bióticos y abióticos, incluido el azar, donde se desarrollan de un modo muy especializado y exclusivo, los ciclos de vida de muchos invertebrados, entre los que insectos son los más abundantes.

En cada oquedad hay una oportunidad de vida para los organismos saproxílicos que son *aquellos que dependen de madera muerta o dañada, savia, hongos de la madera o de cualquier otra especie saproxílica, durante alguna parte de su ciclo de vida* (SPEIGHT, 1989). Por lo tanto, en cada oquedad se desarrolla una auténtica comunidad cuyos miembros interactúan entre sí pudiendo convivir en oquedades del mismo agujero organismos con múltiples formas de vida: saproxilófaga, xilófaga, xilomicetófaga, depredadora, parásita, mutualista, etc.

Si observamos atentamente la oquedad de un árbol, no es improbable ver los insectos que se acercan a depositar sus huevos en ella, siendo de distintas especies según la estación del año. Sin embargo, el desarrollo y la actividad de sus fases inmaduras, permanecen ocultos a nuestros ojos tras la oscuridad del orificio durante largos periodos de tiempo, a veces durante varios años, sin que exteriormente se manifieste ningún cambio apreciable.

A pesar de la escasa atención dedicada al estudio de la vida dentro de estas oquedades, y los ecosistemas mediterráneos no son una excepción, éstas albergan y permiten la vida animal de una gran cantidad de especies entre las que hemos estudiado algunos insectos como son los dípteros sírfidos y el grupo más numeroso, los coleópteros. Para hacernos una idea de la importancia numérica de estos dos grupos de insectos, citaremos algunos datos recientes obtenidos durante el desarrollo de dos Proyectos de Investigación subvencionados por el Ministerio de Ciencia e Innovación (CGL2008-04472 y CGL2009-09656 /BOS), dirigidos por la Dra. Micó y el Dr. Galante respectivamente.

Para el cumplimiento de los objetivos propuestos en estos proyectos, lo primero es conocer las especies de insectos saproxílicos que viven en los árboles de nuestros bosques mediterráneos. Para ello, las prospecciones realizadas a lo largo de un año de estudio, en un total de 87 oquedades, nos han permitido estudiar insectos pertenecientes a más de 40 familias de dípteros y coleópteros, habiendo identificado hasta la fecha un total de 145 especies. Son muchas las especies que, de no haber tenido en cuenta el estudio de las oquedades en troncos, raíces y ramas de nuestros árboles, no habrían sido consideradas en las estimaciones de biodiversidad de especies animales en estos ecosistemas mediterráneos.

Estos insectos, pertenecen al grupo de los holometábolos (con ciclos completos de desarrollo constituidos por: huevo, larva, pupa y adulto) cuyas fases inmaduras transcurren en el interior de la oquedad. Los adultos nacen generalmente en su interior y al poco tiempo salen a la luz para culminar fuera el resto de sus actividades vitales, principalmente la reproducción. En su fase adulta los requerimientos tróficos son distintos a lo que necesitaron en la oquedad, dependiendo ahora su alimentación de otros recursos como el néctar y el polen y participando por tanto en nuevas funciones ecológicas como por ejemplo la polinización. En esta fase adulta presentan una mayor capacidad de dispersión que les permitirá buscar y seleccionar nuevas oquedades donde poder perpetuarse como especie, si bien muchas especies saproxílicas presentan una muy baja capacidad de dispersión, incluso en su fase adulta, siendo éstas muy difíciles de encontrar en el medio si no es dentro de la oquedad.

Además de la importancia cuantitativa en cuanto al número de especies y de individuos, en algunos casos, es significativa la importancia que representan estas especies como bioindicadoras del estado de conservación de nuestros ecosistemas. Algunas de ellas son claves en la definición y establecimiento de estrategias de gestión de las áreas naturales por ser sus poblaciones escasas, presentar alguna categoría de conservación a nivel europeo, o estar en el límite geográfico de su distribución, como en el caso de *Mallota dusmeti* (Diptera, Syrphidae), especie catalogada como VULNERABLE en el *Libro Rojo de los Invertebrados de España* (MARCOS-GARCÍA, 2006) (Fig. 2).

Figura 2: *Mallota dusmeti* (Diptera: Syrphidae) (Foto: José Ignacio Pascual www.inectariumvirtual.com).

Otro ejemplo de esto lo constituye el Elatérido *Limoniscus violaceus* (Müller, 1821) (Fig. 3), coleóptero saproxílico endémico del continente europeo que presenta una distribución severamente fragmentada en todo su rango. Esta especie se encuentra incluida en el Anexo II de la Directiva Europea Hábitat y recientemente ha sido catalogada como EN PELIGRO en la Lista Roja de Coleópteros Saproxílicos Europeos (NIETO & ALEXANDER, 2010).

Figura 3. *Limoniscus violaceus* (Coleoptera: Elateridade) (Foto: E.Micó).

Asimismo, desde el punto de vista de la funcionalidad de las especies, gran parte de la entomofauna saproxílica es la responsable de la fragmentación de los restos de madera tanto directamente, realizando túneles y alimentándose en árboles en pie, en troncos o ramas depositadas en el suelo, como indirectamente a través de relaciones endosimbióticas con hongos y otros microrganismos que humidifican la madera (SPEIGHT 1989). Constituyen muchos de ellos, por lo tanto, un ensamble que actúa como descomponedores de materia vegetal, participando en la fase de fragmentación y facilitando, a los verdaderos organismos degradadores (hongos y bacterias), la transformación de la materia orgánica en elementos inorgánicos, devolviendo así los nutrientes al medio y cerrando el ciclo de materia y energía. Por este motivo, la madera muerta y la fauna saproxílica que sobre ella actua, participan a su vez en un gran número de funciones ecológicas en los ecosistemas terrestres capturando carbono, favoreciendo la formación de humus y contribuyendo en definitiva al mantenimiento de la biodiversidad y al incremento de la productividad (SCHLAGHAMERSKY, 2003; CAVALLI & MASON, 2003). En este sentido, la presencia de madera muerta y de una adecuada comunidad descomponedora (insectos saproxílicos) en áreas boscosas, constituye un indicador de calidad y madurez del hábitat.

Se desconoce el número de especies con hábitos saproxílicos en Europa, pero sólo en el grupo de los coleópteros ya se cuentan por miles. Por ejemplo, en Gran Bretaña el 7% de todos lo animales son saproxílicos y la mitad de ellos coleópteros (NIETO & ALEXANDER, 2010). Muchas de estas especies juegan un importante papel en las interacciones ecológicas dentro de la comunidad saproxílica como ocurre con algunos coleópteros Cerambícidos, cuyas larvas realizan túneles en la madera actuando como verdaderos arquitectos del ecosistema al favorecer la creación de microhábitats para otros insectos saproxílicos (BUSE *et al.*, 2008).

Por lo que hemos estudiado hasta el momento, y considerando lo que aún queda por saber, principalmente en lo que se refiere a las interacciones de las especies dentro de la oquedad y en el contexto general del ecosistema, la atención dedicada al estudio de estos organismos no debe calificarse de preocupación minúscula. Son hábitats lentos en su formación, con algunas características fisicoquímicas permanentes en el tiempo, otras efímeras, pero cuyo estudio tiene una gran trascendencia en el conocimiento de la biodiversidad, en la conservación de los ecosistemas forestales en general y en particular, de la vida de muchos seres vivos ligada a oquedades de ejemplares maduros de árboles.

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MARCOS-GARCÍA, Mª A., 2006. *Mallota dusmeti* Andréu,1926. (En: VERDÚ y E. GALANTE editores). Libro Rojo de los Invertebrados de España: 175. D. G. Biodiversidad. Ministerio de Medio Ambiente, Madrid. Figura 3. *Limoniscus violaceus* (Coleoptera: Elateridade) (Foto: E.Micó)

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APÉNDICE 3

Nueva cita de *Limoniscus violaceus* (Müller, 1821) (Coleoptera: Elateridae) para la región Mediterránea Ibérica

New record of *Limoniscus violaceus* (Müller, 1821) (Coleoptera: Elateridae) in the Iberian Mediterranean Region

Micó, E., **Quinto, J.**, Briones, R., Brustel, H., Galante, E., 2010. Nueva cita de *Limoniscus violaceus* (Müller, 1821) (Coleoptera: Elateridae) para la región Mediterránea Ibérica. Boletín de la Asociación Española de Entomología 34: 427-429.

Resumen

Limoniscus violaceus (Müller, 1821) (Coleoptera: Elateridae) es un coleóptero saproxílico endémico del continente europeo donde presenta una amplia distribución caracterizada por estar severamente fragmentada en todo su rango. En algunos países como Dinamarca está extinta (MARTÍN, 1989), mientras que en otros, sus poblaciones sufren un claro declive debido fundamentalmente a un manejo inadecuado de su hábitat (NIETO & KEITH, 2010). Esta especie se encuentra incluida en el Anexo II de la Directiva Europea Hábitat (http://www.mma.es/portal/secciones/biodiversidad/rednatura2000/normativa/europea/europea) y recientemente ha sido cataloga como En Peligro en la Lista Roja de Coleópteros Saproxílicos Europeos (NIETO & KEITH, 2010). Habita en árboles maduros de los géneros *Fagus*, *Quercus* y *Fraxinus* con amplias cavidades, principalmente basales, donde se acumula abundante materia orgánica derivada de la descomposición de la madera por hongos (LESEIGNEUR, 1972, MURRIA & MURRIA, 2004). Su desarrollo larvario varia entre 15 a 16 meses. La fase de pupa tiene lugar al final del verano o comienzos de otoño y el imago inverna hasta su emergencia en la segunda mitad de la primavera (LESEIGNEUR, 1972, LAIBNER, 2000). La larva parece ser necrófaga, alimentándose de restos de insectos presentes en las oquedades de los troncos (RECALDE & SÁNCHEZ-RUIZ, 2002).

Se trata de una especie presente principalmente en regiones de influencia Atlántica y Continental, siendo muy rara en robledales termófilos Mediterráneos de donde se cuenta con escasos registros: en Francia, la localidad de “Forêt de la Sainte Baume” (Provence, Francia) en *Quercus pubescens* (H. Brustel *leg*), “Les Maures” (Provence, Francia) asociada a *Q. suber* (SERRE & BLANC, 2010), en Grecia “Mont Ossa” (Larissa), asociada a *Q. frenetto* y a *Fagus orientalis* (M Egger *leg*, *com. pers* a H. Brustel) y en Turquía, asociada a diversas especies de *Quercus* (*Q. cerris*, *Q. infectoria* y *Q. ithaburensis*) (Jansson & Coskun, 2008)

En la península Ibérica hasta ahora se conocían tan sólo cuatro registros; uno de Picos de Europa (Asturias) (MÉQUIGNON, 1930), dos del Pirineo Navarro (RECALDE & SÁNCHEZ-RUIZ, 2002) y la más reciente, también del Pirineo, en Aragón (MURRIA & MURRIA, 2004). Con este trabajo aportamos la cita más meridional de la península Ibérica: un macho y una hembra, Parque Nacional de Cabañeros (Ciudad Real) 30SUJ6568, 27/06/2009 y 28/07/2009, Micó, Quinto y Briones *leg*. Ambos ejemplares han sido encontrados en una fresneda termófila, más concretamente en oquedades basales de *Fraxinus angustifolia*. En el primer caso se trata de un fresno de 2,26m de perímetro (medido a 0,30cm del suelo) con una oquedad basal que albergaba en su interior un volumen de materia orgánica de 36dm^3. El otro ejemplar se encontró en un fresno de 1,66m de perímetro, en el interior de una oquedad de raíz que albergaba 21dm^3 de materia orgánica. Entre la fauna acompañante encontrada en estas oquedades destacamos otros elatéridos de interés como *Elater ferrugineus* Linnaeus*, Ampedus (Ampedus) aurilegulus* (Schaufuss) y *Megapenthes lugens* (Redtenbacher).

La presencia de esta especie en una localidad tan termófila amplía en gran medida su distribución conocida para la península Ibérica y revela la necesidad de un mayor esfuerzo de muestreo de *Limoniscus violaceus* en el territorio nacional dirigido fundamentalmente a las cavidades basales de árboles de gran talla de los géneros *Quercus* y *Fraxinus*.

Agradecimientos

Queremos agradecer a todo el personal de Parque Nacional de Cabañeros su inestimable apoyo en la realización de este trabajo, así como a J.L. Zapata de la Vega por su ayuda en la confirmación taxonómica de la especie. Trabajo Financiado por los Proyectos del Ministerio de Ciencia e Innovación, CGL2008-04472 y CGL2009-09656.

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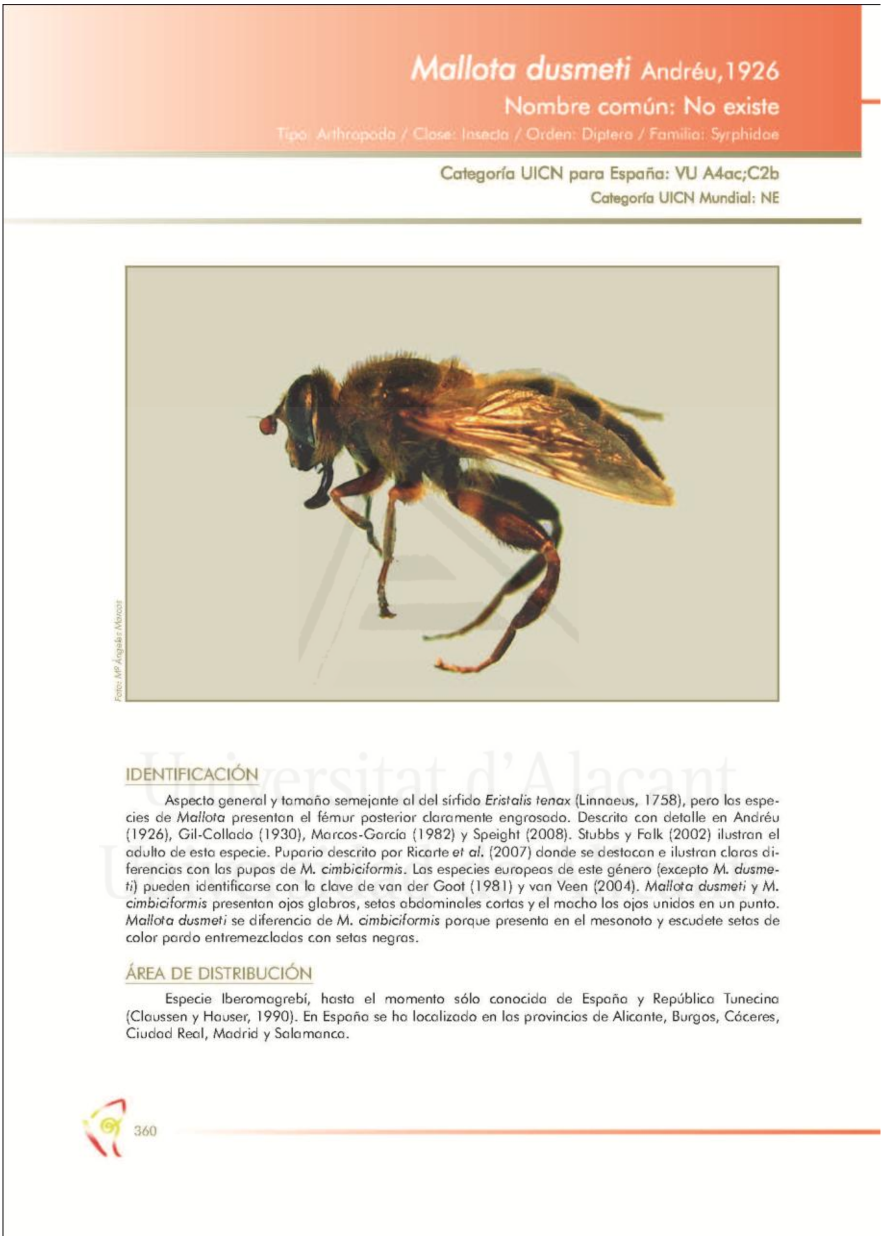
APÉNDICE 4

Mallota dusmeti Andréu, 1926

Marcos-García, M.A., **Quinto, J.**, 2011. *Mallota dusmeti* Andréu, 1926. Atlas y Libro rojo de los Invertebrados Amenazados de España (Especies Vulnerables). Vol: I. Editorial Ministerio de Medio Ambiente, Medio Rural y Marino, pp. 360-364.



Mallota dusmeti Andréu, 1926

Nombre común: No existe

Tipo: Arthropoda / Clase: Insecta / Orden: Diptera / Familia: Syrphidae

Categoría UICN para España: VU A4ac;C2b

Categoría UICN Mundial: NE

Foto: Mª Ángeles Marcos

IDENTIFICACIÓN

Aspecto general y tamaño semejante al del sírfido *Eristalis tenax* (Linnaeus, 1758), pero las especies de *Mallota* presentan el fémur posterior claramente engrosado. Descrito con detalle en Andréu (1926), Gil-Collado (1930), Marcos-García (1982) y Speight (2008). Stubbs y Falk (2002) ilustran el adulto de esta especie. Pupario descrito por Ricarte *et al.* (2007) donde se destacan e ilustran claras diferencias con las pupas de *M. cimbiciformis*. Las especies europeas de este género (excepto *M. dusmeti*) pueden identificarse con la clave de van der Goot (1981) y van Veen (2004). *Mallota dusmeti* y *M. cimbiciformis* presentan ojos glabros, setas abdominales cortas y el macho los ojos unidos en un punto. *Mallota dusmeti* se diferencia de *M. cimbiciformis* porque presenta en el mesonoto y escudete setas de color pardo entremezcladas con setas negras.

ÁREA DE DISTRIBUCIÓN

Especie Iberomagrebí, hasta el momento sólo conocida de España y República Tunecina (Claussen y Hauser, 1990). En España se ha localizado en las provincias de Alicante, Burgos, Cáceres, Ciudad Real, Madrid y Salamanca.

Número de UTM 1x1 Km visitadas	8
Número de UTM 1x1 Km confirmadas	6
Número de poblaciones conocidas antes de este estudio	11
Número de poblaciones nuevas	4
Número de poblaciones extintas	1
Número de poblaciones no confirmadas	9

HÁBITAT Y BIOLOGÍA

Las larvas de esta especie son saproxílicas y se desarrollan en oquedades de árboles maduros (*Quercus rotundifolia, Quercus faginea* y *Fraxinus angustifolia*) donde se dan condiciones de alta humedad, alimentándose de microorganismos procedentes de la descomposición de la materia vegetal. Los adultos son florícolas y visitan flores como la jara (*Cistus ladanifer* L.), próximas a las áreas arboladas en busca de recursos alimenticios como el polen y el néctar.

Especie monovoltina cuyas larvas completan su desarrollo a lo largo del año, pupando a finales del invierno. La pupación se ha constatado en el interior de la oquedad, pero también hay evidencias de una posible pupación en el exterior, cerca de la base del árbol. El periodo de pupación observado en condiciones de laboratorio, oscila entre 2 y 3 meses. Los nacimientos de los adultos en el campo comienzan al inicio de la primavera (de marzo a mayo), extendiéndose su actividad de vuelo hasta el mes de julio.

DEMOGRAFÍA

Se trata de una especie saproxílica cuya existencia depende de los árboles maduros donde se desarrollan sus larvas. Los adultos son raramente observados en la naturaleza desde los meses de abril a julio, alimentándose sobre las flores o volando alrededor de árboles maduros. Cada oquedad suele albergar mas de una larva (per. obs.). Su hábitat de desarrollo larvario se encuentra en franca regresión.

Tabla de localidades

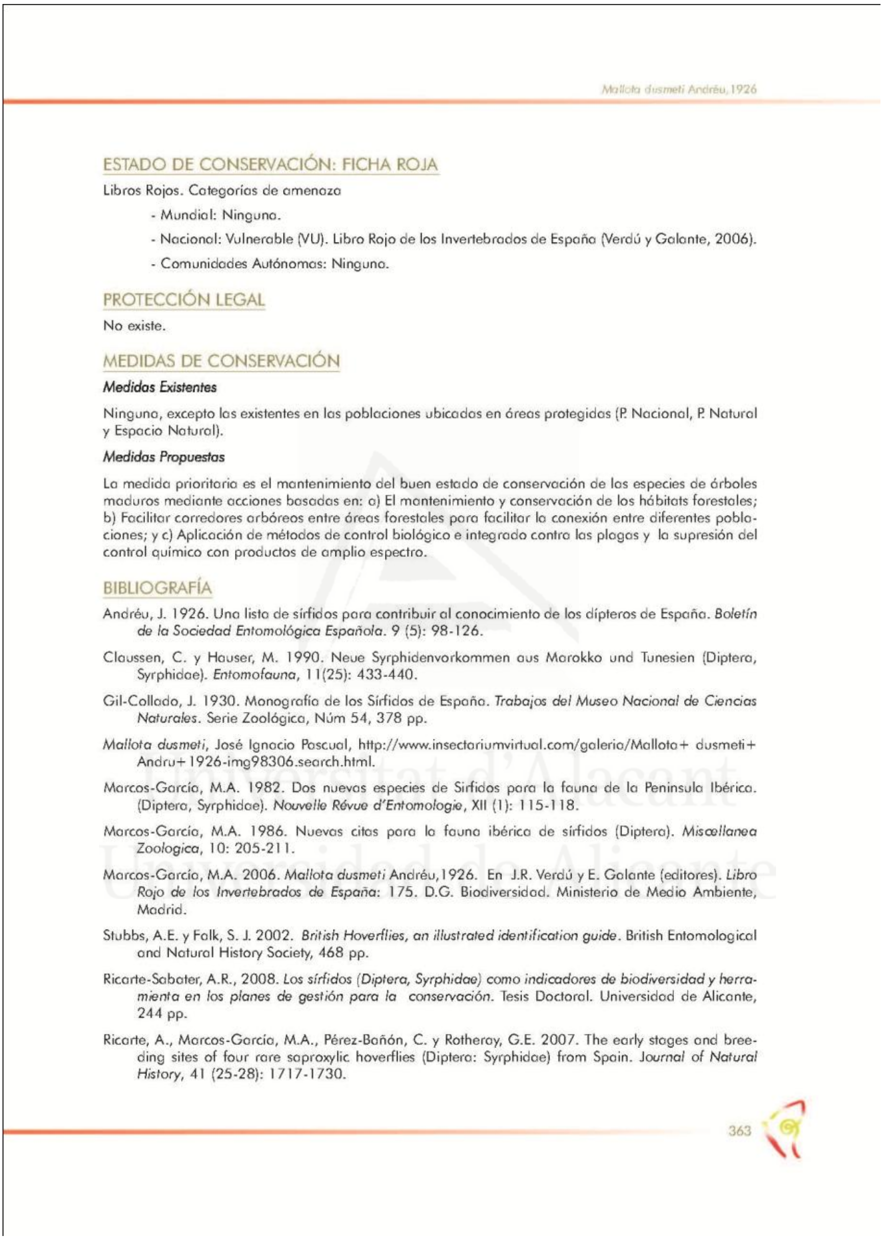
Fuente (año)	Visitada	Localidad	Provincia	UTM	Estado de conservación	Observaciones
Quinto y Briones, 2009	Quinto y Briones, 2009	Bañeres, Parque Natural Sierra de Mariola	Alicante	30SYH18	3	Área protegida con la figura de Parque Natural
Marcos- García, 1986		Cortes	Burgos	30TVM48	NE	Área situada en el ámbito periurbano y próxima al camping Fuentes Blancas con abundante arbolado.
Marcos- García, 1986		Los Membrillares	Cáceres	29TQF22	2	Área pública cercana a un pantano y destinada al baño
Marcos-García y Quinto, 2009	Marcos-García y Quinto, 2009	Parque Nacional de Cabañeros, Garbanzuelo	Ciudad Real	30SUJ66	3	Área protegida con la figura de Parque Nacional
Ricarte *et al.*, 2007	Marcos-García y Quinto, 2009	Parque Nacional de Cabañeros, Gargantilla	Ciudad Real	30SUJ66	3	Área protegida con la figura de Parque Nacional
Ricarte, 2008	Marcos-García y Quinto, 2009	Parque Nacional de Cabañeros, Valle de Canalejas	Ciudad Real	30SUJ76	3	Área protegida con la figura de Parque Nacional
Ricarte *et al.*, 2007	Marcos-García y Quinto, 2009	Parque Nacional de Cabañeros, Valle de Santiago	Ciudad Real	30SUJ76	3	Área protegida con la figura de Parque Nacional
Gil Collado, 1930		El Escorial	Madrid	30TUK09	NE	
Gil Collado, 1930	Pascual, 2009	El Pardo	Madrid	30TUK38	3	Espacio Natural de la Comunidad de Madrid y Patrimonio Nacional protegido
Gil Collado, 1930		Villaviciosa de Odón	Madrid	30TVK26	NE	
Gil Collado, 1930		Aranjuez	Madrid	30TVK53	2	
Gil Collado, 1930		Rivas	Madrid	30TVK56	0	
Marcos- García, 1986		Villaseco de los Gamitos	Salamanca	29TQF34	NE	
Marcos- García, 1986		Topas, Castillo del Buen Amor	Salamanca	30TTL76	NE	

FACTORES DE AMENAZA

Debido al régimen alimenticio de sus larvas, cualquier actividad que incida negativamente en la conservación de los ejemplares maduros de las especies arbóreas citadas como lugares de microhábitat de desarrollo larvario, afectará negativamente a la supervivencia de las poblaciones de esta especie. Por tanto, puesto que *Quercus faginea*, *Quercus rotundifolia* y *Fraxinus angustifolia*, especies arbóreas en cuyas oquedades han sido encontradas las larvas de *M. dusmeti*, son manejadas por el hombre mediante usos agrícolas y culturales, hay que arbitrar medidas para que los árboles viejos o las ramas desprendidas de gran porte que puedan tener oquedades, no sean eliminados del ecosistema.

El uso de productos fitosanitarios no específicos utilizados en el control de plagas forestales, puede afectar negativamente a la supervivencia de las larvas y de los adultos.

Cualquier actividad humana o factor ambiental que afecte a la densidad, supervivencia o estado de salud de los árboles maduros, afectará al hábitat de desarrollo larvario de *Mallota dusmeti*. Los periodos prolongados de sequía, aceleran la desecación en el interior de las oquedades de los árboles, provocando la mortandad de las larvas por deshidratación. Los tratamientos químicos en áreas forestales pueden dejar residuos en los árboles que penetren en las oquedades con el agua de la lluvia.



ESTADO DE CONSERVACIÓN: FICHA ROJA

Libros Rojos. Categorías de amenaza

- Mundial: Ninguna.
- Nacional: Vulnerable (VU). Libro Rojo de los Invertebrados de España (Verdú y Galante, 2006).
- Comunidades Autónomas: Ninguna.

PROTECCIÓN LEGAL

No existe.

MEDIDAS DE CONSERVACIÓN

Medidas Existentes

Ninguna, excepto las existentes en las poblaciones ubicadas en áreas protegidas (P. Nacional, P. Natural y Espacio Natural).

Medidas Propuestas

La medida prioritaria es el mantenimiento del buen estado de conservación de las especies de árboles maduros mediante acciones basadas en: a) El mantenimiento y conservación de los hábitats forestales; b) Facilitar corredores arbóreos entre áreas forestales para facilitar la conexión entre diferentes poblaciones; y c) Aplicación de métodos de control biológico e integrado contra las plagas y la supresión del control químico con productos de amplio espectro.

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AUTORES

Mª Ángeles Marcos García y Javier Quinto Cánovas.

Reunido el Tribunal que suscribe en el día de la fecha acordó otorgar, por a la Tesis Doctoral de D. Javier Quinto Cánovas la calificación de .

Alicante de de

El Secretario,

El Presidente,

UNIVERSIDAD DE ALICANTE

CEDIP

La presente Tesis de D. Javier Quinto Cánovas ha sido registrada con el nº____________ del registro de entrada correspondiente.

Alicante ___ de __________ de _____

El Encargado del Registro,