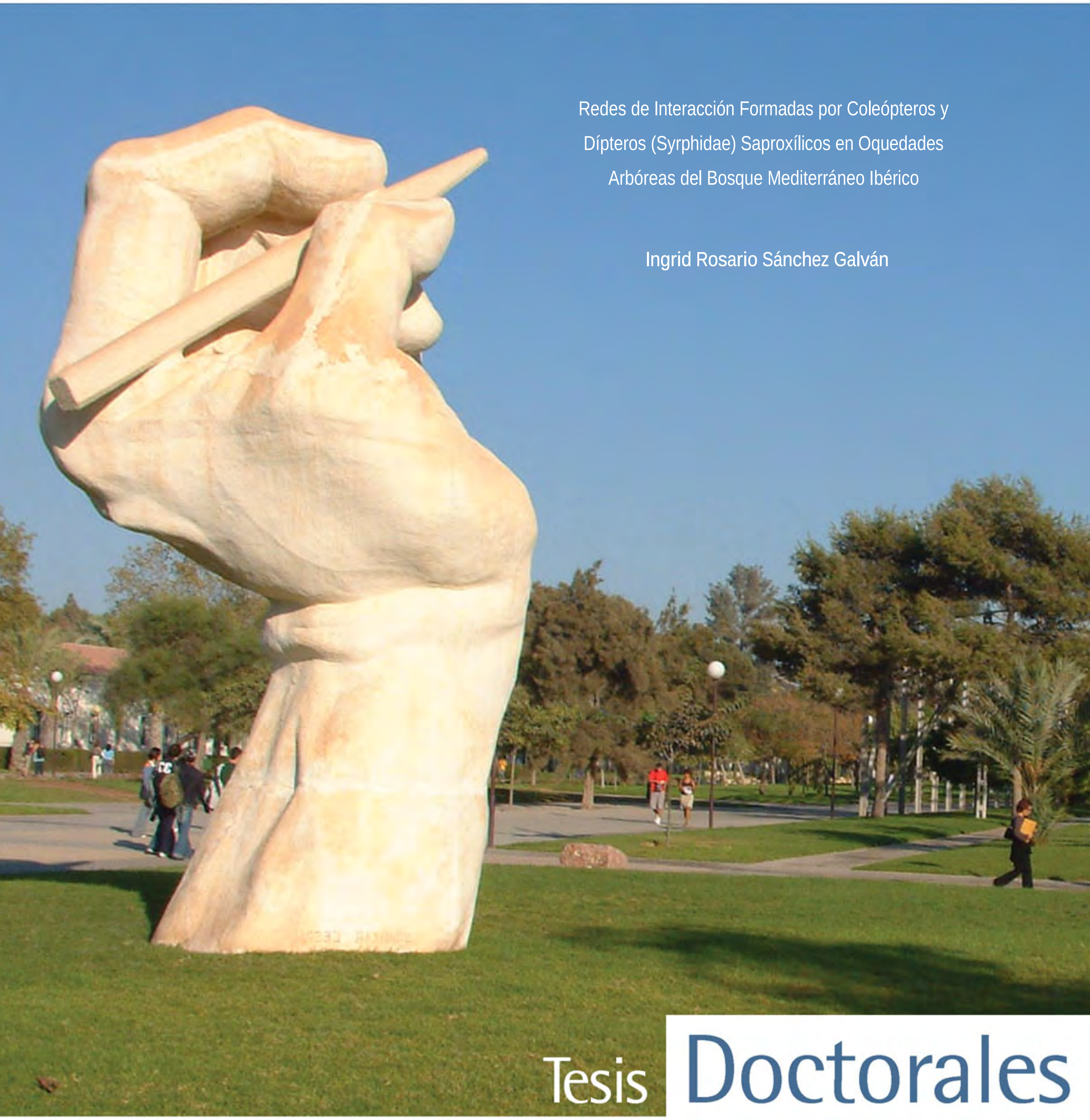

Redes de Interacción Formadas por Coleópteros y Dípteros (Syrphidae) Saproxílicos en Oquedades Arbóreas del Bosque Mediterráneo Ibérico

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Ingrid Rosario Sánchez Galván

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Sección I

Síntesis Inicial

Los insectos saproxílicos, una comunidad de alta diversidad en los ecosistemas forestales

Los organismos saproxílicos conforman una comunidad constituida por especies que al menos, en algún estadio de su ciclo vital, dependen directa o indirectamente de los procesos de descomposición de la madera, estando asociados tanto a árboles vivos como muertos, tanto en pie como caídos (Speight, 1989; Alexander, 2008). Los invertebrados, y especialmente los insectos, conforman en gran parte este grupo de organismos, el cual a su vez constituye la mayor biodiversidad que podemos encontrar en los ecosistemas forestales (Schlaghamersky, 2003; Saint-Germain et al., 2007).

Dentro de los insectos saproxílicos, dos son los grupos taxonómicos más abundantes, los Coleoptera y los Diptera Syrphidae (Dajoz, 1998; Micó et al., 2013a). Sus especies pueden ser clasificadas en diferentes gremios de acuerdo al uso trófico que hacen de los recursos que encuentran en el árbol y que están relacionados con el estado de descomposición de la madera, y con la presencia de los distintos organismos que la colonizan a lo largo del tiempo: xilófagos, saprófagos, saproxilófagos, xilomicetófagos, depredadores y comensales (Speight, 1989; Bouget et al., 2005; Stokland et al., 2012; Micó et al. 2013a) (Figura 1).

Dado que los insectos saproxílicos en general, los coleópteros y dípteros sírfidos en particular, tienen una alta dependencia del proceso y estado de descomposición de la madera, su biología se encuentra ligada a un amplio abanico de microhábitats que ofrecen los árboles a lo largo de su desarrollo, y que están condicionados por la especie arbórea y por el tipo de bosque (Quinto et al., 2014; Ramírez-Hernández et al., 2014a). Los microhábitats donde se encuentran las diferentes especies de insectos pueden ser muy diferentes y hacen referencia a las distintas partes del árbol que, en función de sus características, albergan distintos grupos de especies de insectos saproxílicos (Micó et al., 2013a). En consecuencia, los árboles vivos albergan microhábitats que pueden encontrarse en el interior de oquedades arbóreas, resquicios o rugosidades de la corteza, cuerpos fructíferos de hongos, lesiones por las que rezuma savia, galerías de insectos, etc. (Jonsell et al., 1998; Gouix et al., 2012; Speight & Castella, 2015) (Figura 2).

La importancia ecológica de los insectos saproxílicos estriba en su significativa contribución al mantenimiento de los procesos ecológicos del bosque y a su importante papel en la dinámica de fragmentación, procesado de sustratos de madera y reciclado de los nutrientes (Dajoz, 1998; Brustel, 2001; Cavalli & Mason, 2003; Micó et al., 2011a; 2013a; Stokland et al., 2012; Ulyshen, 2012). Estas diversas formas de vida, estrechamente asociadas a un amplio rango de microhábitats del árbol y de la madera muerta, unida a la alta riqueza y abundancia de especies de estas comunidades, justifican la consideración de que los insectos saproxílicos actúan como buenos indicadores del estado de conservación de los bosques (Ricarte et al., 2009; Marcos-García et al., 2010).

En Europa, desde hace varios años, se considera que los insectos saproxílicos son uno de los grupos animales más amenazados (Speight, 1989; Grove 2002, Nieto & Alexander 2010; Audisio et al., 2014) y en algunos países ya se han establecido medidas para su protección (Rotheray et al., 2009). La pérdida de fauna saproxílica a nivel europeo es consecuencia del progresivo y acelerado cambio de uso y gestión de las masas forestales (Speight, 1989; Haslett, 2007) que afecta de manera particular a los bosques mediterráneos ibéricos donde la pérdida de diversidad paisajística y de la fauna saproxílica asociada son consecuencia directa del creciente abandono de las actividades tradicionales agrosilvopastorales. La introducción de nuevos usos de suelo y de modelos de gestión del monte mediterráneo, ha suprimido en gran parte el uso sostenible de los recursos del árbol como son, entre otros, su madera (Canellas et al., 1996), lo que tiene como consecuencia la existencia de menor dinamismo ecológico de estos ecosistemas forestales con una tendencia a la pérdida de biodiversidad (Barbero et al., 1992; Galante & Marcos-García, 2013).

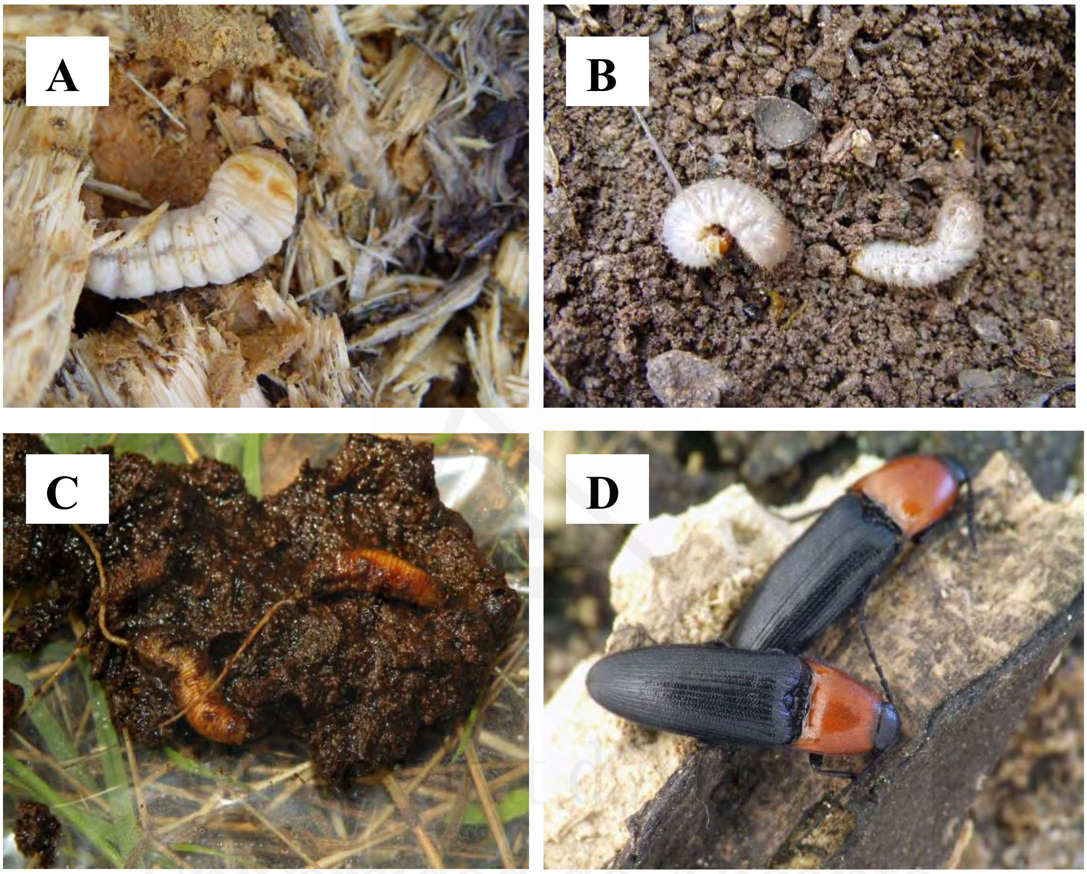

Figura 1 Los insectos saproxílicos (Coleoptera y Diptera: Syrphidae) pueden agruparse en distintos gremios según su régimen alimenticio. (A) Larva de coleóptero xilófago (Coleoptera: Cerambycidae), *foto de: E. Galante*; (B) larvas de coleópteros saproxilófagos (Coleoptera: Cetoniidae), *foto de: E. Galante*; (C) larvas de dípteros saprófagos (Diptera: Syrphidae), *foto de: M. A. Marcos-García*; (D) ejemplares adultos de coleópteros depredadores (Coleoptera: Elateridae), *foto de: T. Németh*.

Figura 2 La madera en descomposición ofrece distintos tipos de microhábitats, que a su vez pueden albergar distintas comunidades de insectos saproxílicos, *fotos de: Eduardo Galante.*

La oquedad arbórea, un medio propicio para el desarrollo de insectos saproxílicos

El objetivo de esta tesis doctoral es el estudio de las interacciones que se producen entre las especies de las comunidades de insectos saproxílicos (Coleoptera y Diptera Syrphidae) que viven dentro de oquedades en árboles de diferentes especies de *Quercus spp* de la península ibérica (Figura 3).

Una de las particularidades del árbol, dentro de ecosistemas de bosques en el mediterráneo ibérico, es la presencia de oquedades arbóreas, buena parte de ellas formadas como consecuencia del manejo tradicional al que han sido sometidas las especies leñosas a lo largo de los años (Marcos-García et al., 2010; Quinto et al., 2012; Micó et al., 2013a; Galante & Marcos-García 2013; Ramírez-Hernández et al., 2014a). Un ejemplo de ello son las oquedades que aparecen dispersas en el arbolado de encinares y robledales ibéricos (*Quercus spp*) y que en gran parte, son el resultado de prácticas de manejo de poda como el olivado y el trasmoche, que favorecen la aparición de heridas en los troncos que al envejecer y descomponerse la madera, causan oquedades donde se puede retener la humedad y el agua de lluvia (Sánchez-Martínez et al., 2013, Ramírez-Hernández et al., 2015) (Figura 3).

Estas oquedades constituyen hábitats particulares donde se acumula materia orgánica junto con el agua de lluvia, donde la actividad desarrollada por la microbiota descomponedora (Walker et al., 1988, 1991; Stokland et al., 2012) y la actividad biológica llevada a cabo por distintas especies animales que van ocupando la oquedad a través del tiempo, dejan sus restos que van enriqueciendo el medio (Micó et al., 2011a, 2015; Sánchez-Sánchez et al., 2017). En conjunto, la actividad biológica de todos estos organismos transforman sucesivamente el sustrato, permitiendo la colonización y desarrollo de otras muchas especies de insectos saproxílicos que sucesivamente se van incorporando a la cavidad del árbol (Micó et al., 2013b; Sánchez-Galván et al., 2014) (Figura 3).

Los distintos gremios tróficos de la comunidad saproxílica (Figura 1) tienen cubiertas sus necesidades de desarrollo en el interior de estas oquedades, donde son numerosos los microhábitats que pueden encontrarse (Quinto et al., 2014). En el interior de una oquedad, existe una alta heterogeneidad estructural y ambiental que permite la presencia de una alta diversidad taxonómica y ecológica de insectos saproxílicos (Quinto et al., 2014) que se encuentra ligada de manera preferente a los bosques de mayor edad y a los árboles de mayor tamaño (Figura 4) (Micó et al., 2011b; Quinto et al., 2014). Los datos obtenidos hasta ahora para bosques mediterráneos ibéricos han puesto de manifiesto que las oquedades arbóreas de mayor amplitud que se encuentran en árboles senescentes, son los reservorios con más alta diversidad y abundancia de coleópteros y dípteros sírfidos saproxílicos (Marcos-García et al., 2010; Micó et al., 2011b, 2013a; Quinto et al., 2012, 2014). Por otra parte, estos registros también han puesto de manifiesto la presencia de un considerable porcentaje de especies amenazadas incluidas en listados tanto de la Directiva Hábitats, como en el Libro Rojo de invertebrados de España (Verdú & Galante, 2006), y que se desarrollan única y exclusivamente dentro de oquedades arbóreas, como es el caso del coleóptero *Limoniscus violaceus* (Müller, 1821) (Elateridae) (Nieto & Alexander, 2010; Gouix, 2011; Micó et al., 2013b) y los sírfidos saproxílicos *Caliprobola speciosa* (Rossi, 1790) y *Mallota dusmeti* Andreu, 1926 (Verdú et al., 2011).

Figura 4 En las quercínas ibéricas las oquedades pueden ser encontradas en diferentes partes del árbol como consecuencia de las prácticas tradicionales de manejo del árbol. Estás oquedades suelen almacenar materia orgánica y agua, *fotos de Eduardo Galante*.

.

Figura 3 En el interior de cada bote colector, se percibe la diferente composición de especies de insectos saproxílicos (Coleoptera y Diptera: Syrphidae) que se desarrollan dentro de cada oquedad arbórea, *fotos de: Ingrid R. Sánchez-Galván*

Interacciones entre especies de insectos saproxílicos dentro de las oquedades: factores biológicos relacionados con el proceso de estructuración de ensambles

Un aspecto central abordado en esta tesis doctoral, es el estudio e investigación de las interacciones específicas insecto-insecto, como mecanismo múltiple que influye en la organización de los ensambles formados por especies de insectos saproxílicos ligados a las oquedades arbóreas, y que condicionan la estructura de la comunidad saproxílica de insectos del bosque mediterráneo ibérico (Sánchez-Galván et al., 2014).

En la naturaleza, las especies animales y vegetales se relacionan entre sí de diferentes maneras, formando una compleja red de interacciones (Thompson, 1994, 2005). Estas relaciones entre las diferentes especies son dinámicas y se desarrollan tanto a escala espacial como temporal, con resultados positivos para ambas especies (mutualismo y comensalismo), negativos (antagonismo) o bien neutros para la supervivencia de las mismas, todo ello a través de distintas y complejas redes de interacción inter e intraespecíficas (Ewald, 1987; Hayashi, 2006; Relman, 2008). A pesar de la importancia que tienen estas interacciones sobre la diversificación y organización de la vida, pocas veces se suele indagar o profundizar en lo que concierne a cómo surgen y evolucionan (Thompson, 1999) o cuál es su papel en la formación de las comunidades biológicas (Thompson, 2005). No obstante, en términos de conservación, manejo y uso de la biodiversidad, es importante considerar también las acciones e iniciativas dirigidas al estudio y conservación de las interacciones biológicas entre las especies (Thompson, 1996).

En un estudio previo sobre una comunidad formada por insectos saproxílicos Coleópteros y Dípteros (Syrphidae) ligada a oquedades arbóreas del bosque mediterráneo ibérico (Quinto et al., 2012), se puso de manifiesto que se encuentra organizada como una compleja red de relaciones que involucra a los diferentes gremios tróficos (xilófagos, saprófagos, saproxilófagos, xilomicetófagos, depredadores y comensales). Estas son redes ecológicas formada por relaciones interespecíficas donde, bien la competencia o bien la facilitación, pueden estar actuando como factores clave para la composición de especies de los ensambles de insectos saproxílicos dentro de cada oquedad (Jönsson et al., 2004; Quinto et al., 2012).

Las relaciones interespecíficas de facilitación ocurren cuando una especie es favorecida por la presencia o actividad previa o simultánea de otra especie (Munguia-Matute et al., 2009). Estudios con un amplio marco teórico referente a este tipo de interacciones positivas han sido tradicionalmente expuestos para comunidades formadas por plantas, las cuales usualmente se han considerado bajo el concepto de "efecto nodriza" (Callaway, 1995; Callaway & Pugnaire, 1999), ejerciendo a su vez una gran influencia sobre la estructuración de los ensambles dentro de la comunidad (Callaway & Lawrence, 1997; Brooker & Callaghan, 1998; Brooker, 2006; Valiente-Banuet & Verdú, 2008; Verdú & Valiente-Banuet, 2008; Maestre et al., 2009). Para las comunidades animales, las interacciones interespecíficas de facilitación se consideran generalmente bajo un concepto distinto al de las plantas, aplicándoles el concepto de "ingeniero del ecosistema", definiendo como tales a aquellas especies que son capaces de transformar física o químicamente el medio, propiciando de este modo, un ambiente más adecuado para la colonización y supervivencia de otras especies (Jones et al., 1994).

Al inicio de esta tesis doctoral nos planteamos que la presencia de especies "ingenieros del ecosistema" dentro de comunidades biológicas formadas por los insectos saproxílicos (Coleoptera y Diptera Syrphidae) en oquedades arbóreas, constituía un escenario potencialmente interesante y muy poco estudiado (Ranius, 2002; Jönsson et al., 2004; Buse et al., 2008; Micó et al., 2011a, 2015; Victorsson, 2012; Sánchez-Galván et al., 2014). Por otra parte resultaban escasos los estudios que abordaban las interacciones de facilitación *per se*, o de otro tipo de interacciones cuando se comparten los mismos recursos como ocurre dentro de una misma oquedad de árbol (Schmidl et al., 2008).

Por ello unas de las primeras preguntas que se plantearon resolver en esta tesis doctoral fue:

i) ¿Cuál es el efecto de facilitación ejercido por la actividad de una especie ingeniero del ecosistema sobre la distribución y supervivencia de otras especies de insectos saproxílicos?

Esta cuestión es abordada en la **Sección II (a)** dentro de esta memoria de tesis doctoral y sus resultados ya han sido publicados:

Sánchez-Galván I.R., Quinto J., Micó E., Galante E. & Marcos-García M. A. (2014) Facilitation Among Saproxylic Insects Inhabiting Tree Hollows in a Mediterranean

Forest: The Case of Cetonids (Coleoptera: Cetoniidae) and Syrphids (Diptera: Syrphidae). *Environmental Entomology*, 43(2): 336–343. Doi: 10.1603/EN13075

Es importante recalcar que las comunidades biológicas que están formadas por múltiples especies de plantas, al igual que aquellas formadas por especies animales, el marco conceptual de las relaciones interespecíficas suele estar definido como la serie de mecanismos biológicos que permiten la coexistencia de las especies que comparten un mismo recurso (Agrawal et al., 2007; Sutherland et al., 2013), todo ello de acuerdo con la teoría de nicho ecológico (Chase & Leibold, 2003; Levine & HilleRisLambers, 2009). Sin embargo, gran parte de los trabajos que estudian estas relaciones, particularmente para comunidades formadas por especies animales, se suelen centrar en las interacciones de competencia (Stachowicz, 2001; Bruno et al., 2003). Por otra parte, son también pocos los ejemplos que involucran especies de insectos saproxílicos ligados a alguna figura de protección, o a sus interacciones de facilitación ejercidas sobre otras especies de insectos saproxílicos (Jönsson et al., 2004; Ranius et al*.,* 2005; Buse et al., 2008; Chiari et al., 2014). Sin embargo, dentro de cada oquedad, un alto número de especies de insectos (coleópteros y dípteros sírfidos principalmente) coexisten e interactúan de diferentes formas entre ellos así como con el sustrato en descomposición donde viven y se desarrollan (Quinto et al., 2012, 2014). Un análisis previo nos reveló como los factores bióticos, como la presencia y/o actividad de especies "ingenieros del ecosistema" dentro de las oquedades, influyen sobre la diversidad de coleópteros saproxílicos (Quinto et al., 2014; Micó et al., 2015). Sabíamos que la acción de grandes cerambícidos, perteneciente al gremio de los xilófagos, así como algunos cetónidos, perteneciente al gremio de los saproxilófagos, al transformar física y químicamente el sustrato dentro de las oquedades, actúan como agentes que podrían facilitar el establecimiento de otras especies (Micó et al., 2011a; 2015). Estos datos nos indicaban que teniendo en cuenta la distribución agregada entre especies comensales y especies xilófagas o saproxilófagas detectadas en los ensambles saproxílicos, podría existir un efecto de facilitación directa asociada a los procesos de colonización sucesiva del medio (Buse et al., 2008; Sánchez-Galván et al., 2014; Micó et al., 2015; Zuo et al., 2016).

Para evaluar la presencia de interacciones de facilitación, tomamos como modelo de estudio la coincidencia previamente observada en campo entre cetónidos (Coleoptera Cetoniidae) y sírfidos (Diptera) saproxílicos. En este sistema, las larvas de cetónidos son capaces de transformar grandes fragmentos de celulosa y lignina, material complejo proveniente de las paredes de la oquedad, y producir una gran cantidad de heces que perduran a lo largo del tiempo (Micó et al., 2011a), y que enriquecen el sustrato dentro de la oquedad (Micó et al., 2011a, 2015; Sánchez-Sánchez et al., 2017), lo que podría facilitar la presencia de otros insectos saproxílicos. Como resultado de nuestras investigaciones, se puso de manifiesto que la actividad de las larvas de los cetónidos (registrada como la presencia de larvas/o presencia de heces) fue la variable que mejor explica la presencia de sírfidos saprófagos en las oquedades del árbol. A su vez, encontramos que bajo condiciones de laboratorio, un sustrato enriquecido con heces de *Cetonia aurataeformis* Curti, 1913, mejora la tasa de crecimiento larvario, así como la eficacia biológica de los adultos de sírfidos saprófagos de la especie *Myathropa florea* Linnaeus 1758. A partir de estos resultados, se puede considerar que larvas de escarabajos de la familia Cetoniidae, particularmente de la especie *C. aurataeformis*, pueden actuar como especies ingenieros del ecosistema en los ensambles de insectos saproxílicos que viven en las oquedades arbóreas del bosque mediterráneo Ibérico.

No obstante, no todas las relaciones que se producen en una comunidad son interacciones de facilitación (Buse et al., 2008; Micó et al., 2011, 2015; Sánchez-Galván et al., 2014; Zuo et al., 2016), existiendo otros tipos de interacciones biológicas en la comunidad saproxílica (*ej.* Rankin & Borden, 1991; Dodds et al., 2001; Hughes & Grabowski, 2006; Johansson et al., 2007). A pesar de la importancia de estas interacciones, se conoce muy poco acerca de cómo los múltiples tipos de interacciones insecto-insecto afectan la estructuración de estos ensambles. Por ello consideramos como otro objetivo en esta tesis, el poder comprender e interpretar cómo las distintas relaciones de interacción entre las especies saproxílicas pueden moldear la estructura de sus ensambles (Coleoptera y Diptera Syrphidae) en el interior de las oquedades y para ello nos planteamos nuevas preguntas:

ii)¿De qué tipo son las relaciones interespecíficas de los insectos saproxílicos (Coleoptera y Diptera: Syrphidae) dentro de oquedades arbóreas en el bosque mediterráneo ibérico?

iii) ¿cuál es la influencia de estas interacciones biológicas sobre la distribución espacial de las especies y qué papel juegan en la presencia de especies incluidas en listados de especies amenazadas en Europa?

Estas cuestiones son abordadas en la **Sección III** y sus resultados se encuentran en revisión por evaluadores:

Sánchez-Galván, I. R., Marcos-García, M. A., Azeria, E., Galante, E., & Micó E. Unravelling Saproxylic Insect Interactions in Tree Hollows from Iberian Mediterranean Forest. *Biodiversity and Conservation* (submitted 2017).

Partimos de una base conceptual en la que las relaciones interespecíficas pueden ser entendidas como los mecanismos que dirigen la estructuración de los ensambles biológicos (*i.e.* la distribución espacial de las especies) (Camarota et al., 2016) y así nos planteamos profundizar en el estudio del efecto que tienen las diferentes relaciones interespecíficas (*ej.* competencia, depredador-presa, comensalismo, facilitación, etc.) sobre los patrones de asociación de las especies de coleópteros y sírfidos saproxílicos.

Para alcanzar este objetivo, hemos utilizado grandes bases de datos que reflejan la distribución absoluta de especies de coleópteros y dípteros sírfidos saproxílicos (de diferentes gremios tróficos) tomando en cuenta los datos de 72 oquedades arbóreas dentro tres espacios forestales protegidos (Parque Nacional de "Cabañeros"; Reserva Natural de "Campanarios de Azaba" y Espacio protegido "Sierra de las Quilamas") (Figura 5). Nuestra estrategia de análisis ha sido la utilización de modelos nulos (Gotelli, 2000) para evaluar patrones de coocurrencia (*i.e.* agregaciones o segregaciones entre pares de especies). Este meta análisis permite la identificación de patrones no aleatorios de asociación de especies dentro de una distribución global de las mismas que conforman grandes inventarios biológicos y así inferir sobre los mecanismos responsables de su estructuración (Gotelli, 2000; Ulrich & Gotelli, 2007; Gotelli & Ulrich, 2012).

Para el análisis de los datos se tuvo en cuenta que no siempre la presencia de interacciones interespecíficas son la pronta respuesta ante la detección de patrones no aleatorios de distribución y en particular cuando se encuentra una marcada segregación entre pares de especies (Connor & Simberloff, 1979, 1984; Peres-Neto et al., 2001), ya que otros factores como la capacidad de dispersión de las especies, o la alta especificidad en los requerimientos de hábitat, pueden producir también patrones de este tipo (Sanderson et al., 2004; Sfenthourakis et al., 2006; Azeria et al., 2012). También, la presencia de un proceso conocido como "filtración de nicho", donde bien las similitudes o las diferencias en la ocupación del nicho ecológico por parte de las especies pueden ser los mecanismos que condicionan la estructuración de los ensambles de la comunidad, y pueden dar la respuesta causal de la presencia de patrones no aleatorios de distribución agregada o segregada entre las especies (Fowler et al., 2014; Camarota et al., 2016).

De acuerdo con nuestros resultados a nivel de matriz, se muestra que regionalmente hay una tendencia general hacía la segregación de las especies, lo que hace tentador especular sobre una dominancia de interacciones de competencia, o que estas segregaciones sean causadas por las diferencias en la ocupación de las oquedades por parte de las especies. Sin embargo este nivel de análisis cuando es aplicado a grandes bases de datos, puede enmascarar el sentido biológico de la existencia de múltiples interacciones interespecíficas, que quizás otros patrones no aleatorios como aquellos detectados en parejas individuales de especies sí podrían aportarlo. Por ejemplo, el análisis a nivel de pares de especies nos mostró un mayor número de patrones no aleatorios agregados que segregados, a nivel local y regional. Aun así, los patrones no aleatorios tanto agregados como segregados, fueron más numerosos entre parejas de especies pertenecientes a diferentes gremios tróficos, siendo en un porcentaje más alto aquellas parejas que implican agregaciones espaciales entre depredadores y presas. Nuestros resultados sugieren que interacciones biológicas como depredador-presa e interacciones de facilitación, actúan como los principales factores biológicos que moldean la estructura y organización espacial de los ensambles de insectos saproxílicos (Coleoptera y Diptera Syrphidae) formados dentro de las oquedades. Además esta investigación, nos ha puesto de manifiesto la importancia en términos de conservación biológica, de la existencia de diversas relaciones interespecíficas donde especies consideradas “ingenieros del ecosistema”, “especies amenazadas” o “casi amenazadas” tienen un papel fundamental dentro de la estructuración y dinamismo del ensamblaje saproxílico.

Finalmente, como una de las aportaciones al conocimiento sobre las interacciones interespecíficas, de importante calado en la elaboración de estrategias de conservación de insectos saproxílicos, es el estudio del conjunto de los agentes bióticos que determinan la biodiversidad saproxílica dentro de las oquedades (Quinto et al., 2014). De ahí surgió la necesidad de explorar aquellos organismos que constituyen la microbiota que se desarrolla en las oquedades y sus interacciones biológicas con los insectos saproxílicos con los que coinciden en el tiempo y espacio.

Bajo este escenario biológico, nos planteamos como pregunta a resolver:

iv) ¿existen interacciones biológicas entre insectos saproxílicos y la microbiota dentro de oquedades arbóreas y cómo son estas relaciones?

Los resultados se recogen en la **Sección II (b)** de esta memoria de tesis doctoral, dentro de la publicación:

Sánchez-Galván, I. R., Ferrer, J., Galante, E., & Marcos-García, M. A. (2016). Bacteria and Hoverflies (Diptera: Syrphidae) in Tree Hollows From the Iberian Mediterranean Forest. *Environmental Entomology*. 46(1): 137–142. Doi: 10.1093/ee/nvw158.

El proceso de descomposición de la madera y de la materia orgánica, depende principalmente de microorganismos descomponedores como son los hongos y las bacterias. Ellos son los principales agentes que transforman la materia orgánica devolviendo los nutrientes al medio (Lavelle et al., 1993; Cornwell et al., 2009; Marcos-García et al., 2010; Micó et al., 2013a). En la naturaleza existe una gran diversidad de microorganismos que viven a expensas de la madera, exhibiendo una amplia gama de estrategias y de mecanismos de descomposición (Greaves, 1971; Stokland et al., 2012). La microbiota que se encuentra en el interior de las oquedades puede realizar su acción descomponedora al actuar directamente sobre la madera o bien de forma indirecta, una vez que esa madera ya se encuentra en el tracto digestivo de algunos insectos, como es el caso de ciertos coleópteros saproxílicos (Bayon, 1981; Kukor & Martin, 1986; Kukor et al., 1988; Martin et al., 1991; Stokland et al., 2012, Engel & Moran, 2013). Para dar respuesta a esta cuestión, se tomó como modelo de estudio el medio líquido que se forma en algunas oquedades arbóreas donde previamente habíamos comprobado que se desarrollan las fases larvarias de dípteros (Syrphidae) saproxílicos.

A pesar de que en Europa los sírfidos saproxílicos en estado adulto son uno de los grupos taxonómicos más estudiados y reconocidos (Speight & Castella, 2015; Ricarte & Marcos-García, 2017), y para los que en algunos países se contemplan medidas de conservación (Rotheray et al., 2009), nada se sabía de las relaciones que establecen entre sus fases larvarias acuáticas y las especies de bacterias que se desarrollan en su medio de crecimiento. El único precedente existente sobre estos estudios en sírfidos, se desarrolló en condiciones muy diferentes por tratarse de las relaciones establecidas entre las larvas de especies saprófagas del género Neotropical *Copestylum* (Eristalinae: Syrphidae) y las bacterias asociadas al tejido acuoso de cactáceas en estado de descomposición donde se desarrollan las larvas de algunas especies de este género (Martínez-Falcón et al., 2011). No obstante, se sabía que en el medio saproxílico el papel de las bacterias es muy importante al actuar como organismos descomponedores de madera, principalmente en condiciones de alta humedad (Stokland et al., 2012). Tal es el caso del interior de las oquedades de *Quercus spp.,* donde con frecuencia se almacenan grandes cantidades de agua de lluvia (Quinto et al., 2014; Ramírez-Hernández et al., 2015) que pueden además permanecer durante largos periodos de tiempo, pese a las condiciones estivales propias de la región mediterránea (Marcos-García et al., 2010). Estas oquedades son el único hábitat de desarrollo larvario de muchas de las especies de sírfidos saproxílicos (Quinto et al., 2014), y de entre ellas cabe mencionar a *Mallota dusmeti* Andreu, 1926, especie endémica de estos particulares ecosistemas mediterráneos. Sus larvas son conocidas como "larvas cola de ratón" por su largo espiráculo respiratorio que les permite obtener el oxígeno atmosférico cuando están sumergidas en el agua. Estas larvas acuáticas son saprófagas y se alimentan de pequeñas partículas orgánicas y de la microbiota existente en el medio acuoso que permanece estancado en el interior de las oquedades y que obtienen mediante mecanismos especializados de filtración (Rotheray & Gilbert, 2011; Rotheray & Lyszkowski, 2015).

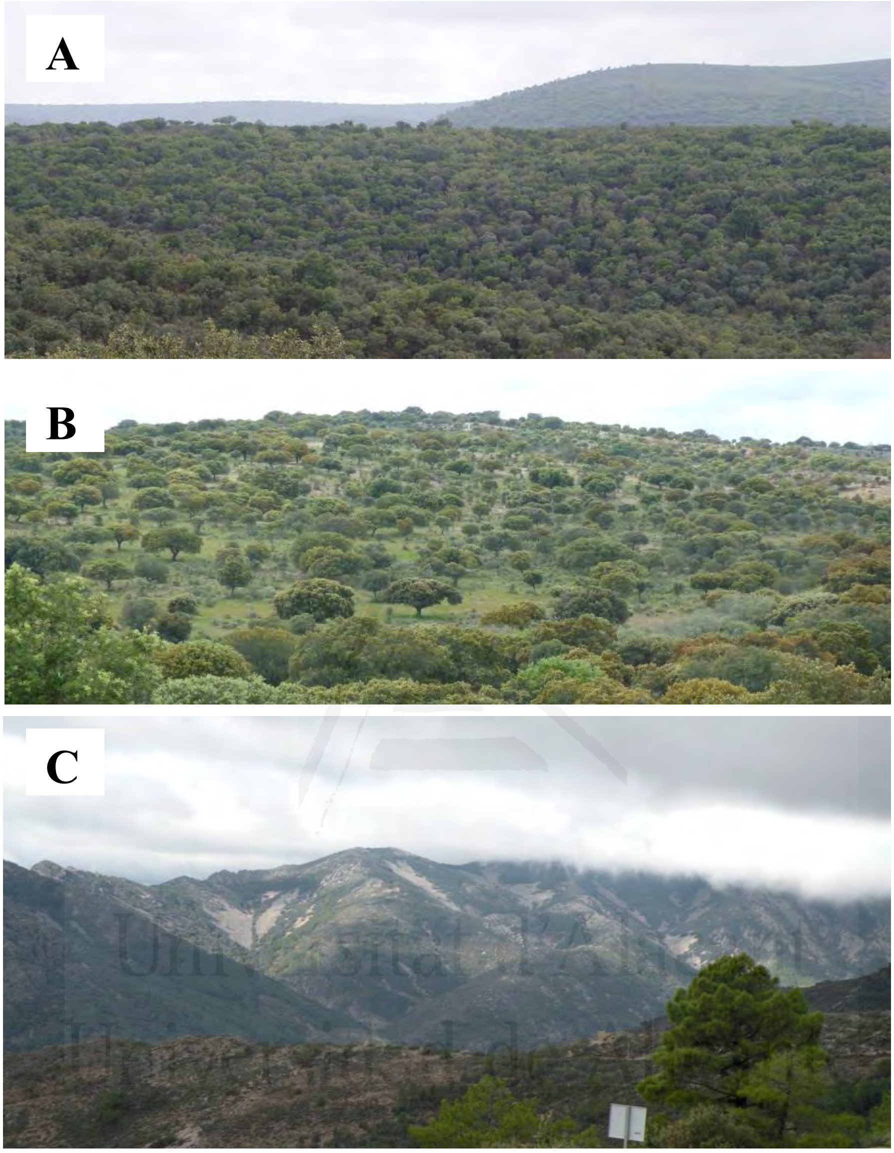

Figura 5 (A) El parque Nacional de “Cabañeros” (39º 23’ 47’’ N, 4º 29’ 14’’ W), abarca una extensión de 40, 856 ha y se encuentra ubicado en los montes de Toledo, en el centro de la Península Ibérica, extendiéndose a través de macizos y sierras no muy elevadas (900 a 1400 m);(B) La Reserva Biológica de “Campanarios de Azaba” (40º 29’ 76’’N, 6º 47’ 55’’ W) abarca una extensión de 522 ha, a una altitud de 800 m, se encuentra situada al sudoeste de la provincia de Salamanca, entre el municipio de Espeja y la Alamedilla (Castilla y León); (C) Espacio natural protegido “Sierra de las Quilamas” (40º 30’ 10’’ N, 6º 05’ 15’’ W), se encuentra situado al sur de la provincia de Salamanca, en la parte occidental de la península, abarca una extensión de 11,100 ha, con una altitud que oscila entre los 600 – 1, 400 m., *fotos de: E. Galante*.

Con el fin de profundizar en los hábitos de filtración larvaria de estas especies de sírfidos y analizar su relación con la microbiota del medio, se ha abordado en esta tesis doctoral por primera vez el estudio de las relaciones entre larvas de sírfidos y su microbiota asociada, habiendo seleccionado como modelo de estudio *M. dusmeti*. Nuestros resultados muestran importantes indicios de relaciones tróficas entre especies de bacterias del grupo *cereus* (*Bacillus cereus*, *Bacillus toyonensis*, *Lysinibacillus sphaericus*) con los estados inmaduros de sírfidos saprófagos como *M. dusmeti.* Estas bacterias se hallaron tanto en el medio líquido contenido en las oquedades arbóreas donde las larvas se desarrollaban, como también en el tracto digestivo de éstas. Teniendo en cuenta que las larvas del sírfido saproxílico *M. dusmeti* son dependientes de las oquedades de árboles maduros que almacenan agua, y que a su vez estas oquedades son hábitats ideales para el desarrollo de microrganismos que se encuentran íntimamente relacionadas con *M. dusmeti*, se pone de manifiesto que para asegurar la conservación de estas comunidades saproxílicas se debe evitar el uso de tratamientos agroquímicos que afecten negativamente a la microbiota contenida en el agua de estas oquedades.

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Sección II (a)

Interacciones de Facilitación entre Insectos Saproxílicos dentro de Oquedades Arbóreas en Ecosistemas de Bosque Mediterráneo Ibérico

Sánchez-Galván, I. R., Quinto, J., Micó, E., Galante, E., & Marcos-García, M. A. (2014). Facilitation among saproxylic insects inhabiting tree hollows in a Mediterranean forest: the case of cetonids (Coleoptera: Cetoniidae) and syrphids (Diptera: Syrphidae). Environmental entomology, 43(2): 336-343.

Facilitation Among Saproxylic Insects Inhabiting Tree Hollows in a Mediterranean Forest: The Case of Cetonids (Coleoptera: Cetoniidae) and Syrphids (Diptera: Syrphidae)

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ABSTRACT Tree hollows offer an ideal niche for saproxylic insects in mature Mediterranean forests, where Diptera and Coleoptera are the richest groups. Co-occurrence is frequently observed among many species of both groups in these microhabitats, and some of these species have been considered to facilitate the presence of other species by acting as ecosystem engineers. One of the systems that is found in Mediterranean tree hollows is formed by cetonid (Coleoptera: Cetoniidae) and syrphid (Diptera: Syrphidae) larvae. Here, cetonid larvae feed on wood and litter and produce a substrate that is easier to decompose. To assess the possible role of these larvae as facilitating agents for the saproxylic guild, we studied whether the presence of saprophagous Syrphidae inside tree hollows is associated with the activity of cetonid larvae. Furthermore, in laboratory conditions, we tested whether cetonid larvae activity can improve the development and fitness of the saprophagous syrphid species. Our results show that "cetonid activity" was the variable that best explained the presence of saprophagous syrphid species in natural conditions. *Myathropa florea* (L., 1758) was one of the species most influenced by this activity. The laboratory experiment gave similar results, demonstrating that an enriched substrate with *Cetonia aurataeformis* Curti, 1913 larval feces improves syrphid larval growth rate and fitness of adults (measured as longer wing length) of *M. florea*.

KEY WORDS Mediterranean forest, *Cetonia aurataeformis*, *Myathropa florea*, co-occurrence, ecosystem engineer

Saproxylic insects depend on decaying processes that occur in woody substrates, associated with living and dead trees (standing or fallen wood) in extensive types of microhabitats (Speight 1989, Alexander 2008). These natural microhabitats have proved to be particularly attractive for studies of community organization and as a model to study factors that determine the structure of a community (Barrera 1996). Tree hollows house a rich biota of microorganisms and arthropods (Bell et al. 2005), and in Europe, the arthropod fauna comprises mainly the immature stages of more or less specialized Diptera and Coleoptera. Tree hollows are one of the most important habitats for saproxylic insects in Iberian Mediterranean forests (Marcos-García et al. 2010, Micó et al. 2010; Fig. 1A). The insect community linked to tree hollows is organized into interacting groups of a complex network that involves different trophic guilds: xylophagous, saproxylophagous, xylomycetophagous, predators, and commensals. Competition and facilitation relationships among different species are important factors that condition the community composition of each particular tree hollow (Jönson et al. 2004, Quinto et al. 2012). Bradshaw and Holzapfel (1992) and Schmidl et al. (2008) examined intra- and interspecific interactions among insects living in these microhabitats. Other commensalistic interactions within tree hollow communities have been studied by Heard (1994), Paradise and Dunson (1997), Paradise (1999), and Paradise and Kuhn (1999), but no work has been dedicated to the study of the facilitation process among different animal species inside the tree hollow itself.

Facilitation relationships occur when one species is favored by the previous presence and activity of another species (Munguia et al. 2009). This positive interaction has been studied extensively in plant–plant interactions as a "nurse effect" (Callaway and Pugnaire 1999, Valiente-Banuet and Verdú 2008, Verdú and Valiente-Banuet 2008), as well as in insect–plant interactions, that is, the nest-building activity of *Macrotermes* spp. (Isoptera: Macrotermitinae), which provides nutrient-enriched microhabitats in savanna soils, supporting a high density of woody plant species (Moe et al. 2009). Facilitation relationships are also known in insect–insect interactions, for example, building of shelters has been reported in leaf rollers (*Anacampsis niveopulvella* (Chambers, 1875) and *Pseudotelphusa* sp.; Martinsen et al. 2000, Lill and Mar-

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Abstract

Tree-hollows offer an ideal niche for saproxylic insects in mature Mediterranean forests, where Diptera and Coleoptera are the richest groups. Co-occurrence is frequently observed among many species of both groups in these microhabitats, and some of these species have been considered to facilitate the presence of other species by acting as ecosystem engineers. One of the systems that is found in Mediterranean tree-hollows is formed by cetonid (Coleoptera: Cetoniidae) and syrphid (Diptera: Syrphidae) larvae. Here, cetonid larvae feed on wood and litter and produce a substrate that is easier to decompose. In order to assess the possible role of these larvae as facilitator agents for the saproxylic guild, we studied whether the presence of saprophagous Syrphidae inside tree-hollows is associated with the activity of cetonid larvae. Furthermore, in laboratory conditions we tested whether cetonid larvae activity can improve the development and fitness of the saprophagous syrphid species. Our results show that "cetonid activity" was the variable that best explained the presence of saprophagous syrphid species in natural conditions. *Myathropa florea* (Linnaeus, 1758) was one of the species most influenced by this activity. The laboratory experiment gave similar results, demonstrating that an enriched substrate with *Cetonia aurataeformis* Curti, 1913 larval feces improves syrphid larval growth rate and fitness of adults (measured as longer wing length) of *Myathropa florea.*

Keywords

Mediterranean Forest, *Cetonia aurataeformis*, *Myathropa florea,* co-occurrence, ecosystem engineer.

Introduction

Saproxylic insects depend on decaying processes that occur in woody substrates, associated with living and dead trees (standing or fallen wood) in extensive types of microhabitats (Speight, 1989; Alexander, 2008). These natural microhabitats have proved to be particularly attractive for studies of community organization and as a model to study factors that determine the structure of a community (Barrera, 1996). Tree-hollows house a rich biota of microorganisms and arthropods (Bell et al., 2005), and in Europe their arthropod fauna is comprised mainly of the immature stages of more or less specialized Diptera and Coleoptera. Tree-hollows are one of the most important habitats for saproxylic insects in Iberian Mediterranean forests (Marcos-García et al., 2010; Micó et al., 2010) (Figure 1A). The insect community linked to tree-hollows is organized into interacting groups of a complex network that involves different trophic guilds: xylophagous, saproxylophagous, xylomycetophagous, predators and commensals. Competition and facilitation relationships among different species are important factors that condition the community composition of each particular tree-hollow (Jönson et al., 2004; Quinto et al., 2012). Bradshaw & Holzapfel (1992) and Schmidl et al., (2008) examined intra- and inter-specific interactions among insects living in these microhabitats. Other commensalistic interactions within tree-hollow communities have been studied by Heard (1994), Paradise & Dunson (1997), Paradise (1999), and Paradise & Kuhn (1999), but no work has been dedicated to the study of the facilitation process among different animal species inside the tree-hollow itself.

Facilitation relationships occur when one species is favored by the previous presence and activity of another species (Munguía et al., 2009). This positive interaction has been studied extensively in plant-plant interactions, as a “nurse effect” (Callaway & Pugnaire, 1999; Valiente-Banuet & Verdú, 2008; Verdú & Valiente-Banuet, 2008), as well as in insect-plant interactions, *i.e.* the nest building activity of *Macrotermes* spp. (Isoptera: Macrotermitinae), which provides nutrient-enriched microhabitats in savanna soils, supporting a high density of woody plant species (Moe et al., 2009). Facilitation relationships are also known in insect-insect interactions, *e.g.,* building of shelters has been reported in leaf-rollers (*Anacampsis niveopulvella* (Chambers, 1875) and *Pseudotelphusa* sp.) (Martinsen et al., 2000, Lill et al., 2003; Diniz et al., 2012); gall makers (*Pemphigus betae* Doane, 1900) (Waltz & Whitham, 1997); leaf miners (*Phyllonorycter pastorella* Zellar, 1846) (Johnson et al., 2002; Kagata et al., 2004) and stem-borers (*Oncideres albomarginata chamela* Chemsak & Giesbert, 1986) (Calderón-Cortés et al., 2011). A common denominator of these examples is the existence of ecosystem engineer species that act as chemical or physical transformers that determine a more suitable environment (Jones et al., 1994; Jönson et al., 2004) for the subsequent colonization and development of secondary species (Bronstein, 2009; Connell & Slatyer, 1997).

One classic example of ecosystem engineer insects linked to dead-wood is *Cerambyx cerdo* (Linnaeus, 1758) (Coleoptera: Cerambycidae), whose larvae create galleries within trunks of living trees, facilitating colonization by other saproxylic species (Buse et al., 2008). The presence of *Osmoderma eremita* (Scopoli, 1763) (Coleoptera: Cetoniidae) larvae in tree-hollows also seems to favor the saproxylic beetle diversity of the assemblage (Jönsson et al., 2004; Ranius et al., 2005).

Leaf litter is the main energy source in tree-hollow systems, however, an additional supply of nutrients for the saprophagous fauna within tree-hollows is provided by arthropod cadavers and residues (*e.g.,* molts and feces) (Yee & Juliano, 2006). Saproxylic Cetoniidae larvae develop inside tree-hollows in Mediterranean forests, where they become abundant (Micó & Galante, 2002; Ricarte et al., 2009; Micó et al., 2011). These cetonid larvae transform large fragments of rotten wood and litter into feces that are richer than the original substrate (Murayama, 1931; Micó et al., 2008; Micó et al., 2011) (Figure 1B). This enriched and thinner substrate could facilitate the occurrence of other saproxylic organisms, such as those species with filtering mouthparts (Rotheray & Gilbert, 2010) (Figure 1C). Therefore, cetonid larvae could also be considered to be ecosystem engineers in tree-hollows in Mediterranean forests. Quinto et al., (2012) provided a first approach to characterizing and analyzing specialized interacting patterns that occur in quantitative tree-hollow/saproxylic insect (Coleoptera, Diptera: Syrphidae) food webs in the Cabañeros National Park (Spain). In that study we reported that cetonid beetles and saprophagous Syrphidae (Diptera) co-occur in tree-hollows in Mediterranean forests (Figure 1). However, to our knowledge, there are no studies that analyze these spatio-temporal co-occurrences, nor whether this co-occurrence is mediated by facilitation events. Here, we extend the studies of Quinto et al., (2012) to assess whether the presence of saprophagous Syrphidae inside tree-hollows is related to the activity of cetonid larvae (feces' presence), and whether cetonid larvae feces improve the development and fitness of the saprophagous syrphid species in laboratory conditions.

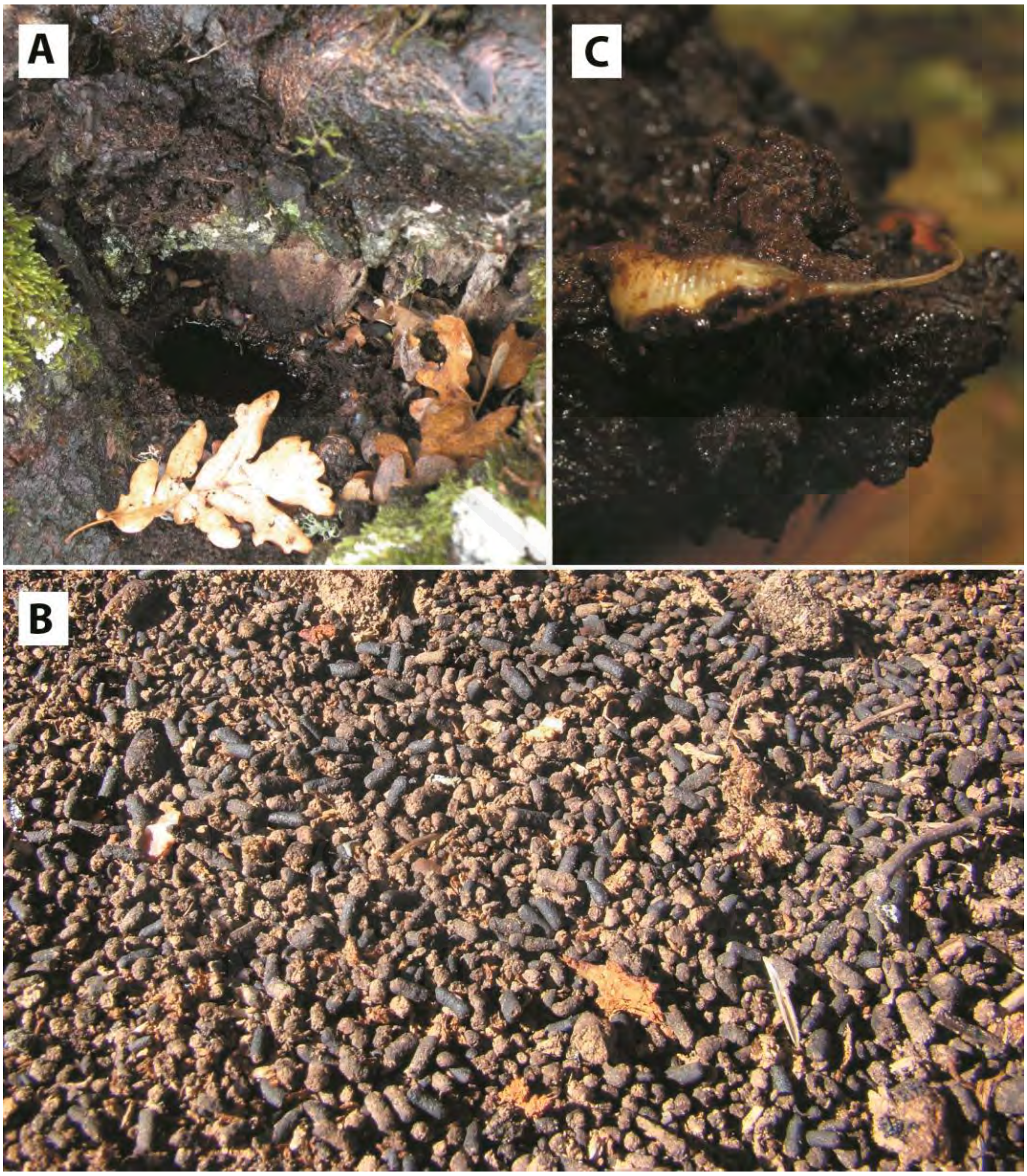

Figure 1 (A) The interior of a tree-hollow with accumulated rain water and organic matter. (B) Cetonid larvae feces in a tree-hollow showing the amount and shape of feces. (C) A saprophagous syrphid larva with its typical long tail, feeding on the organic matter containing cetonid feces inside a tree-hollow.

Materials and Methods

Study area

The study was conducted from February 2009 to February 2010 in the Cabañeros National Park (39º 23'47"N, 4º29'14"W), Spain. This protected area has a wide diversity of habitats formed by well-preserved Mediterranean woodlands (Vaquero, 1997). The area of the park is 40,856 ha and altitude ranges from 560 to 1448 m. This zone belongs to the Mediterranean region, where the climate is characterized by a dry summer period, with annual rainfall from 500 to 750 mm. The average annual temperature varies from 12.9 ºC to 15.6 ºC, with maximum temperatures of 40 ºC in summer and minimum temperatures of -12 ºC in winter (Vaquero, 1997).

Field Experiment

In order to evaluate whether the presence of saprophagous Syrphidae in the study area was related to cetonid larval activity, our field work was carried out in the most representative Mediterranean forests of the National Park: sclerophyllous forest of *Quercus rotundifolia* Lamarck, mixed deciduous forest dominated by *Quercus pyrenaica* Willdenow and *Quercus faginea* Lamarck, and riparian forest of *Fraxinus angustifolia* Vahl (Quinto et al., 2012; Micó et al., 2013). We selected 30, 30 and 27 tree-hollows from each forest type respectively; these were then monitored using emergence traps (Colas, 1974; Gouix & Brustel, 2001; Quinto et al., 2012). Each tree-hollow was covered with acrylic mesh and sealed up with staples. Adults emerged and came into a collecting pot that contained ethylene glycol as a preservative. This kind of trap has been proved to be the most effective for sampling saproxylic insects in tree-hollows in Mediterranean areas (Quinto et al., 2013). Pots were replaced every month for a year (February 2009 - March 2010).

Before installing the traps, we registered the presence of cetonid feces in the substrate contained in the tree-hollow; cetonid larvae eat large quantities of wood, and their feces, which remain in the substrate for long time, are often a dominant content in the tree-hollow (Jönsson et al., 2004; Micó et al., 2011). The feces are easily distinguishable from the rest of the substrate due to their shape, size and abundance (Figure 1B).

In order to assess the effect of cetonid activity (Cet Act) on syrphid species distribution, we recorded the presence and absence of cetonid larvae or larval feces in each of the 87 tree-hollows selected. We measured 10 variables in each hollow in order to model Syrphidae saproxylic assemblages at microhabitat scale (further details in J.Q., unpublished data): 1) trunk diameter (Diam). We measured the tree perimeter at 0.30 and 1.30 cm, and applied the equation

$$diam = \frac{P}{\pi} \text{ (cm)},$$

where P is the mean perimeter of the two heights considered; 2) tree-hollow volume (Volth). We homogenized 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 of the hollow opening level (the unique measurable radius in many cases) and h the total height of the tree-hollow; 3) organic matter volume contained in each hollow (Volmo). This was estimated by considering the volume as a hypothetical semi-sphere, and then

$$Volwm = \frac{2}{3}\pi r^3 \text{ (cm}^3\text{)},$$

where r is the radius of the upper level of the organic matter; 4) height of hollow from the ground (Height); 5) distance (cm) from the lower hollow opening point to the ground; 6) hollow opening area (Area): considering the opening area as an ellipse; 7) hollow orientation (Orient): this value considered eight cardinal and intermediate directions from North to Northwest, and horizontal hollows were considered as “without orientation”; 8) accumulated water presence (Water) in the hollow. Before trap installation, we registered the presence or not of accumulated water in each selected tree-hollow; 9) presence of Scolytinae galleries (Scolyt); 10) activity of vertebrates (Verteb). We also recorded tree-hollows that presented vertebrate activity (hairs, feathers, nests, etc).

Laboratory Experiment

The experiment was performed using *Myathropa florea*, the most abundant syrphid species living inside tree-hollows in the study area (Quinto et al., 2012). The larvae of this species live in liquefied decaying vegetal matter (Hartley, 1960). On the other hand, one of the most abundant cetonid species living inside tree-hollows is *Cetonia aurataeformis* (Micó et al., 2011).

The laboratory experiment was conducted to assess the effect of the presence of feces of *Cetonia aurataeformis* larvae on the life cycle and fitness of *Myathropa florea.* In January 2011, we collected sixty third-instar larvae of *Myathropa florea* (L3) by hand from several tree-hollows of *Q. pyrenaica* Willdenow in the Cabañeros National Park. Species identification and L3-instar of the larvae were confirmed in the laboratory using Rotheray (1993). Each larva was placed in a 100 ml plastic box with three different breeding media (see below). This box was open at the top and was placed inside a larger box with sawdust in order to provide a dry substrate for larva pupation. A *Q. pyrenaica* stump was also placed inside the breeding box, to allow larvae to go out and pupate in the dry substrate (Figure 2). The top of the large box containing sawdust was closed with fine mesh. The larvae were reared until adult emergence in a climatic room under dark conditions (T= 20 ±1ºC; RH = 75 ± 10%). The three different breeding media were tested using 20 larvae per treatment.

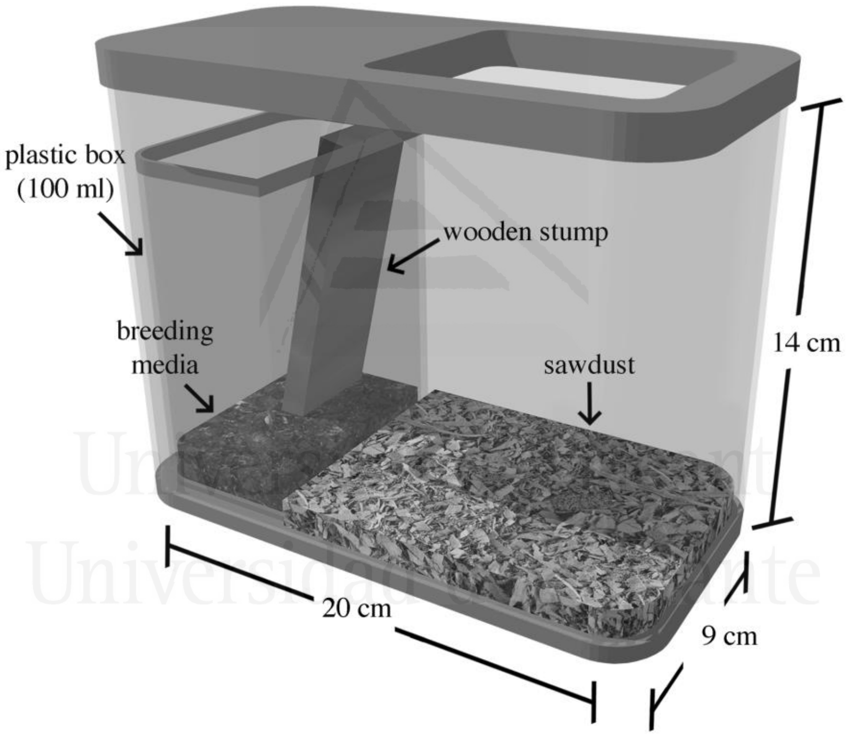

Figure 2 Rearing box with breeding media where larvae of *M. florea* were placed until pupation. A plastic box containing the breeding media was placed inside a larger plastic box. We placed a wooden stump in the breeding media to enable the syrphid larvae to access the dry area to pupate.

Treatment 1. Optimal conditions for saprophagous syrphid larvae growth, simulating natural conditions for larvae inside tree-hollows (*sensu* Rotheray, 2012). This treatment consisted of 40 ml of detritus (*Q. pyrenaica* wood sawdust) and 60 ml of purified water.

Treatment 2. Substrate enriched with feces of *Cetonia aurataeformis* larvae. This treatment consisted of 20 ml of detritus (*Q. pyrenaica* wood sawdust), 20 ml feces of *Cetonia aurataeformis* larvae and 60 ml of purified water.

Treatment 3. Sub-optimal treatment (*sensu* Rotheray, 2012). This treatment consisted of 20 ml of detritus (*Q. pyrenaica* wood sawdust) and 80 ml of purified water.

At the beginning of each treatment, a drop of the original liquid collected from tree-hollows in the field was added to the substrate in order to accelerate bacterial growth (Rotheray, 2012).

Each L3 larva and newly formed pupa was weighed using a precision scale (Acculab ALC-110.4 Analytical Balance, CE, Germany). Larval growth rate (measured as the increase in weight per week) and pupal weight were considered as indicators for the breeding success of each treatment (greater weight is better) (Kingsolver & Huey, 2008).

We compared larval growth rate during development until pupation per treatment. The duration of the larval period was regarded as a surrogate for the quality of larva food (a shorter developmental period is better) (Amorós-Jiménez et al., 2012; Dziock, 2005).

Each pupa was placed separately in a Petri dish until adult emergence. The weight of the pupae in all treatments was recorded the day after pupation as in Amorós-Jiménez et al., (2012). We registered the number of pupae that developed to adults in order to obtain adult emergence rate for each treatment. Wing length of the emerged adults was also measured as a surrogate for total body size in syrphids, and a good indicator for adult fitness (Kingsolver & Pfennig, 2004; Dziock, 2005; Kingsolver & Huey, 2008). Specifically, the shortest length between the junction of the costal vein (C) with the humeral cross vein (h) and the junction of R4+5 with the medial vein (M) were measured (Dziock, 2005) (Figure 3). Measurements were analyzed separately for each sex, due to differences between males and females, and the right wing was always used to avoid any effect caused by asymmetry. We used an Image Analyzer LEIKA (M205C/DFC425, Cambridge, United Kingdom) for wing length measurements.

Statistical Analysis

We used CANOCO 4.5 (ter Braaak & Smilauer, 2002) to assess the influence of cetonid activity on syrphid species distribution in tree-hollows (Table 1), as well as to discover which syrphid species is most affected by this biotic variable. This is a canonical correspondence analysis for the total abundance of each syrphid species (CCA, Hill's scaling, down-weighting rare species). The species most related to a variable is represented by those points that are distributed closest, representing the weights with a higher linear correlation index (Morrison, 1967).

The data with normal distribution, such as larval growth rate, pupal weight, and wing length of the adults of *Myathropa florea* were tested with one way-ANOVA tests to evaluate intrinsic differences among treatments. Moreover, a non-parametric Kaplan–Meier test was performed to find out whether there were any differences between mean larval growth period and adult emergence rate among treatments (Zar, 1999).

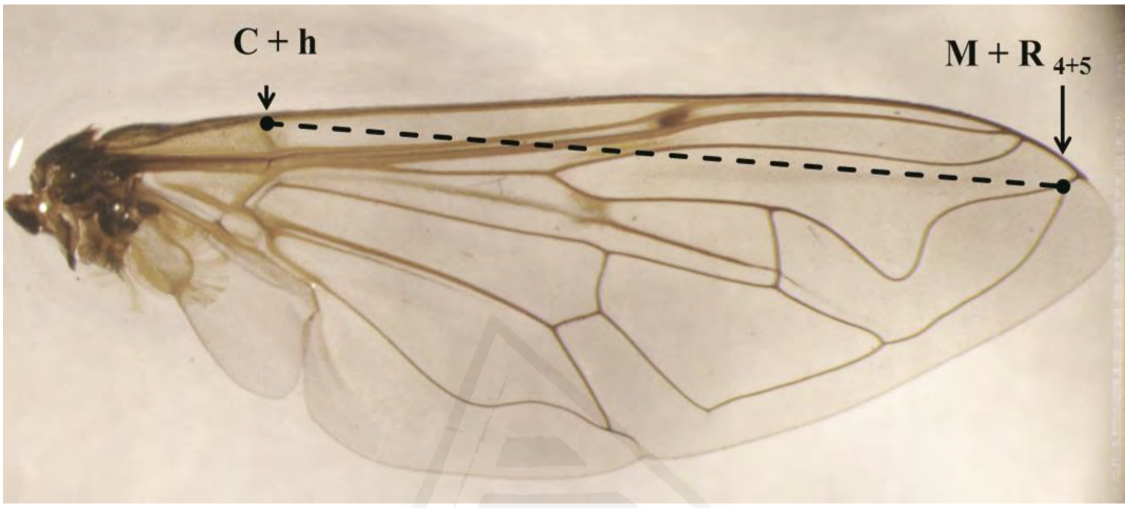

Figure 3 Wing of *M. florea*. The distance between the two marked points is the shortest length between the junction of the costal vein (C) with the humeral cross vein (h) and the junction of R4 + 5 with the medial vein (M) (Dziock, 2005).

Table 1. Saproxylic Syrphidae species composition in tree-hollows in the Cabañeros National Park (Spain) collected from emergence traps (modified from Quinto et al., 2012)

Species	Abundance (No. of individuals)	CCA labels
Brachyopa grunewaldensis (Kassebeer, 2000)	11	S1
Brachypalpoides lentus (Meigen, 1822)	2	S2
Brachypalpus valgus (Panzer, 1798)	4	S3
Callicera aurata (Rossi, 1790)	4	S4
Callicera spinolae Rondani, 1844	29	S5
Ceriana vespiformis (Latreille, 1804)	9	S6
Criorhina floccosa (Meigen, 1822)	8	S7
Criorhina pachymera Egger, 1858	4	S8
Ferdinandea aurea Rondani, 1844	24	S9
Ferdinandea cuprea (Scopoli, 1763)	3	S10
Ferdinandea fumipennis Kassebeer, 1999	1	S11
Ferdinandea ruficornis (Fabricius, 1775)	6	S12
Mallota cimbiciformis (Fallen, 1817)	33	S13
Mallota dusmeti Andréu, 1926	97	S14
Mallota fuciformis (Fabricius, 1794)	11	S15
Milesia crabroniformis (Fabricius, 1795)	1	S16
Myathropa florea (Linnaeus, 1758)	203	S17
Myolepta dubia (Fabricius, 1805)	1	S19
Myolepta obscura Becher, 1882	4	S20
Sphiximorpha subsessilis (Illiger in Rossi, 1807)	1	S21
Spilomyia digitata (Rondani, 1865)	6	S22

Results

Influence of Cetonid Activity on Saprophagous Syrphidae Presence

Just over sixty three per cent (63.22%) of the studied tree-hollows exhibited evidence or/and presence of feces of *Cetonia aurataeformis* larvae. The CCA analysis showed that six micro-environmental variables influence Syrphidae species distribution (Figure 4; Table 2 and 3), with "cetonid activity" being the variable that explains the highest percentage of the variation (*Monte Carlo test* = 1.67, F = 2.55, $P < 0.01$), followed by hollow height from the ground (F=2.19, $P < 0.01$), presence of Scolytinae galleries (F = 1.88, $P < 0.05$), presence of accumulated water (F =1.65, P = 0.026), internal volume of hollow (F = 1.67, $P < 0.05$) and hollow orientation (F = 1.58, $P < 0.05$).

The syrphid species most related to cetonid activity was *Myathropa florea* (present in 35% of the tree-hollows examined), followed by *Brachyopa grunewaldensis* (Kassebeer, 2000) (13%), *Myolepta dubia* (Fabricius, 1805) (10%) and *Spilomyia digitata* (Rondani, 1865) (7%).

Scolytinae galleries were found to be particularly related to the presence of the syrphid *Criorhina pachymera* Egger**,** 1858, whereas hollow orientation and water content were mainly related to the presence of *Myolepta obscura* Becher, 1882, and *Mallota dusmeti* (Andreu, 1926). Furthermore, both water presence and height of hollow from the ground positively promoted the presence and abundance of *Criorhina pachymera*; *Mallota fuciformis* (Fabricius, 1794); *Spilomyia digitata*; *Brachypalpus valgus* (Panzer, 1798). Finally, the species most influenced by hollow volume was *Brachyopa grunewaldensis* (Figure 4).

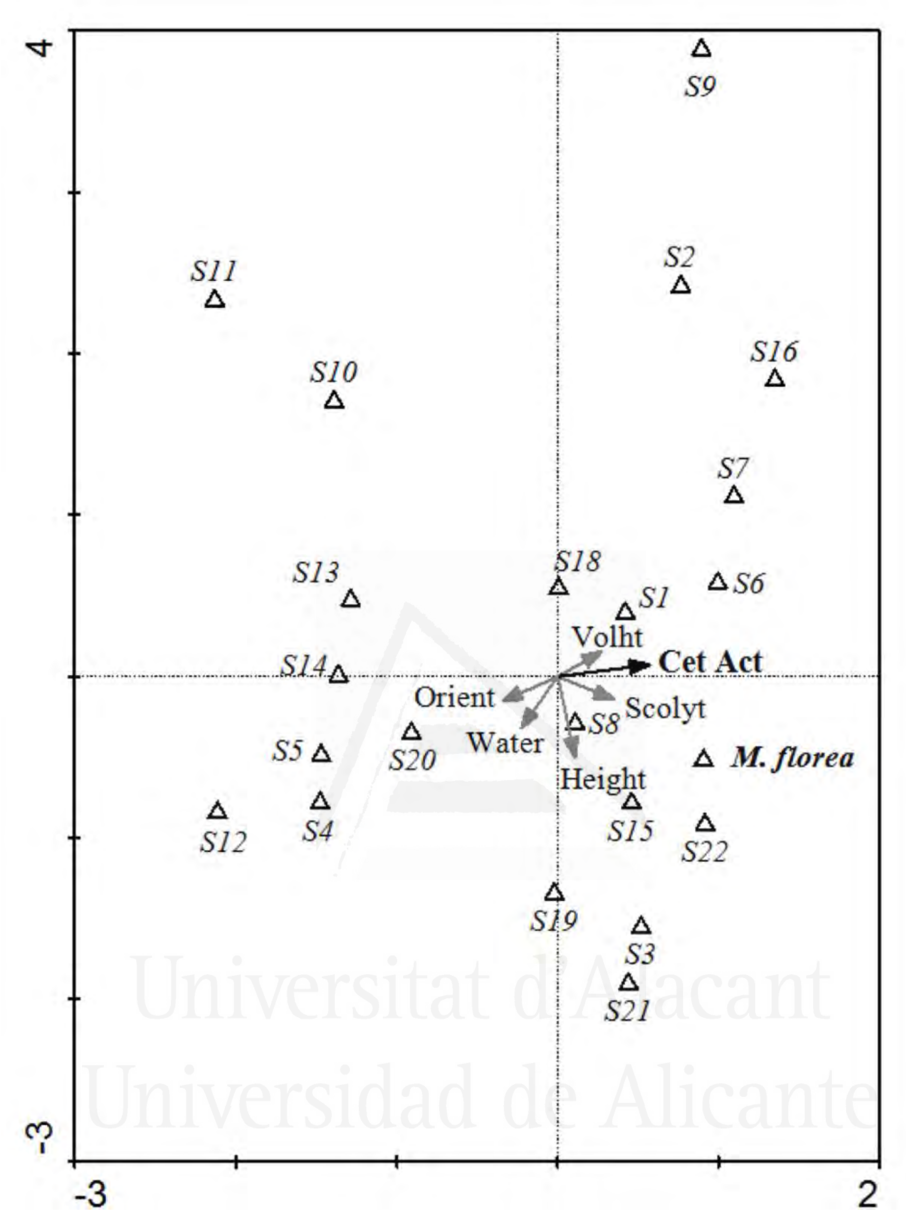

Figure 4 CCA representation of the significant micro-environmental variables that affect the Syrphidae species distribution. The syrphid species other than *M. florea* labels (S17) can be found in Tables 2 and Table 3. Cet Act, Cetonid activity; Volth, tree-hollow volume; Scolyt, presence of Scolytinae galleries; Height, height of hollow from the ground; Water, water presence; and Orient, hollow orientation.

Table 2. Results of canonical correspondence analysis of syprhid larvae abundance as a function of the micro-environmental variables studied

Micro-environmental variables	***F-ratio***	***P-value***
Cetonid activity (Cet Act)	2.55	0.002*
Height of hollow from the ground (Height) (cm)	2.19	0.002*
Water presence (Water)	1.65	0.026*
Presence of Scolytidae galleries (Scolyt)	1.88	0.030*
Hollow orientation (Orient)	1.58	0.030*
Tree hollow volume (Volth) (cm^3)	1.67	0.046*
Hollow opening area (Area) (cm^2)	1.19	0.504
Vertebrate presence (Verteb)	0.75	0.804
Organic matter volume (Volmo) (cm^3)	0.68	0.892
Diameter of trunk (Diam) (cm)	0.53	0.942

An asterisk indicates those micro-environmental factors that significantly explain a major percentage of variation ($P < 0.05$) of the distribution of saprophagous syrphids in tree-hollows.

Table 3. Eigenvalues and correlation coefficients for axes 1 and 2, and canonical coefficients for each micro-environmental variable

	Canonical axes	
CCA outputs	**1**	**2**
Eigenvalues	0,545	0,521
Species-environment correlations	0,8	0,754
% variance species data	6,1	11,9
% variance species-environment relationship	28,9	56,5
Canonical coefficients of the environmental variables		
Cetonid activity	0,845 *	0,101 *
Height of hollow from the ground	0,16	-0,724
Presence of Scolytiinae galleries	0,517	-0,204
Presence of accumulated water	-0,338	-0,458
Internal volume of hollow	0,407	0,22
Hollow orientation	-0,507	-0,221

An asterisk indicates the highest eigenvalue corresponding to “Cetonid activity”.

Influence of Cetonid Feces on *Myathropa florea* Larval Development and Adult Fitness

The larval growth rate of *Myathropa florea* for treatment 2 (enriched with cetonid feces) was significantly higher than for the other two treatments (F= 7.50, df = 2, P < 0.01). In addition, wing length average was also significantly greater in adults from treatment 2 ($F=3.54$, df = 2, $P < 0.05$), which indicated an improvement of adult fitness. Differences in larval mortality rate, pupal weight and period of larval development among treatments were not statistically significant. However, in all cases, better performance was obtained in treatment 2 (*chi-square* = 4.43, df = 2, $P > 0.05$) (Table 4).

Table 4. Metrics of the syrphid *Myathropa florea* for each treatment.

Metrics	**Treatment 1**	**Treatment 2**	**Treatment 3**	***P-values***
N	20	20	20	
Larval growth rate per week (g)	0.0393 ± 0.0188	0.0525 ± 0.0195	0.0275 ± 0.0175	*P* = 0.0016 *
Pupal weight (g)	0.1228 ± 0.0092	0.1316 ± 0.0064	0.1117 ± 0.0150	*P* = 0.4030
Median larval growth period (d)	26	23	33	*P* = 0.1089
Adult emergence rate (%)	65	80	60	*P* = 0.3679
Average wing length (mm)	4.48 ± 3.77	5.21 ± 3.52	2.28 ± 3.58	*P* = 0.0354 *

Treatment 1, Optimal conditions for saprophagous syrphid larvae growth; Treatment 2, Substrate enriched with feces of *Cetonia aurataeformis* larvae; Treatment 3, Sub-optimal treatment (see details in Materials and Methods).

An asterisk indicates significant differences ($P < 0.05$) among treatments.

Discussion

It has been suggested that several beetle species considered as ecosystem engineers (*i.e. C. cerdo* and *O. eremita*) could be important facilitation factors that determine higher species richness of saproxylic insects in tree-hollows (Jönson, 2004; Ranius, 2005; Buse, 2008). The study of the ecological role of these species in these microhabitats, where species of different trophic guilds live together and interact, is of the utmost importance in order to understand the biodiversity hosted by tree-hollows.

Our results show that cetonid activity (as feces and/or larval presence in tree-hollows) was the most important micro-environmental factor determining the presence of saprophagous syrphid species. In particular, this was the case of *Myathropa florea,* whose larvae were present in 35% of the tree-hollows studied with observed cetonid activity.

Myathropa florea is a cosmopolitan saprophagous hoverfly (Speight & Castella 2011), whose distribution in the Iberian Peninsula is wide (Marcos-García, 1985). The aquatic larvae of *Myathropa florea* filter microorganisms and are common in the metazoan communities that occur in water-filled tree-hollows in European temperate deciduous forests with low litter content (Schmidl et al., 2008). Nevertheless, this species is not an obligatory dendrolimnetobiont, species that only occur in tree-hollows or similar phytotelmata (Yanoviak, 2001), and whose larvae require a high supply of organic substrates on which to feed (Rotheray & Gilbert, 2011). They have also frequently been observed developing in decaying vegetal matter such as ripe fruit of *Opuntia* (M.A.M.G., unpublished data). The nutrients provided by the cetonid feces represent a facilitating factor for the successful development of *Myathropa florea*, which can extend to over a year in natural conditions (Rotheray & Gilbert, 2011). This food enrichment provided by cetonid feces can lead to a lack of synchrony in the life cycle of *Myathropa florea* at local scale (*i.e.* shortening the life cycle of *Myathropa florea* in hollows with feces). This asynchrony can be considered as an advantage as it enables the mixing of individuals from different generations and contributes to genetic variability. This can also partially explain why populations of saproxylic larvae in tree-hollows frequently consist of different sizes and instars (Rotheray & Gilbert, 2011).

The laboratory experiment corroborates our field facilitation results, demonstrating that *Myathropa florea* larvae had a higher growth rate when reared in an enriched substrate with *C. aurateoformis* feces. In addition, the wing length average was significantly greater in adults reared with the enriched substrate. Longer average wing length indicates an increase in adult fitness of this syrphid species and a better flight capacity (Dziock, 2005). However, other studies on larval interspecific relations undertaken with *Myathropa florea* and three other common insects (two Nematocera and one Coleoptera species) living in tree-hollows have not shown any evidence of facilitation interaction (Schmidl et al., 2008).

The higher occurrence of some syrphids in tree-hollows with cetonid activity is probably due to the attractiveness for elective oviposition exerted on gravid syrphid females by tree-hollows enriched with organic matter (Speight & Castella, 2008). This attraction seems to be mediated by a combination of physical and chemical volatile compounds emitted by biological processes of decomposition, as has been reported for other species of Diptera (Kellner, 2002). However, without further and more extensive and rigorous comparisons with other similar field situations, no particular mechanism can be indicated. We conclude that cetonids in general, particularly *Cetonia aurataeformis,* act as ecosystem engineers within tree-hollows, favoring the establishment, survival and fitness of *Myathropa florea* and probably other saprophagous syrphid species.

Nevertheless, our results show that not all syrphid species are equally affected by cetonid activity. For instance, *Ferdinandea* spp., whose facultative saproxylic larvae live in tree-hollows and sap-runs located on different parts of the tree trunk surface (Rotheray, 1993, Speight & Castella, 2011), are not dependent on cetonid larvae activity.

Moreover, richness and abundance of syrphid species are favored in tree-hollows containing accumulated water, with horizontal openings that are highest from the ground. The majority of saprophagous syrphid species have aquatic larvae (Rotheray & Gilbert, 2011) that require deep hollows to survive the long drought periods that are characteristic of the Mediterranean climate. These horizontal hollows constitute a very suitable habitat for the development of large *Myathropa florea* larvae (Schmidl et al., 2008). The preference of this species for tree-hollows with a greater volume of water, as observed in *Mallota obscura* and *Mallota dusmeti*, is related to their long respiratory processes that allow them to obtain oxygen from the air outside (Rotheray, 1993). In addition, other species such as *Criorhina pachymera*, *Mallota fuciformis* and *Brachypalpus valgus* tend to occupy higher tree-hollows, which is consistent with their adult habits. These are primarily arboreal, flying high and descending to flowering under-storey trees to feed (Speight & Castella, 2011).

Taking into account that saproxylic insects are one of the most threatened groups in Europe (Nieto & Alexander, 2010; Radenkovic et al., 2013), the identification of ecosystem engineer species is of the utmost importance to understand the key processes that structure the community. As a consequence, when conservation programs for saproxylic communities are being established, interspecific relationships should be taken into consideration and special attention ought to be paid to the facilitation processes that model these communities.

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Sección II (b)

Relaciones entre Sírfidos Saproxílicos (Diptera: Syrphidae) y Bacterias dentro de Oquedades Arbóreas en Bosques del Mediterráneo Ibérico

Sánchez-Galván, I. R., Ferrer, J., Galante, E., & Marcos-García, M. A. (2016). Bacteria and Hoverflies (Diptera: Syrphidae) in Tree Hollows From the Iberian Mediterranean Forest. Environmental Entomology, 46(1):137-142.

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Bacteria and Hoverflies (Diptera: Syrphidae) in Tree Hollows From the Iberian Mediterranean Forest

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Abstract

Saproxylic insect communities inhabiting tree hollows in Mediterranean forests depend on a combination of physical characteristics and interactions occurring between community member species. Despite the need to preserve these organisms, little is known about their interrelationships, in particular those relationships between saproxylic insects and microbiota occurring in these microhabitats. In tree hollows of *Quercus rotundifolia* Lamark that hold water and contain dead leaves, abundant microbial populations can be found. Developing on them are the larvae of *Mallota dusmeti* Andréu, 1926 (Diptera: Syrphidae), a vulnerable species (IUCN category: Marcos-García and Quinto 2011). This study provides the first data on the microbiota living inside the gut of the larvae of *M. dusmeti*, as well as the microbiota in the hollow where these larvae develop. Bacteria were identified by amplification and partial sequencing of the V1–V3 regions and the complete nucleotide sequence of 16S rRNA genes. We found eight species of bacteria living in tree hollows and three species in the gut of *M. dusmeti* larvae: *Bacillus cereus*, *Bacillus toyonensis, and Lysinibacillus sphaericus*. The filter-feeding mechanism characteristic of *M. dusmeti* larvae is selective in enabling ingestion of bacteria only above 2.1 µm in diameter.

Key words: bacteria–insect association, filter-feeder larvae, vulnerable hoverfly, *Mallota dusmeti*, *Quercus rotundifolia*

Saproxylic organisms are dependent on dead or dying wood, sap, wood-inhabiting fungi, or other saproxylic species during some part of their life cycle (Speight 1989, Bouget et al. 2005). Coleoptera and Diptera are the most common taxa (Dajoz 1998, Ricarte et al. 2009). These organisms play a key role in nutrient recycling (Schlaghamersky 2003) and make a significant contribution to the maintenance of the trophic chain in forest ecosystems (Thompson and Rotheray 1998, Brustel 2001).

Understanding the relationships between saproxylic insect assemblages and woodland composition and management is very important (Grove 2002, Fayt et al. 2006, Saint-Germain et al. 2010, Stokland et al. 2012, Sebek et al. 2012, Micó et al. 2013b, García-López et al. 2016), but we also need to investigate more about the influence of abiotic and biotic characteristics of wood microhabitats (tree hollows) on insect saproxylic diversity and distribution (Micó et al. 2011, 2013a; Quinto et al. 2012, Sánchez-Galván et al. 2014). Our previous studies in the Mediterranean Iberian Peninsula have shown that old trees maintain particular “habitat islands” (tree hollows), considered one of the most important microhabitats for the conservation of these species of insects (Ricarte et al. 2009, Marcos-García et al. 2010, Micó et al. 2011, Quinto et al. 2014, Ramírez-Hernández et al. 2014).

In most of the world’s forests, species of Diptera Syrphidae can be found whose larvae develop in water-filled tree hollows or rot holes (Rotheray and Gilbert 2011). In the Iberian Peninsula, 68 saproxylic species are known (Ricarte et al. 2009, Marcos-García et al. 2010, Quinto et al. 2014, Sánchez-Galván et al. 2014). The main sources of food for larvae of these syrphids are rich communities of microbiota associated with their development sites (Walker and Merritt 1988, Walker et al. 1991, Bell et al. 2005, Martínez-Falcón et al. 2012). To extract microbiota, saprophagous syrphid larvae possess the typical filtering mechanism of cyclorrhaphan Diptera larvae, the cibarial or pharyngeal ridges (Dowding 1967), which enable separation of particulate food from a fluid suspension (Rotheray and Gilbert 2011).

Cibarial ridges are a series of up to 10 longitudinal, somewhat parallel, T- or Y-shaped ridges that run along the floor of the pharynx, contained within the basal sclerite of the head skeleton. Ingested microbial suspensions are pressed against the cibarial ridges through which liquid passes, while microbiota are retained that are too large to pass through the gaps between the ridges (Dowding 1967).

However, relationships between saprophagous syrphid larvae and microbiota associated with development sites are poorly known (Mahmoud et al. 1999, Lobkova et al. 2007). Martínez-Falcón et al. (2012) analyzed feeding in larvae of the syrphid genus *Copestylum* Macquart in decaying tissues of the columnar cactus, *Isolatocereus dumortieri* (Scheidw.) Backeb. (Cactaceae) and found that through

Abstract

Saproxylic insect communities inhabiting tree hollows in Mediterranean forests depend on a combination of physical characteristics and interactions occurring between community member species. Despite the need to preserve these organisms, little is known about their interrelationships, in particular those relationships between saproxylic insects and microbiota occurring in these microhabitats. In tree hollows of *Quercus rotundifolia* Lamark that hold water and contain dead leaves, abundant microbial populations can be found. Developing on them are the larvae of *Mallota dusmeti* Andréu, 1926 (Diptera: Syrphidae), a Vulnerable species (IUCN category: Marcos-García & Quinto2011). This study provides the first data on the microbiota living inside the gut of the larvae of *M. dusmeti*, as well as the microbiota in the hollow where these larvae develop. Bacteria were identified by amplification and partial sequencing of the V1-V3 regions and the complete nucleotide sequence of 16S rRNA genes. We found eight species of bacteria living in tree hollows and three species in the gut of *M. dusmeti* larvae: *Bacillus cereus*, *Bacillus toyonensis* and *Lysinibacillus sphaericus*. The filter feeding mechanism characteristic of *M. dusmeti* larvae is selective in enabling ingestion of bacteria only above 2.1 µm in diameter.

Keywords

Bacteria-insect association; filter-feeder larvae; Vulnerable hoverfly; *Mallota dusmeti*; *Quercus rotundifolia.*

Introduction

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The hoverfly *Mallota dusmeti* Andréu 1926 (Syrphidae, Eristalini) is a threatened species in Europe (Ricarte et al., 2009; Marcos-García & Quinto, 2011; Quinto et al., 2012, 2014; Micó et al., 2013b; Ramirez-Hernández et al., 2013). It is also an Ibero Maghrebian endemic whose adults are rarely observed at the field (Marcos-García & Quinto, 2011). The saprophagous larva of *M. dusmeti* is found in water-filled tree hollows of Mediterranean species of *Quercus* and *Fraxinus* where it develops over a period of at least 2 yr (Marcos-García & Quinto, 2011; Quinto et al., 2014). These saprophagous syrphid larvae are filter feeders (Rotheray & Gibert, 2011), and the hypothesis is that the larvae of *M. dusmeti* may feed on the bacteria in the tree hollows. The main aim of this study was to determine which bacteria species present in the tree hollows could also be found in the larval gut of *M. dusmeti*.

Material and Methods

Field collection of *M. dusmeti* larvae

Larvae of *M. dusmeti* (Figure 1) were collected from two Spanish localities separated by 250 km and known to hold populations of this species (Ricarte et al., 2009; Quinto et al., 2014; Ramirez-Hernández et al., 2014). The first is the Biological Reserve "Campanarios de Azaba" (Camp), a private, protected area of 522 ha of the typical landscape ''dehesa'', savannah- like open woodland with scattered trees (Gómez-Gutiérrez, 1992), dominated by *Quercus pyrenaica* Willdenow and *Q. rotundifolia* Lamark that coexist with some individuals of *Q. faginea* Lamark, at an altitude of 800 m, close to the border with Portugal (Ramirez-Hernández et al., 2014). The second is the National Park of Cabañeros (Cab), an area of 40,856 ha located in Central Spain (Micó et al., 2013a, 2015). Special permission to collect these vulnerable larvae was obtained from the respective managing authorities.

At each locality, >30 tree hollows of *Quercus spp.* were searched manually each year for 2 yr during the *M. dusmeti* larval growth period (November to March, 2012-2013). However we only found larvae in three hollows of *Q. rotundifolia*. A total of 20 third stage (L3) larvae were obtained in two hollows of Cab and one of Camp. A higher number of samples were unavailable, since the larvae are rare and since listed as a vulnerable species and collecting and killing specimens is very limited. The other organisms found and the characteristics of these tree hollows were documented in previous studies (Quinto et al., 2014; Ramirez-Hernandez et al., 2014; Sánchez-Galván et al., 2014). Larvae were placed in sterile plastic containers (100 mL) with perforated caps. The liquid substrate was collected at the same level as the live larvae and was kept in sterile containers (100 mL at 4ºC).

Figure 1 Saprophagous long-tailed larvae of *M. dusmeti* and decomposing organic matter present at the bottom of the hollows.

Identification, preservation and measurement

The collected larvae were immediately stored in the field at 4ºC and transported to the laboratory, where they were killed and preserved by freezing (-80º) and then dissected. In order to make the identification of the larvae to the species level easier, dissected specimens were preserved by placing larvae in water and heating slowly for about 4 min, and then fixed separately in KAAD solution following methods described in Ricarte et al., (2015). The identification was done by comparison with preserved larvae in the CIBIO Entomological Collection, University of Alicante (CEUA) and the original description (Ricarte et al., 2007).

Head skeletons (Figure 2) were carefully extracted from the antero-ventral margin of emerged puparia and cleaned in a bath of 10% KOH for 1 h. They were then preserved in glycerin for further analysis and measured using the Image Analyzer LEIKA (M205C/DFC 425, Cambridge, United Kingdom). The distance between the ridges of each cibarial lobe piece was measured in 7third instar larvae (L3). The maximum distance between cibarial ridges was measured with a stereomicroscope fitted with an eyepiece reticle.

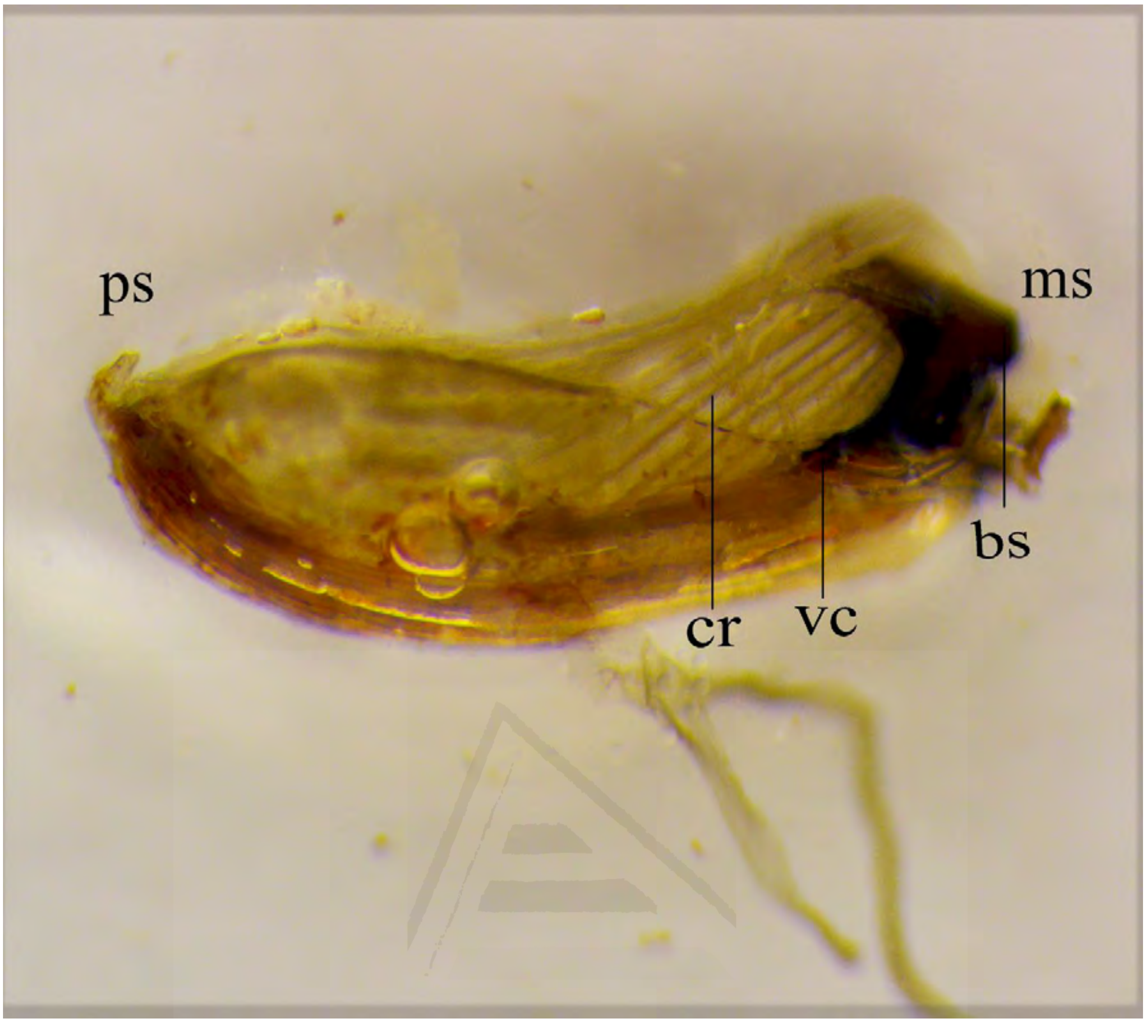

Figure 2 Head skeleton of *M. dusmeti* larvae: bs, basal sclerite; vc, ventral cornu; cr, cibarial ridges; ms, mouth side; ps, posterior side.

Bacterial analyses

Each larva was dissected aseptically under a binocular microscope to extract the intestinal tract with the aid of sterile forceps and micro scissors. The three sections of the intestinal tract (foregut, midgut and hindgut; Figure 3) were separated and placed individually into marked tubes and frozen (-80º) until further analysis.

The larval gut was soaked in 200 µl of sterile distilled water to obtain bacteria for analysis. In addition, 200 µl of liquid from tree hollows was assessed for bacteria. Aliquots of 100 µl from each sample were transferred to solid medium (peptone 10 g/l; yeast extract 5 g/l; tryptone 5 g/l; pH < 7; agar 1.5%) distributed in Petri dishes, and incubated for 24h at 37ºC. After incubation, individual bacterial colonies of different sizes were selected, transferred to liquid medium (same composition as solid medium excluding agar) to obtain pure cultures, and incubated for12h at 37ºC, and shaken with an orbital speed 144 rpm.

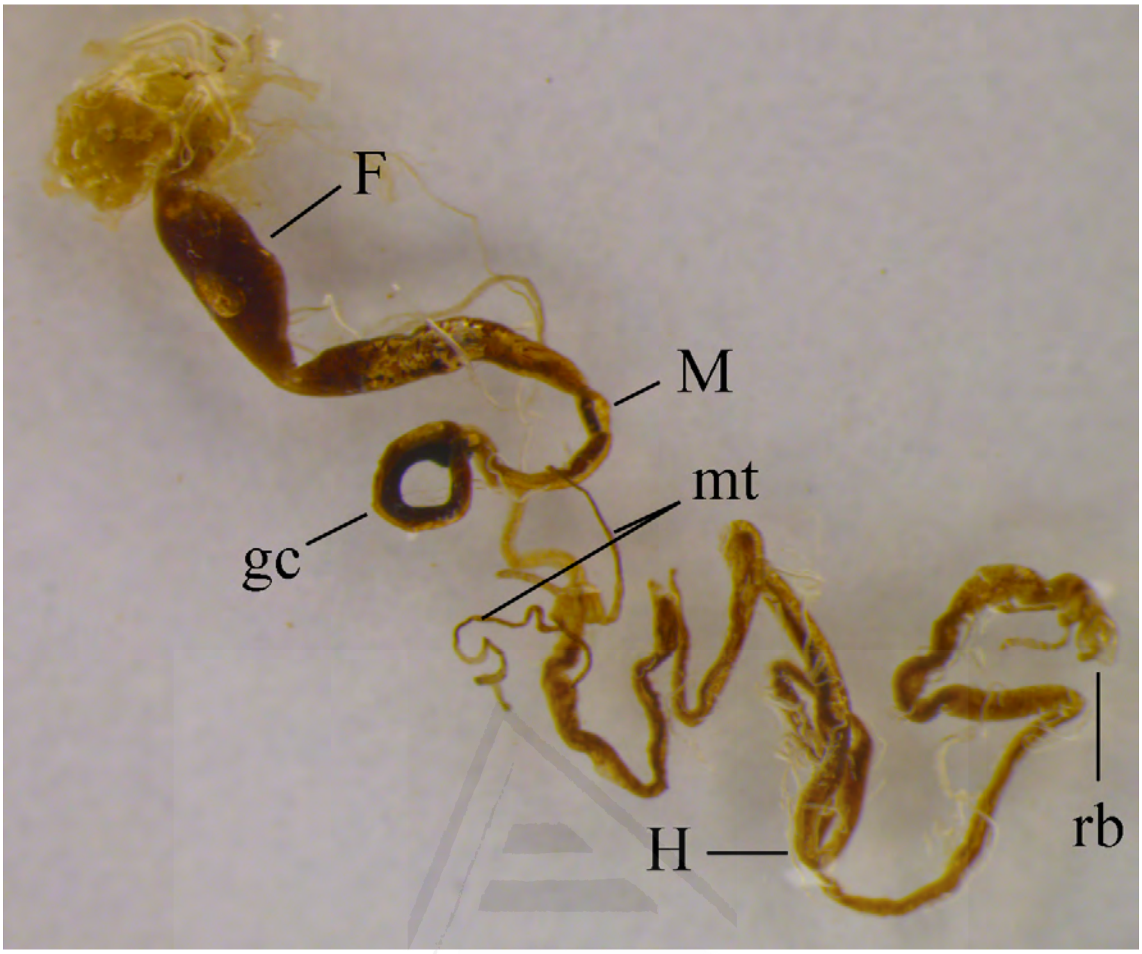

Figure 3 Intestinal tract of *M. dusmeti* larvae: F, foregut; M, midgut; H, hindgut; mt, Malpighian tubules; gc, gastric caecum; rb, rectal bulb.

The liquid material from the tree hollows where the larvae were collected was analyzed separately. Each sample was placed in sterile containers and frozen at -80ºC until analysis. The liquid was filtered to remove the macroscopic organic material. Later, the filtrate was centrifuged at 10,000 g for 5 min, to obtain pellets of bacterial cells. These pellets are suspended in tampon solution (tampon phosphate 10 mM, pH 7). One fraction was used to extract the DNA, and the other one to culture the bacteria.

Bacteria were identified through their 16S rRNA sequence. Amplification of the 16S rRNA gene was by PCR. Two strategies of analysis were taken. The first involved the generation of PCR 750 bp fragments of the V3-V5 region from 16S rRNA gene (Baker et al., 2003), obtained by primers E334F (5'-CCAGACTCCTACGGGAGGCAGC-3') and E939R (5'-CTTGTGCGGGCCCCCGTCAATTC-3'). The second strategy involved the generation of PCR 1500 bp fragments, obtained by primers E8F (5'-AGAGTTTGATCCTGGCTCAG-3') and E1541R (5'-AAGGAGGTGATCCANCCRCA-3'), which included the complete 16S rRNA gene sequence (Baker et al., 2003).

PCR conditions were an initial denaturation step at 95ºC/5min, followed by 35 cycles of a denaturation step at 94ºC/30s, a primer annealing step at 55ºC/30s, an extension step at 72ºC/90s, and a final step at 72ºC/7min. PCR products were verified with gel electrophoresis and purified using the SpeedTools PCR Clean-up Kit from BIOTOOLS.

Purified fragments of 1,500 pb were cloned using the kit pGem-T II Easy Vector Systems (Promega, USA) in *Escherichia coli* DH5α. Cloned fragments were sequenced with universal primers that hybridize with sequences of plasmid flanking the cloned fragment, primers M13FpUC (5'-GTAAAACGACGGCCAG-3') and M13RpUC (5'-CAGGAAACAGCTATGAC-3'). Sequencing was carried out with the Big Dye Terminator Kit (Applied Biosystems, Foster City, CA) on an ABI Prism 377 DNA sequencer (Applied Biosystems). Similarities to the obtained sequences were sought at the GenBank nucleotide database using BLAST (Benson et al., 2013).

ResultsThe three sections of the larval *M. dusmeti* gut were readily distinguished morphologically: 1) foregut with a separate crop for temporary food storage, 2) midgut, with crypts and a gastric caecum, being the primary area of digestion and absorption of nutrients, and 3) hindgut including excretory organs as Malpighian tubules, that are extensions of the anterior hindgut extending into the body cavity (Terra et al., 1996) (Figure 3).

M. dusmeti larval head skeletons have a set of cibarial ridges acting as a filtering area (Figure 2). The results of our measurements show that the maximum gap between cibarial ridges is 2.1 ± 0.04 µm.

DNA analysis revealed a total of eight species of bacteria in the tree hollow liquid: *Bacillus cereus* Franklandand Frankland, 1887; *Bacillus mojavensis* (Roberts, Nakamura & Cohan, 1994) Wang et al., 2007; *Bacillus subtilis* (Ehrenberg, 1835) Cohn, 1872; *Bacillus toyonensis* Jimenez et al., 2014; *Brevibacterium frigoritolerans* Delaporteand Sasson, 1967; *Lysinibacillus sphaericus* (Meyer & Neide, 1904) Ahmed et al., 2007; *Pectobacterium carotovorum* Jones, 1901; *Brenneria alni* (Surico et al., 1996) Hauben et al., 1999 (Table 1). After analysis of 16S rRNA sequences of the bacteria, only three of the tree hollow bacteria were found inside the larva: *Bacillus cereus* (51%), *Bacillus toyonensis* (46%) and *Lysinibacillus sphaericus* (3%). These results indicate that the larvae only allow a few of the species found in the tree hollows to enter their guts (Table 1). The aerobic endophytic species *Bacillus mojavensis* (2%) and *Bacillus subtilis* (4%), as well as *Brenneria alni* (6%), *Pectobacterium carotovorum* (4%), and *Brevibacterium frigoritolerans* (10%), were detected in the cultures from larvae breeding media, but not in cultures from the larval intestinal tract (Table 1).

Table 1 Bacteria species found within intestinal tract of the larvae of *M. dusmeti* and their liquid breeding media from tree hollows.

	Species of bacteria found (% identity)		**Intestinal Tract**			**Camp**	**Cab**	**Breeding media**	**Intestinal tract of the larvae**
			F	**M**	**H**				
Baciliaceae	*Bacillus cereus* (99)	P,C	no	yes	yes	yes	yes	39% (52)*	51% (36)
	Bacillus toyonensis (99)	P,C	yes	yes	yes	yes	yes	29% (39)*	46% (32)
	Bacillus mojavensis (99)	C	no	no	no	no	yes	2% (3)*	----
	Bacillus subtilis (97)	C	no	no	no	no	yes	4% (5)*	----
	Lysinibacillus sphaericus (99)	P,C	no	no	yes	yes	no	6% (8)*	3% (2)
	Brevibacterium frigotolerans (99)	P,C	no	no	no	no	yes	10% (13)*	----
Enterobacteriaceae	*Brenneriaalni* (98)	C	no	no	no	no	yes	6% (8)*	----
	Pectobacterium carotovorum (97)	P,C	no	no	no	no	yes	4% (5)*	----

F, foregut; M, midgut; H, hindgut codes corresponding to each part of intestinal tract of the larvae of *M. dusmeti*. P, sequencing partial; C, complete sequencing codes are indicating the routes of analysis (*see* Material and Methods).

* Number of sequences obtained of each bacteria.

Discussion

In the Iberian Peninsula, the traditional management of Mediterranean forests is pollarding and light pruning (Sebek et al., 2012; Ramírez-Hernández et al., 2014; Quinto et al., 2014). These techniques initiate the formation of most tree hollows (Figure 4) into which organic material, such as dead leaves, falls and is trapped. In wet conditions, rich populations of bacteria develop on this material, decomposing and recycling it (Walker et al., 1988, 1991). The results indicate there is a possible relationship between the microbiota found in tree hollows, where *M. dusmeti,* a vulnerable syrphid species, is found, and the bacteria thriving in the guts of these larvae that develop in this microhabitat.

Enterobacteriaceae are sometimes referred to as "survival packs" because of their role in the gut of insects in facilitating the assimilation of nitrogen (*e.g.,* Lauzon et al., 1998; Martínez-Falcón et al., 2012), especially during the period of early growth (Ben-Yosef et al., 2008; Engel & Moran, 2013). Our results indicate that two species of this group, *Brenneria alni* and *Pectobacterium carotovorum*, are present in tree hollows. However, they were not detected in the gut of *M. dusmeti* larvae (Table 1).

Figure 4 On Iberian Mediterranean forest, many hollows in the trees are a consequence of traditional management in the past known as "pollarding".

These two bacteria species play an important role in the decomposition of the plant tissues. *Brenneria alni* is a plant pathogenic bacterium responsible for plant diseases, such as bark canker, phloem canker and drippy nut disease (Kado, 2006; Poza-Carrión et al., 2008). It causes lesions on trunk bark of *Quercus* species in Spain from which fluids exude (Surico et al*.,* 1996; Biosca et al*.,* 2003). *Pectobacterium carotovorum* is a soil borne pathogen and the cause of diseases such as soft rots (Thomas et al., 2011), and is associated with the hollows nearest the soil. These bacteria are also associated with sapwood through wounds on the trees (Stokland et al., 2012), activating the fermentation of the sap in anaerobic conditions by producing methane and carbon dioxide, increasing the pressure on wood and producing fluid exudates or sap runs (Stokland et al., 2012). Sap runs are an attractive food for the adults of saproxylic syrphids, such as species of *Ferdinandea* Rondani, 1844 whose presence is known in these two areas of the Mediterranean forests (Ricarte et al., 2010; Quinto et al., 2014).

Two bacteria that produce glycopeptides with antifungal activity (Arima et al., 1968; Bacon & Hinton 2006; Snook et al., 2009; Youcef-Ali et al., 2014), *Bacillus mojavensis* and *Bacillus subtilis* (Table 1), may inhibit the growth of fungi inside tree hollows. Our results indicate that these bacteria are not ingested by the larvae of *M. dusmeti* living on the water contained inside tree hollows.

Brevibacterium frigotolerans was also recorded in tree hollows and not found in the gut of *M. dusmeti* (Table 1). It is a known pathogen of insect larvae living in the soil, such as those of the Scarabaeidae (Selvakumar et al., 2011). The presence of *Brevibacterium frigotolerans* might be related to the presence of Coleoptera that colonize tree hollows during dryer periods (Sánchez-Galván et al., 2014; Micó et al., 2015; unpublished data).

In the Eristalini, ingestion of bacteria is facilitated by mouthparts adapted for filtering (Harley, 1963; Mohamoud et al., 1999). The larva of *M. dusmeti* possesses cibarial ridges (Dowding, 1967) that allow filtering of particles smaller than 2.1 µm in diameter, while the bacteria that are larger are retained on the cibarial ridge surfaces and not allowed to pass posteriorly to the foregut (Rotheray & Gilbert, 2011).

The gap between cibarial ridges is wide enough to allow passage of the three Bacillaceae species found in the larval gut of *M. dusmeti*. However, microbial colonization inside depends on the physicochemical conditions in the different gut compartments, and these can display extreme variation in both pH and oxygen availability. The basic design of insect guts displays many modifications reflecting adaptations to specialized niches and feeding habits, and many of these specializations have evolved for housing gut microorganisms in specific gut compartments (Engel & Moran, 2013).

Bacillaceae species are regularly associated with the digestive system of soil-dwelling arthropod species, where they can also cause insect disease (Margulis et al., 1998; Damgaard, 2000, Jensen et al., 2003; Stenfors et al., 2007). Two of them, *Bacillus cereus* and *Bacillus* *toyonensis,* are facultative aerobic bacteria living in the soil where they are saprophytic (Jiménez et al., 2013). *Bacillus cereus* is a common filamentous spore-forming bacteria frequently found as part of the midgut microflora (Margulis et al., 1998; Jensen et al., 2003; Vilain et al., 2006). The third bacterium species found in the gut of *M. dusmeti*, *Lysinibacillus sphaericus*, was found in relatively low proportions and only in the hindgut, the area of the intestine where the largest microbiota concentration occurred (Engel & Moran, 2013), and where it is expected that the host is equipped with appropriate regulatory systems to sustain gut integrity and tolerate high microbial loads (Hongoh, 2010; Martinson et al., 2012).This bacteria is an aerobic microorganism commonly isolated from soil and water and surprisingly, is a common pathogen of insects frequently used as a bio-insecticide of aquatic mosquitos (Peña-Montenegro et al., 2015), although it seems to have no such negative effects on *M. dusmeti* larvae.

It is likely that the three species found inside the gut of *M. dusmeti* are ingested from the breeding medium and lysed by extracellular enzymes secreted by symbiotic bacteria on the anterior part of the digestive tract, with absorption of resulting products occurring in the midgut (Lemos & Terra, 1991; Lobkova et al., 2007). However, it is possible that they could also play a role in the digestion of the organic material ingested by the larvae, since they secrete hydrolytic enzymes (Terra et al., 1996; Lobkova et al., 2007).

Tree hollows are the main reservoirs of diversity for threatened species of saproxylic insects such as *M. dusmeti* in the Iberian Mediterranean forest (Ricarte et al., 2009; Micó et al., 2013; Ramírez-Hernández et al., 2014). Our results show that the populations of *M. dusmeti* are dependent on the existence of water in the tree hollows, generally rich in organic matter and an excellent broth culture for microbiota (Quinto et al., 2014). The bacteria species passing through the gut, ingested with fermented food, provide acritical food source enabling development of the filter-feeder larvae of *M. dusmeti*. In consequence, a priority for conservation of this species of syrphids should be to ensure the protection of the mature trees with hollows that are able to keep water for long time periods (Ramirez-Hernández et al., 2014),and to prevent the use of certain pesticide treatments, which may negatively affect hollow microbial diversity (Hussain et al., 2009).

These results suggest the need for up studies concerning the microbiota of tree cavities and their relationships with insects in order to improve the conservation programs of saproxylic diversity.

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Sección III

Relaciones Interespecíficas entre Insectos Saproxílicos dentro de Oquedades Arbóreas en Zonas de Bosque del Mediterráneo Ibérico

Sánchez-Galván, I. R., Marcos-García, M. A., Azeria, E., Galante, E., & Micó E. Unravelling Saproxylic Insect Interactions in Tree Hollows from Iberian Mediterranean Forest. Biodiversity and Conservation (submitted May 2017).

Abstract

Tree hollows are complex microhabitats in which a variety of abiotic and biotic factors shape the community assembly of saproxylic insects. To detect non-random species co-occurrence patterns (aggregated or segregated) is a fundamental goal in ecology in order to understand the assembly mechanisms of communities, including interspecific interactions. Here, we studied association patterns of species of Syrphidae (Diptera) and Coleoptera (belonging to different trophic guilds) on 72 tree hollows at a local and regional scale in three protected areas in Mediterranean forests using a null model. The matrix-level analysis showed a tendency for segregation in species association at both regional and site level but it failed to support a satisfactory biological explanation for inter-guilds interactions. However, pairwise analysis showed a dominance of non-random aggregation patterns at both local and regional level. Both aggregation and segregation non-random patterns were more common among species from different trophic guilds than within the same guilds, with predators being a common denominator of a high percentage of the inter-guild pairs. These results highlight that predation and facilitation interactions, together with habitat segregation, are the main factors shaping tree-hollow assemblages. Our study implies the importance of interspecific interactions, where "ecosystem engineers" and threatened and near-threatened species form an important part of the process of assemblage structuration and aid conservation of tree hollow assemblages.

Key words

Co-occurrence analysis, matrix level approach, pair-wise level approach, trophic guilds, Coleoptera, Diptera (Syrphidae)

Introduction

Tree hollows are complex ecological systems that make up an important resource in forests for a wide array of biological groups including saproxylic insects (Quinto et al., 2012, 2013; Müller et al., 2013), which are dependent on the decay process of woody substrates, associated with living and dead trees at least during some part of the life cycle (Speight, 1989; Alexander, 2008). In addition, tree hollows are considered as "keystone" structures in European forests because they harbour higher functional and phylogenetic diversity than other saproxylic microhabitats (Müller et al., 2013). Moreover, several endangered species depend on this peculiar microhabitat (Dajoz, 1998; Ranius, 2002; Sverdrup-Thygeson, 2009; Ramírez-Hernández et al., 2014).

In each tree hollow, a high number of insect species, mainly Coleoptera and Diptera (Syrphidae) coexist and interact in different ways among themselves, and with the woody substrates (Speight, 1989; Quinto et al., 2014). Saproxylic beetles inhabiting tree hollows can be categorized into different trophic guilds such as: predators, saprophagous, saproxylophagous, xylomycetophagous and xylophagous, which have different degrees of dependence upon the substrate and on other organisms (Quinto et al., 2012).

Previous studies have demonstrated the importance of biotic factors in tree-hollows in driving beetle diversity (Quinto et al., 2014; Micó et al., 2015). The presence of "ecosystem engineer" species such as Cerambycids and Cetoniids (Coleoptera), can transform the substrate in tree-hollows both physically and chemically, and consequently, can act as a facilitator for some trophic guilds (Micó et al., 2015). In this way, the activity of several species of xylophagous and saproxylophagous beetle larvae of Coleoptera has been suggested to allow the subsequent establishment of larvae of other saproxylic insects (Buse et al., 2008; Micó et al., 2015; Zuo et al., 2016). Predator-prey interactions can also be key in the assemblage structuration; Hughes & Grabowski (2006) showed that predator-prey interactions could result in aggregation patterns, in which saproxylic predators tend to aggregate where their prey species are abundant (Johansson et al., 2007; Azeria et al., 2012). On the other hand, it has been reported that spatially segregated distribution between saproxylic species occurs as the result of resource competition (Rankin & Borden, 1991) and antagonistic larval interactions (Dodds et al., 2001).

However, our understanding of the prevalence of insect-insect interactions (Jönsson et al., 2004; Ranius et al., 2005; Buse et al., 2008; Chiari et al., 2014), and to what extent species interactions could be influencing the diversity and the structure of the saproxylic insect assemblages inside tree-hollows remains insufficient.

To address the role of interspecific interactions occurring in community assembly is a central challenge to the field of community ecology. Null model analysis of species' co-occurrence patterns has been shown to provide a valuable tool in identifying non-random association patterns, from distribution data to large biodiversity inventory data, and to infer their causal mechanisms (Gotelli, 2000; Ulrich & Gotelli, 2007; Gotelli & Ulrich, 2012). For example, non-random patterns of segregation have been attributed to competitive interactions (Diamond, 1975; Connor & Simberloff, 1979; Rejmánek & Lepš, 1996; Gotelli, 2000) or habitat segregations (Gotelli et al., 2002; Peres-Neto et al., 2004; Azeria et al., 2009, 2012), while non-random patterns of aggregation may suggest mutualistic or cooperative interactions (Wright & Biehl, 1982; Holt, 1984; Gotelli & Graves, 1996; Peres-Neto, 2004), predator-prey interactions (Hughes & Grabowski, 2006), or similar niche preferences between a pair of species when resource is non-limiting (Peres-Neto, 2004).

In this study, we assess the role of interspecific interactions in the structure of saproxylic insect assemblages by examining the non-random patterns of aggregation and segregation between species pairs belonging to two abundant taxa, Coleoptera and Syrphidae (Diptera) within tree hollows in *Quercus pyrenaica* Willdenow forest in the Iberian Mediterranean region. Our main aims were: (i) to examine whether tree hollow insect assemblages in Iberian *Q. pyrenaica* forest show a whole trend toward aggregation or segregation of species, and (ii) to explore pairwise co-occurrence patterns at two spatial scales (local and regional level) in order to detect non-random patterns between species pairs and trophic guilds with an emphasis on the association patterns between threatened and near-threatened saproxylic species and other saproxylic taxa to highlight the potential role interspecific interaction might have for conservation.

Materials and Methods

Study area

The study was conducted in three protected areas within the Iberian Mediterranean region: "Cabañeros National Park" (henceforth Cab), "Campanarios de Azaba" Biological Reserve (henceforth Camp), and "Sierra de las Quilamas" Natural Area (Site of Community Importance 92/43/CEE, code ES4150108-Quilamas) (henceforth Quil), (Micó et al., 2011, 2013; Quinto et al., 2012; Ramírez-Hernández et al., 2014). Cab (Central Spain) is a National Park of 40,856 ha with altitudes between 560 and 1448 m, and is a well-preserved Mediterranean landscape with several patches of forest dominated by *Quercus* species (*Q. rotundifolia* Lamarck, *Q. faginea* Lamarck, and *Q. pyrenaica* Willdenow) (Quinto et al., 2012; Micó et al., 2013). Camp (Western Spain) is a private biological reserve belonging to the "dehesa ecosystem" with an area of 522 ha, located at an altitude of 800 m and dominated by *Q. rotundifolia* and *Q. pyrenaica*

(Ramírez-Hernández et al., 2014). Quil (Western Spain) is a natural protected area of 11,100 ha, spanning an altitude of between 600 and 1400 m, whose forest habitats are dominated by *Q. pyrenaica* (Micó et al., 2011, 2013). Quil and Camp have been managed in the past by pollarding trees, while signs of ancient pollard activity in *Q. pyrenaica* trees of Cab are not noticeable. Currently, no active management is carried out in any of the studied areas (Quinto et al., 2012, 2014; Ramírez-Hernández et al., 2014).

Sampling methods and species identification

Seventy-two emergence traps were used for collecting saproxylic insects inhabiting tree hollows of *Q. pyrenaica*: 30 tree hollows in Cab, 15 tree hollows in Camp and 27 tree hollows in Quil. Emergence traps consist of a black acrylic mesh that covers and seals the tree hollow with a collecting pot containing ethylene–glycol or propylene–glycol as a preservative (Gouix & Brustel, 2011; Quinto et al., 2013). Traps were replaced monthly from May to November in the year 2009 in Cab, 2010 in Camp, and 2012 in Quil.

This study focused on saproxylic insect species of 26 families belonging to Coleoptera and Diptera (Syrphidae) (Annex I). Syrphids were identified using the van Veen (2004) and Speight & Castella (2015) keys and other specialized bibliography. The beetle nomenclature is according to the Fauna Europaea (http://www.faunaeur.org/) (Bouchard et al., 2011), and the Catalogues of Palearctic Coleoptera (Löbl & Smetana, 2004, 2006, 2007, 2008). The specimens are deposited in the entomological collection of the University of Alicante (Collection CEUA) at CIBIO. The species were classified into six trophic guilds (Bouchard et al., 2011; Speight and Castella 2015): predators (P); saprophagous coleopterans (CSA); saproxylophagous (SX); xylomycetophagous (XM); xylophagous (X) and saprophagous syrphids (DSA) (see Quinto et al., 2012, 2014 for more details).

Data analysis

Saproxylic insects collected in all the selected sites were organized in a presence/absence matrix and abundance matrix (Annex 1). Species data were also organized as separate matrices for each study site (Annex II). Singleton and doubleton species were excluded from each matrix for co-occurrence analyses as in Colwell & Coddington (1994) and Gotelli (2000) (Annex I).

Completeness of the saproxylic species inventory per woodland site (Cab, Camp and Quil) was evaluated as the percentage of observed species in relation to the number of species predicted by the sample coverage estimator, as suggested by Chao & Jost (2012), which is a less biased estimator of sample completeness.

To detect differences in species diversity among woodland sites we calculated the number of effective species for each site using the actual number of species counted. We used the measure of true diversity of order q =2 (D^2) that is the inverse Simpson concentration index, which can be interpreted as the effective number of 'dominant' species (Magurran, 1988; Chao & Shen 2003; Jost, 2006, 2010; Hsieh & Linsenmair, 2012; Alencar et al., 2015). We calculated this using the minimum variance unbiased estimator (MVUE) (Moreno et al., 2011; Chao & Jost 2015; Benítez-Malvido et al., 2016). Sample coverage and true diversity metrics were calculated using the SPADE software (Chao & Shen, 2010).

To assess the variability of species composition among woodlands we used the Bray-Curtis index of similarity among them (Anderson, 2001). Differences were analysed with ANOSIM, a non-parametric method producing a permutation statistic R, which is an absolute measure of distance between the groups using PRIMER V. 6. (Clarke & Gorley, 2009). Matrices of abundance data were square root transformed to reduce the potentially large contribution of common species to the similarity.

Analyses of species co-occurrence

We used null models (Gotelli & Graves, 1996; Gotelli, 2000) to quantify and assess whether the observed patterns of species associations were different from patterns calculated from a random distribution (Azeria et al., 2009; Gotelli & Ulrich, 2010). We chose the fixed-fixed algorithm, which maintains the species occurrence (fixed row totals) and the total number of species at sites (i.e. fixed column totals) during the randomization process (Gotelli, 2000). The algorithm assumes that tree hollows differ in the number of species they harbour due to their differences in physic-chemical attributes (Micó et al., 2015; Sánchez- Sánchez, 2017) and their microhabitat characteristics (Quinto et al., 2014). The algorithm also reflects species differences in the number of tree hollows they can occupy. For the application of a fixed-fixed null model at a pairwise level approach, we generated 1,000 random matrices using the "permatswap" function and the "quasiswap" method (mtype = "count") for abundance data, and at matrix level approach, we generated 1,000 random matrices using the "oecosimu" function and the "quasiswap" method for presence/absence data. Both functions were implemented in the "vegan" package in R software (Oksanen et al., 2015).

Detection of non-random co-occurrence patterns

Pair-wise level approach

We used the Bray-Curtis dissimilarity index (BCD) (Faith et al., 1987) to measure the degree of co-occurrence for pairs of species, separately taking account of the abundance of species in tree hollows. BCD is computed as:

$$BCD\ (Sp1 - Sp2) = (\Sigma\left|Xi - Xj\right|)/\Sigma(Xi + Xj)\ ,$$

where the dissimilarity between specie 1 ($_{\text{Sp-1}}$) and specie 2 ($_{\text{Sp-2}}$) involves summing the absolute differences between the abundance of each pair of species, and dividing this by sum of the total abundance of both species in each matrix. This measure takes values between zero (absolute aggregation) and one (species completely segregated) (Faith et al., 1987; Oksanen et al., 2015).

We generated three species-by-species dissimilarity matrices for each for each woodland site (Cab, Camp and Quil separately), as well as by combining the assemblage data of all three sites at a regional level (henceforth Global) using the function "vegdist", and the method "bray" in the Vegan R-package (Oksanen et al., 2015). Next, for each BCD index, calculated per species pair, we determined their individual significance of aggregation or segregation by determining the *p*-values and effect sizes (SES). Each effect size was calculated as (BCD_{obs} – BCD_m)/SD, where BCD_{obs}= observed BCD index, BC_m= mean BCD index calculated from a simulated matrices (1,000 null matrices), and SD= standard deviation of the test distribution (Gotelli & McCabe, 2002). Here the *p*-values test the significance of the hypotheses (H_0: $BCD_{obs} = BCD_m$; H_1: $BCD_{obs} > BCD_m$ or H_1: $BCD_{obs} < BCD_m$), and the effect size determines how large the effect is (Ellis, 2011). Values of BCD SES which are greater (or lower) than zero indicate prevailing spatial segregation (or aggregation) between pairs of species, respectively (Maestre et al., 2009). Assuming a normal distribution of deviations, BCD SES values should fall between -2 and 2 if co-occurrences are not different from what would be expected by chance alone (Azeria et al., 2012; López et al., 2013; Šálek et al., 2014). Hence, BCD SES values greater than 2 indicate a non-randomly segregated distribution (p<0.05) and values less than -2 indicate a non-randomly aggregated distribution (p<0.05).

Matrix-level approach

To measure co-occurrence patterns as a property of the whole abundance matrix and the whole presence/absence matrix, we performed a co-occurrence analysis based on community-wide association indexes at the regional level (Global) and per woodland site (Cab, Camp and Quil). The association indexes (i.e. mean index value of matrices between all species pairs) are a tool to simplify the overall non-randomness of the species distribution, and their whole trend towards aggregation or segregation (Gotelli, 2000; Gotelli & McCabe, 2002; Azeria et al., 2012; Šálek et al., 2014). Moreover, to test the significance of general community-wide patterns, we converted these community-wide association indexes into standardized effect sizes (SES) (Gotelli & McCabe, 2002). At this level, SES measures by how many standard deviations the mean value of the community-wide association is greater (or lower) than the values computed for the null matrices. Inferences of community-wide summaries may differ among association indexes depending, in part, on whether they standardize for species incidences in the computation (Stone & Roberts, 1992; Azeria et al., 2012).

Using presence-absence data, we used the following wide association indexes (Azeria et al., 2012): (1) the checkerboard index of Stone & Roberts (Stone & Roberts, 1992): C-score: CU = (N1-A) x (N2–A); (2) the incidence-standardized form of C-score (Clarke & Gorley, 2009; Azeria et al., 2012): StC-score: SCU = (B x C)/ (N1 x N2); (3) the Sorensen index: SOR = 2A/ (2A+B+C) (Dice, 1945); and (4) the Jaccard index (Jaccard, 1912): JAC =A/(A+B+C). Using abundance data, we used (5) the BCD as a wide association index in the same way as the pair-wise level approach.

The C-score, StC-score, SOR and JAC, N1 and N2 are incidences of Species-1 and Species-2; A is the number of sites where both species are present; B is the number of sites where Species-1 is present but Species-2 is absent, and C is the converse.

SES values greater than 2 ($p< 0.05$) indicate a segregated distribution using the C-score, StC-score and BCD indexes, and conversely, when SES values are less than -2 ($p<0.05$) this indicates an aggregated distribution using SOR, JAC and BCD indexes.

Results

We identified a total of 117 species and 2,747 individuals belonging to Coleoptera and 18 species and 351 individuals belonging to hoverflies (Syrphidae, Diptera). Saproxylic Coleoptera guilds were composed of xylophagous (12 species, 326 individuals); saproxylophagous (32 species, 1,040 individuals); saprophagous (23 species, 624 individuals); xylomycetophagous (16 species, 311 individuals) and predators (34 species, 446 individuals). All syrphid species were considered as saprophagous in the larval stage (Annex I).

Results on the completeness of the saproxylic species inventory showed that a large proportion of the species present in each forest type was recorded (sample coverage > 97 %; Table 1). Cab and Quil had the same effective species while Camp had a lower diversity value. Species composition varied significantly among the studied areas (R=0.403, $p<0.001$) while Camp and Quil were the most similar sites (Table 2).

Table 1. Estimates per woodland site, of species richness (S), abundance (Ind), completeness of the sample coverage estimator (Cn), true diversity of order 2 (D^2).

Woodland Site			
Estimators	**Cab**	**Camp**	**Quil**
S	102	55	68
Ind	1740	619	560
Cn	0.984	0.977	0.984
D^2	24.18	16.09	24.30

Table 2. Values of permutation statistic R and significance from the pairwise tests of ANOSIM analysis among woodland sites. Significant values in bold.

Pair of woodland sites	**Pairwise test**	
	Statistic R	***p*-value**
Cab–Camp	**0,543**	$p<0.001$
Cab–Quil	**0,408**	$p<0.001$
Camp–Quil	**0,246**	$p<0.001$

Cab (“Cabañeros” National Park), Camp (“Campanarios de Azaba” Biological Reserve), Quil (“Sierra de las Quilamas” Natural Area).

Matrix-level approach

After omitting rare species (singletons and doubletons) (Annex I), the community-wide co-occurrence analysis focused on 89 saproxylic species (65.92% of a total of 135 species) on 72 tree hollows. The regional assemblage exhibited a significant trend toward segregation [Global: BCD SES >2, $p<0.05$] (Table 3). However, at the local level only assemblages in Cab indicated a segregation co-occurrence trend [Cab: CU SES >2; JAC SES <-2 and SOR SES <-2 indexes, $p<0.05$] (Table 3).

Pairwise-level approach

Threatened and near-threatened species were involved in 57 non-random patterns, of which 39 were aggregations and 18 were segregations at a regional level (Annex III). Moreover, species considered as ecosystem engineers (*Cerambyx welensii* and *Cetonia aurataeformis)* were involved in 13 aggregations. Few non-random patterns of aggregation/segregation were shared among woodland sites (Table 5). The pairwise co-occurrence analysis at the regional level indicated that 10.3% of 3,916 pairs of species had significant non-random association patterns, of which 8.30% (336 pairs) were aggregated pairs and 1.8% (69 pairs) were segregated species (Annex III; Figure 1). Most of the significant aggregated (76.4%) and segregated (88.4%) associations detected were between species that belong to different trophic guilds. Predator species tended to have the most frequent aggregated association with saproxylophagous species (43 pairs, 12.79%) and xylomycetophagous species (32 pairs, 9.52%), followed by saproxylophagous and xylomycetophagous species (32 pairs, 9.52%) (Table 4). On the other hand, saproxylophagous (13 pairs, 18.84%) and saprophagous beetles (10 pairs, 14.49%) had the most frequent segregated association with saprophagous syrphids (Table 4). At the local level, pairwise co-occurrence analysis revealed that 9.62% of 2,016 species pairs in Cab assemblages had significant associations (Figure 1). In Camp, 8.9% of 861 species had significant associations whereas only 5.9% of 1,061 pairs had significant association in Quil (Figure 1, details in Annex IV).

Furthermore, we found that in all sites, predators were involved in most of the non-random aggregated pairs: in Cab, most common non-random aggregated pairs occurred between predator-xylomycetophagous species (23 pairs, 12%) and saproxylophagous species (17 pairs, 9%) (Table 4). In Camp, non-random aggregated pairs were most common between predator-saproxylophagous species (6 pairs, 1%) (Table 4). Finally, in Quil, non-random aggregated pairs were most common between predator-saproxylophagous (10 pairs, 16%) and saprophagous beetles (10 pairs, 16%) (Table 4).

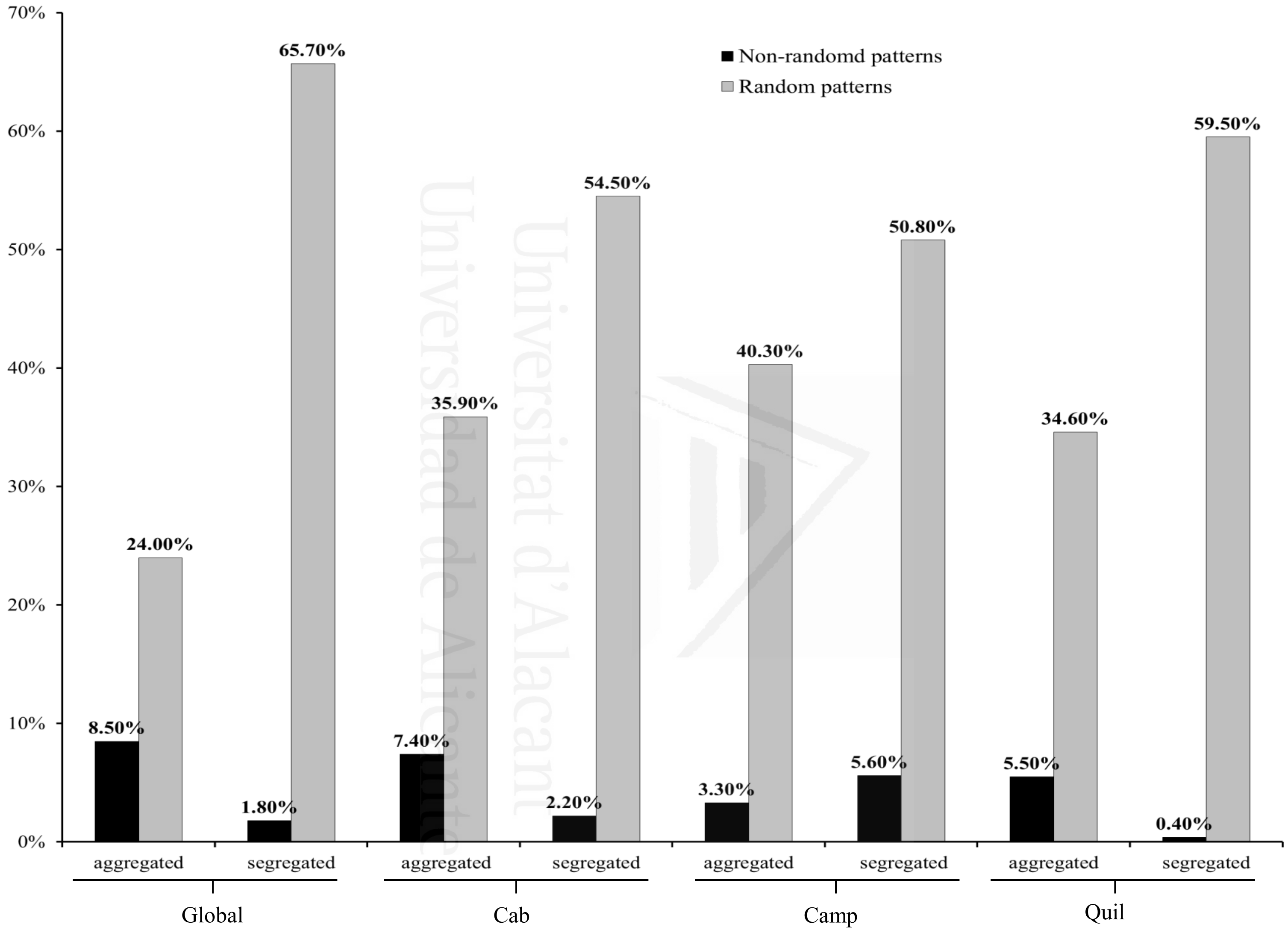

Figure 1 Low percentages of non-random patterns derived of pairwise analysis

Table 3 Community-wide association indices based on data for all saproxylic insects (Diptera: Syrphidae and Coleoptera) breading in tree-hollows.

Protected Area	**Index**	**SES values**	***p-value***
Global	CU	1.6853	0.1209
	SCU	-1.3047	0.2068
	JAC	-0.47005	0.6044
	SOR	-1.8471	0.07493
	BCD	**3.7115 (S)**	**0.001**
Cab	CU	**2.5563(S)**	**0.01499**
	SCU	1.1669	0.2727
	JAC	**-2.2054 (S)**	**0.04296**
	SOR	**-2.1147 (S)**	**0.04496**
	BCD	-1.0000	0.149
Camp	CU	-0.3260	0.8002
	SCU	-0.0989	0.9181
	JAC	-0.0036	0.9021
	SOR	0.6776	0.5145
	BCD	1.9463	0.018
Quil	CU	-0.9193	0.3606
	SCU	1.1033	0.2488
	JAC	1.2333	0.1908
	SOR	1.7197	0.0509
	BCD	0.974045	0.17

Standardized effect sizes (SES values) and permutation-based *p*-values were computed under the fixed-fixed null model (Gotelli, 2000) for the five community wide association indices: C-Score (CU; (Stone & Roberts, 1992)), standardized C-score (SCU; (Clarke & Gorley, 2006)), Jaccard index (JAC; (Gotelli & Entsminger, 2004)); Sorensen index (SOR; (Stone & Roberts, 1990)), and Bray-Curtis dissimilarity index (BCD; (Faith et al., 1987)). * Significant differences between observed data and null model outputs ($p<0.05$) are in bold.

Table 4 Number of non-random patterns performed between functional guilds couples derived of pairwise co-occurrence analysis applied to whole assemblage (matrix Global) and to local level per woodland site (Cab, Camp and Quil matrices).

Couples formed by trophic guilds couples	**Global**		**Cab**		**Camp**		**Quil**	
	A	**S**	**A**	**S**	**A**	**S**	**A**	**S**
X - XM	13	0	7	0	0	1	1	0
X - SX	18	5	6	2	3	0	3	0
X - CSA	5	6	0	5	1	1	2	0
X - P	19	2	11	1	1	0	3	0
X - DSA	8	5	2	1	0	2	2	0
XM - SX	32	0	15	1	2	1	1	0
XM - CSA	14	1	7	2	0	1	1	0
XM – P	32	0	23	0	5	0	3	0
XM - DSA	6	3	4	0	0	8	0	0
SX - CSA	15	8	3	10	1	0	9	0
SX – P	43	2	17	1	6	0	10	1
SX - DSA	20	13	9	0	0	14	3	1
CSA - P	20	3	6	5	3	0	10	0
CSA - DSA	3	10	2	11	1	6	1	0
DSA – P	9	3	4	0	0	10	1	0

A: aggregated non-random patterns; S: segregated non-random patterns; DSA: saprophagous syrphids; CSA: coleopterans saprophagous; SX: saproxylophagous; X: xylophagous; XM: xylomycetophagous and P: predators.

On the other hand, saprophagous beetles showed the most frequent non-random segregated association in Cab with saprophagous syrphids (8 pairs, 4%) (Table 4); and in Camp this was between saproxylophagous beetles and saprophagous syrphids (14 pairs, 18%) (Table 4). Finally, in Quil few significant segregated associations were detected (2 pairs, 3%) (Table 4).

Table 5 Non-random patterns of aggregation/ segregations shared among woodland sites.

Species pair		**Cab** BCD SES	**Camp** BCD SES	**Quil** BCD SES
Camptorhinus statua (CSA)	*Xyleborus dryographus* (X)	-2.03 (A)	-------	-2.03 (A)
Cryptophagus aurelioi (SX)	*Cryptophagus scanicus* (XM)	-2.42 (A)	--------	-2.37 (A)
Cryptophagus scanicus (XM)	*Paromalus flavicornis* (P)	-3.16 (A)	---------	-2.17 (A)
Epuraea fuscicollis (CSA)	*Mallota cimbiciformis* (DSA)	2.28 (S)	4.41 (S)	-------
Soronia oblonga (CSA)	*Mallota cimbiciformis* (DSA)	2.15 (S)	2.13 (S)	-------
Mallota dusmeti (DSA)	*Epuraea fuscicollis* (CSA)	2.33 (S)	3.07 (S)	-------
Mallota dusmeti (DSA)	*Soronia oblonga* (CSA)	2.17 (S)	2.78 (S)	-------

A: aggregated non-random patterns; S: segregated non-random patterns; DSA: saprophagous syrphids; CSA: coleopterans saprophagous; SX: saproxylophagous; X: xylophagous; XM: xylomycetophagous and P: predators.

Discussion

Even though there is evidences regarding the existence of several interspecific interactions on saproxylic insect communities (Dodds et al., 2001; Buse et al., 2008; Micó et al., 2011, 2015; Sánchez-Galván et al., 2014; Zuo et al., 2016), little is known about how these different interactions affect the structure of saproxylic insect assemblages. This study analyzed for the first time non-random patterns of aggregation and segregation between species pairs and trophic guilds in tree hollows of *Q. pyrenaica* trees from Iberian Mediterranean forests. Our findings indicate the existence of significant association patterns of pairs of species and trophic guilds in these particular systems within, the assumption of the fixed-fixed null model.

Compositions of saproxylic insect assemblages (Coleoptera and Diptera: Syrphidae) formed in tree hollows varied significantly among woodland sites (Tables 1 and 2), causing a low number of co- occurrence non-random patterns of aggregation/segregation which are shared among woodland sites (Table 5).

The analyses at matrix level were only significant at regional level and at local level in Cab. At both levels, a whole trend toward segregation among insect species was found (Table 3). It could be tempting to speculate about the dominance of cases of competitive exclusions (Connor & Simberloff, 1979, 1984) in these microhabitats, or to attribute this observations to niche dissimilarities (niche filtering effect) (Fowler et al., 2014). A segregation pattern was expected at regional level due to the difference in species composition between the three studied localities. Moreover, when using large data sets, the matrix-level approach could fail to detect patterns of species association and their biological explanation (Azeria et al., 2012; Camarota et al., 2016).

In this regard, the pairwise-level analyses indicated there were more non-random aggregated than non-random segregated patterns (Figure 1). In general, the proportion of significant non-random pairs was moderately low (6-10%) (Figure1), compared with other similar studies, for example 28.7% for beetles in boreal forest (Azeria et al., 2012), and less than 5% in other context (Sfenthourakis et al., 2006).These moderately low percentages of non-random patterns could be the consequence of the high complexity of tree hollow microhabitats, which increases the stochastic nature of patterns in general. Besides, the Iberian Mediterranean ecosystems are characterized by a bimodal Mediterranean climate, i.e. there is a high seasonal and annual variability of environmental conditions that might add randomness to these patterns (Blondel & Aronson, 1999).

Aggregated non-random patterns could be interpreted as species sharing habitat affinity (Peres-Neto, 2004; Azeria et al., 2009, 2012). However, only 23.5% (for whole assemblage expressed in Global) and 16-23% (for each site) of the non-random co-occurrences were composed of species belonging to the same trophic guild. Therefore, the aggregated patterns in these systems may be attributed to interspecific interactions. Indeed, the majority of these patterns constituted pairs of species belonging to different trophic guilds, such as saproxylophagous, saprophagous or xylomycetophagous beetle species with predator species (Table 4). This fact could corroborate the assertion that tree hollows hosting more potential preys are expected to be colonized by more predator species (Kenis et al., 2004; Johansson et al., 2007; Azeria et al., 2012).

Segregation among species is traditionally considered the result of competitive interactions when resources are a limiting factor (Connor & Simberloff, 1979, 1984; Gotelli & Graves, 1996). However, we only found ~ 12% (from a total of 69 pairs) of non-random segregated pairs composed of species of the same trophic guild, denoting the limited possibility of competitive interactions among species. On the contrary, ~ 88% (from a total of 69 pairs) belonged to different trophic guilds (details in Annex III). Other studies have suggested also that habitat segregation rather than competition is the main force driving species segregation (Azeria et al., 2012). In fact, different characteristics of tree hollows affect different trophic guilds to a different extend (Quinto et al., 2014). In this way, many of the spatial segregations found in this study may be the result of dissimilarity in hollow occupation of the two taxonomic orders studied: Diptera (Syrphidae) and Coleoptera. In Camp, the majority of significant segregations were formed by syrphids and coleopteran species (Table 4). Here, ecological requirements of long-tailed larvae of saprophagous hoverflies such as *Mallota* species, whose larvae live in water retained in tree hollows, or in high humidity conditions, could explain these kinds of segregations (Rotheray & Gilbert, 2011; Přikryl et al., 2012; Ramírez-Hernández et al., 2014). A clear example of segregation is the case of the Vulnerable syrphid *Mallota dusmeti* Andréu, 1926 and the beetle predator *Dendrophilus punctatus* (Histeridae) (BCD SES=-2.99, see Annex IV, Table B). In other systems Histeridae species such as *D. punctatus* act as principal predators of immature stages of several Diptera families, however, this occurs in dry conditions (Wills & Mullens, 1991).

Tree hollows harbour many endangered species (Dajoz, 1998; Ranius, 2002; Sverdrup-Thygeson, 2009; Ramírez-Hernández et al., 2014). However, the examples involving the conservation of endangered saproxylic species by their insect-insect interactions are scarce. Our results reveal the implication of threatened and near-threatened saproxylic species in 57 non-random patterns, of which 39 were aggregations and 18 were segregations (Annex III). Among the inter-guilds couples, some interactions of facilitation could be revealed; for example the endangered species *Limoniscus violaceus* (Elateridae) (species included in the Habitat Directive) was associated with the Vulnerable predator *Ischnodes sanguinicollis* (Elateridae)

(BCD SES=-3.92, Annex III). This association, pointed out previously (Gouix & Brustel, 2011; Gouix et al., 2012), could be the result of the biology of *L. violaceus* that exploits the nutrients of the dead animals resulting in the predatory activity of the other Elateridae beetles (Gouix et al., 2012; Micó et al., 2015). Moreover, our results showed non-random aggregation patterns between ecosystem engineer species, such as *Cerambyx* (Cerambycidae) and Cetoniidae species, and some trophic guilds. In Cab, *Cerambyx welensii* showed aggregation patterns with the predators *Abraeus perpusillus* (BCD SES=-3.37, see Annex IV, Table A) and *E. ferrugineus* (BCD SES=-2.59, Annex IV, Table A). It is well known that galleries made by the *Cerambyx* larvae facilitate the species richness of predators (Buse et al., 2008; Micó et al., 2015). Cetoniid species have also been considered ecosystem engineers which facilitate the establishment of mainly other saprophagous and saproxylophagous species in tree-hollows (Micó et al., 2015; Sánchez-Sánchez et al., 2017). Our results highlight the formation of couples, at the regional level (Annex III), by *Protaetia cuprea* and the saprophagous *Attagenus incognitus* (Anobiidae) (BCD SES=-2.97), *Palorus depressus* (Tenebrionidae) (BCD SES=-2.67) and the saproxylophagous *Melanothus dichrous* (Elateridae) (BCD SES=-2.28) and *Mycetochara linearis* (Alleculinae) (BCD SES=-2.23), or by *P. mirifica* with the saproxylophagous *Cryptophagus reflexus* (Cryptophagidae) (BCD SES=-3.53) and *Probaticus anthracinus* (Tenebrionidae) (BCD SES=-2.26).

Our findings, based on the FF null models, suggest that interspecific interactions such as predation and facilitation, as well as habitat segregation, are the main factors shaping tree-hollow assemblages, while competition seems to have less importance, indicating that resources are not a limiting factor in tree-hollows. Consequently, an effective conservation of saproxylic insect assemblages on these complexes micro-environments implies taking into account, not only tree hollow heterogeneity but also the interspecific interactions with special attention to the "ecosystem engineers", and the threatened and near-threatened species.

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Annex I- Total list of saproxylic Coleoptera and Diptera: Syrphidae species, collected in tree-hollows from whole selected sites. All species were included in the Global matrix. Singletons/doubletons were excluded of co-occurrence analyses. The IUCN categories of threatened and near threatened species are indicated: (**EN**) Endangered; (**VU**) Vulnerable; and (**NT**) Near Threatened (Verdú & Galante, 2006; Nieto & Alexander, 2010).

Order	**Trophic Guild**		**Species**	**Total abundance**
Coleoptera	Predators **(P)**	1	*Abraeus perpusillus*	16
		2	*Ampedus aurilegulus*	32
		3	*Amphotis marginata*	2
		4	*Anthocomus fenestratus*	14
		5	*Aplocnemus nigricornis*	1
		6	*Axinotarsus marginalis*	2
		7	*Brachygonus megerlei* (NT)	4
		8	*Colobicus hirtus*	1
		9	*Colydium elongatum*	5
		10	*Corticeus fasciatus*	1
		11	*Dasytes pauperculus*	1
		12	*Dendrophilus punctatus*	40
		13	*Ectamenogonus montandoni* (NT)	25
		14	*Elater ferrugineus* (NT)	57
		15	*Gnathoncus communis*	35
		16	*Gnathoncus nannetensis*	14
		17	*Hetaerius ferrugineus*	1
		18	*Hypebaeus albifrons*	16
		19	*Hypebaeus flavipes*	6
		20	*Ischnodes sanguinicollis* (VU)	37
		21	*Lacon punctatus*	13
		22	*Margarinotus brunneus*	1
		23	*Margarinotus merdarius*	22
		24	*Margarinotus uncostriatus*	2
		25	*Mauroania bourgeoisi*	1
		26	*Megapenthes lugens* (NT)	22
		27	*Melanotus villosus*	2
		28	*Merohister ariasi*	2
		29	*Paromalus flavicornis*	26
		30	*Platylomalus gardineri*	1
		31	*Platysoma filiforme*	1
		32	*Procraerus tibialis*	15
		33	*Troglops furcatus*	26
		34	*Uleiota planata*	2
	Saprophagous **(CSA)**	35	*Ahasverus advena*	1
		36	*Anthrenus angustefasciatus*	2
		37	*Anthrenus festivus*	1
		38	*Anthrenus minutus*	5
		39	*Atomaria pusilla*	1
		40	*Attagenus incognitus*	6
		41	*Attagenus schaefferi*	1
		42	*Attagenus trifasciatus*	2
		43	*Cryptophagus distinguendus*	1
		44	*Cryptophagus micaceus*	65
		45	*Cryptophagus saginatus*	17

		46	*Dermestes bicolor*	1
		47	*Dermestes erichsonii*	1
		48	*Dermestes hispanicus*	1
		49	*Dermestes undulatus*	6
		50	*Epuraea fuscicollis*	160
		51	*Epuraea ocularis*	2
		52	*Limoniscus violaceus* $^{(EN)}$	5
		53	*Orphilus niger*	4
		54	*Palorus depressus*	8
		55	*Prionocyphon serricornis*	127
		56	*Soronia oblonga*	174
		57	*Tenebrio punctipennis*	33
	Saproxylophagous **(SX)**	58	*Aderus populneus*	12
		59	*Alocerus moesiacus*	3
		60	*Anaspis (Anaspis) ruficollis*	5
		61	*Anaspis regimbarti*	10
		62	*Camptorhinus simplex*	7
		63	*Camptorhinus statua*	129
		64	*Cetonia aurataeformis*	208
		65	*Cryptophagus aurelioi*	48
		66	*Cryptophagus jakowlewi*	102
		67	*Cryptophagus punctipennis*	15
		68	*Cryptophagus reflexus*	63
		69	*Dendarus pectoralis*	13
		70	*Dorcus parallelipipedus*	50
		71	*Hemicoelus nitidus*	2
		72	*Ischnomera xanthoderes*	27
		73	*Isomira hispánica*	3
		74	*Melanotus dichrous*	4
		75	*Mycetochara linearis*	18
		76	*Mycetochara quadrimaculata*	24
		77	*Nalassus laevioctostriatus*	5
		78	*Oryctes nasicornis*	7
		79	*Otolelus neglectus*	2
		80	*Prionychus ater*	27
		81	*Prionychus fairmairei*	11
		82	*Probaticus anthracinus*	43
		83	*Protaetia cuprea*	63
		84	*Protaetia mirifica* $^{(VU)}$	9
		85	*Protaetia opaca*	1
		86	*Pseudocistela ceramboides*	35
		87	*Scraptia testacea*	91
		88	*Stagetus elongatus*	1
		89	*Stenohelops montanus*	2
	Xylomycetophagous **(XM)**	90	*Cryptophagus cylindrellus*	4
		91	*Cryptophagus dentatus*	40
		92	*Cryptophagus scanicus*	124
		93	*Diplocoelus fagi*	8
		94	*Dorcatoma agenjoi*	8
		95	*Dorcatoma chrysomelina*	2
		96	*Eledonoprius armatus*	7
		97	*Endophloeus marcovichianus*	20
		98	*Gasterocercus hispanicus*	2
		99	*Litargus balteatus*	1
		100	*Litargus connexus*	9
		101	*Mycetaea hirta*	2
		102	*Mycetophagus quadriguttatus*	48
		103	*Orchesia micans*	4

		104	*Rhamna semen*	23
		105	*Symbiotes gibberosus*	9
	Xylophagous **(X)**	106	*Cerambyx welensii* **(NT)**	74
		107	*Eurythyrea quercus*	2
		108	*Lobonyx aeneus*	1
		109	*Oligomerus brunneus*	21
		110	*Platypus cylindrus*	1
		111	*Rhyncolus reflexus*	6
		112	*Stictoleptura trisignata*	20
		113	*Trichoferus fasciculatus*	1
		114	*Xestobium rufovillosum*	3
		115	*Xyleborinus saxesenii*	14
		116	*Xyleborus dryographus*	9
		117	*Xyleborus monographus*	174
Diptera: Syrphidae	Saprophagous **(DSA)**	1	*Brachypalpoides lentus*	1
		2	*Callicera aurata*	2
		3	*Callicera spinolae*	7
		4	*Ceriana vespiformis*	1
		5	*Criorhina floccosa*	16
		6	*Criorhina pachymera*	1
		7	*Ferdinandea aurea*	27
		8	*Ferdinandea cuprea*	4
		9	*Ferdinandea fumipennis*	2
		10	*Ferdinandea ruficornis*	16
		11	*Mallota cimbiciformis*	118
		12	*Mallota dusmeti* **(VU)**	71
		13	*Myathropa florea*	63
		14	*Myolepta difformis*	4
		15	*Myolepta dubia*	11
		16	*Myolepta obscura*	1
		17	*Spilomyia digitata*	5
		18	*Myolepta vara*	1

Annex II

Table A. - Local list of saproxylic insect species (Coleoptera and Diptera: Syrphidae) selected to form part of the matrix "Cab". The IUCN categories of threatened and near threatened species are indicated: (**EN**) Endangered; (**VU**) Vulnerable; and (**NT**) Near Threatened (Verdú & Galante, 2006; Nieto & Alexander, 2010).

Order	Trophic Guild		Species	Abundance	Number of tree hollows occupied
Coleoptera	Predators **(P)**	1	*Abraeus perpusillus*	14	5
		2	*Ampedus aurilegulus*	28	10
		3	*Anthocomus fenestratus*	11	7
		4	*Colydium elongatum*	5	2
		5	*Elater ferrugineus* (NT)	25	11
		6	*Gnathoncus communis*	30	6
		7	*Gnathoncus nannetensis*	6	3
		8	*Hypebaeus albifrons*	3	2
		9	*Ischnodes sanguinicollis* (VU)	19	3
		10	*Lacon punctatus*	4	4
		11	*Margarinotus merdarius*	6	6
		12	*Megapenthes lugens* (NT)	13	5
		13	*Paromalus flavicornis*	21	3
		14	*Troglops furcatus*	25	9
	Saprophagous **(CSA)**	15	*Cryptophagus micaceus*	61	4
		16	*Cryptophagus saginatus*	14	6
		17	*Dermestes undulatus*	5	1
		18	*Epuraea fuscicollis*	113	11
		19	*Prionocyphon serricornis*	122	16
		20	*Soronia oblonga*	128	20
		21	*Tenebrio punctipennis*	29	9
	Saproxylophagous **(SX)**	22	*Aderus populneus*	9	6
		23	*Anaspis regimbarti*	10	5
		24	*Camptorhinus statua*	89	23
		25	*Cetonia aurataeformis*	144	20
		26	*Cryptophagus aurelioi*	11	6
		27	*Cryptophagus jakowlewi*	60	16
		28	*Cryptophagus punctipennis*	8	6
		29	*Dorcus parallelipipedus*	34	10
		30	*Ischnomera xanthoderes*	3	3
		31	*Mycetochara linearis*	4	4
		32	*Mycetochara quadrimaculata*	21	7
		33	*Oryctes nasicornis*	7	1
		34	*Prionychus fairmairei*	8	7
		35	*Probaticus anthracinus*	17	7
		36	*Protaetia cuprea*	6	4
		37	*Pseudocistela ceramboides*	35	10
		38	*Scraptia testacea*	25	11
	Xylomycetophagous **(XM)**	39	*Cryptophagus cylindrellus*	4	2
		40	*Cryptophagus dentatus*	8	6
		41	*Cryptophagus scanicus*	67	13
		42	*Diplocoelus fagi*	8	8
		43	*Dorcatoma agenjoi*	8	2
		44	*Eledonoprius armatus*	7	2
		45	*Endophloeus marcovichianus*	20	8
		46	*Litargus connexus*	9	4
		47	*Mycetophagus quadriguttatus*	23	4
		48	*Orchesia micans*	4	2
		49	*Rhamna semen*	13	5

	Xylophagous **(X)**	50	*Cerambyx welensii* $^{(NT)}$	3	1
		51	*Oligomerus brunneus*	20	10
		52	*Stictoleptura trisignata*	20	5
		53	*Xyleborinus saxesenii*	11	8
		54	*Xyleborus dryographus*	6	6
		55	*Xyleborus monographus*	165	20
Diptera; Syrphidae	Saprophagous **(DSA)**	56	*Callicera spinolae*	3	2
		57	*Criorhina floccosa*	7	2
		58	*Ferdinandea aurea*	24	2
		59	*Ferdinandea ruficornis*	6	1
		60	*Mallota cimbiciformis*	17	2
		61	*Mallota dusmeti* $^{(VU)}$	17	2
		62	*Myathropa florea*	41	6
		63	*Myolepta difformis*	4	3
		64	*Spilomyia digitata*	3	2

Table B. - Local list of saproxylic insect species (Coleoptera and Diptera: Syrphidae) selected to form part of the matrix "Camp"**.** The IUCN categories of threatened and near threatened species are indicated: (**EN**) Endangered; (**VU**) Vulnerable; and (**NT**) Near Threatened (Verdú & Galante, 2006; Nieto & Alexander, 2010).

Order	**Trophic Guild**		**Species**	**Abundance**	**Number of tree hollows occupied**
Coleoptera	Predators **(P)**	1	*Anthocomus fenestratus*	3	3
		2	*Brachygonus megerlei* (NT)	4	3
		3	*Dendrophilus punctatus*	39	9
		4	*Ectamenogonus montandoni* (NT)	23	6
		5	*Elater ferrugineus* (NT)	14	8
		6	*Gnathoncus communis*	5	3
		7	*Gnathoncus nannetensis*	6	3
		8	*Lacon punctatus*	5	4
		9	*Margarinotus merdarius*	13	5
		10	*Megapenthes lugens* (NT)	5	3
		11	*Procraerus tibialis*	5	3
	Saprophagous **(CSA)**	12	*Attagenus incognitus*	3	2
		13	*Cryptophagus micaceus*	4	1
		14	*Cryptophagus saginatus*	3	3
		15	*Epuraea fuscicollis*	43	7
		16	*Palorus depressus*	5	3
		17	*Soronia oblonga*	42	10
	Saproxylophagous **(SX)**	18	*Aderus populneus*	3	3
		19	*Camptorhinus statua*	13	2
		20	*Cetonia aurataeformis*	10	6
		21	*Cryptophagus aurelioi*	29	3
		22	*Cryptophagus reflexus*	63	8
		23	*Dorcus parallelipipedus*	4	3
		24	*Mycetochara linearis*	3	3
		25	*Mycetochara quadrimaculata*	3	3
		26	*Prionychus ater*	13	6
		27	*Probaticus anthracinus*	26	7
		28	*Protaetia cuprea*	38	9
		29	*Protaetia mirifica* (VU)	9	4
		30	*Scraptia testacea*	4	3
	Xylomycetophagous **(XM)**	31	*Cryptophagus dentatus*	30	3
		32	*Cryptophagus scanicus*	49	6
		33	*Mycetophagus quadriguttatus*	21	6
		34	*Rhamna semen*	10	2
		35	*Symbiotes gibberosus*	5	5
	Xylophagous **(X)**	36	*Cerambyx welensii* (NT)	48	9
		37	*Xyleborinus saxesenii*	3	3
		38	*Xyleborus monographus*	4	2

Diptera; Syrphidae	Saprophagous **(DSA)**	39	*Mallota cimbiciformis*	101	1
		40	*Mallota dusmeti* (VU)	47	3
		41	*Myathropa florea*	5	4
		42	*Myolepta dubia*	10	2

Table C. - Local list of saproxylic insect species (Coleoptera and Diptera: Syrphidae) selected to form part of the matrix "Quil". The IUCN categories of threatened and near threatened species are indicated: (**EN**) Endangered; (**VU**) Vulnerable; and (**NT**) Near Threatened (Verdú & Galante, 2006; Nieto & Alexander, 2010).

Order	**Trophic Guild**		**Species**	**Abundance**	**Number of tree hollows occupied**
Coleoptera	Predators **(P)**	1	*Ampedus aurilegulus*	4	4
		2	*Elater ferrugineus* $^{(NT)}$	18	10
		3	*Hypebaeus albifrons*	13	5
		4	*Hypebaeus flavipes*	6	3
		5	*Ischnodes sanguinicollis* $^{(VU)}$	18	4
		6	*Lacon punctatus*	4	3
		7	*Margarinotus merdarius*	3	3
		8	*Megapenthes lugens* $^{(NT)}$	4	3
		9	*Paromalus flavicornis*	3	3
		10	*Procraerus tibialis*	10	5
	Saprophagous **(CSA)**	11	*Anthrenus minutus*	5	4
		12	*Epuraea fuscicollis*	4	3
		13	*Limoniscus violaceus* $^{(EN)}$	4	2
		14	*Palorus depressus*	3	3
		15	*Prionocyphon serricornis*	4	3
		16	*Soronia oblonga*	4	4
		17	*Tenebrio punctipennis*	4	3
	Saproxylophagous **(SX)**	18	*Anaspis (Anaspis) ruficollis*	5	4
		19	*Camptorhinus simplex*	7	4
		20	*Camptorhinus statua*	27	9
		21	*Cetonia aurataeformis*	54	12
		22	*Cryptophagus aurelioi*	8	3
		23	*Cryptophagus jakowlewi*	42	14
		24	*Cryptophagus punctipennis*	6	4
		25	*Dendarus pectoralis*	13	4
		26	*Dorcus parallelipipedus*	12	8
		27	*Ischnomera xanthoderes*	24	9
		28	*Isomira hispanica*	3	1
		29	*Melanotus dichrous*	4	1
		30	*Mycetochara linearis*	11	7
		31	*Nalassus laevioctostriatus*	5	3
		32	*Prionychus ater*	14	11
		33	*Prionychus fairmairei*	3	1
		34	*Protaetia cuprea*	19	10
		35	*Scraptia testacea*	62	10
	Xylomycetophagous **(XM)**	36	*Cryptophagus scanicus*	8	3
		37	*Mycetophagus quadriguttatus*	4	4
	Xylophagous **(X)**	38	*Cerambyx welensii* $^{(NT)}$	23	7
		39	*Rhyncolus reflexus*	6	4
		40	*Xestobium rufovillosum*	3	1
		41	*Xyleborus dryographus*	3	1

		42	*Xyleborus monographus*	5	2
Diptera; **Syrphidae**	Saprophagous **(DSA)**	43	*Criorhina floccosa*	9	3
		44	*Ferdinandea cuprea*	3	2
		45	*Ferdinandea ruficornis*	9	4
		46	*Mallota dusmeti* (VU)	7	1
		47	*Myathropa florea*	17	7

ANNEX III- Aggregated and segregated non-random association patterns calculated by pairwise co-occurrence analysis to regional level. The panel show B-C SES < -2 values indicating a significant aggregated distribution between pair of species (p smaller <0.05), whereas B-C SES > 2 values are indicating significant segregated distribution between individual pair of species (p larger <0.05). In the first column is distinguished the species trophic guild: saprophagous syrphids (DSA); saprophagous (CSA); saproxylophagous (SX), xylophagous (X), xylomycetophagous (XM) and predators (P).

Id	Trophic guild couple	Pairs of species		B-C SES
1	DSA_5-DSA_17	*Callicera spinolae*	*Myolepta difformis*	-8.15
2	XM_5-XM_7	*Dorcatoma agenjoi*	*Eledonoprius armatus*	-7.94
3	XM_11-P_9	*Litargus connexus*	*Colydium elongatum*	-7.76
4	XM_11-XM_7	*Litargus connexus*	*Eledonoprius armatus*	-7.37
5	P_29-CSA_23	*Paromalus flavicornis*	*Tenebrio punctipennis*	-6.57
6	XM_11-XM_5	*Litargus connexus*	*Dorcatoma agenjoi*	-6.55
7	XM_7-P_9	*Eledonoprius armatus*	*Colydium elongatum*	-6.39
8	XM_5-P_9	*Dorcatoma agenjoi*	*Colydium elongatum*	-6.28
9	CSA_18-SX_12	*Limoniscus violaceus*	*Dendarus pectoralis*	-5.84
10	SX_21-DSA_9	*Oryctes nasicornis*	*Ferdinandea aurea*	-5.61
11	P_15-P_29	*Gnathoncus communis*	*Paromalus flavicornis*	-5.59
12	SX_27-P_13	*Protaetia mirifica*	*Ectamenogonus montandoni*	-5.37
13	P_1-XM_15	*Abraeus perpusillus*	*Rhamna semen*	-5.22
14	XM_16-CSA_6	*Symbiotes gibberosus*	*Attagenus incognitus*	-5.17
15	SX_5-CSA_4	*Camptorhinus simplex*	*Anthrenus minutus*	-5.06
16	P_15-XM_5	*Gnathoncus communis*	*Dorcatoma agenjoi*	-4.79
17	XM_14-XM_8	*Orchesia micans*	*Endophloeus marcovichianus*	-4.78

18	SX_2-P_9	*Alocerus moesiacus*	*Colydium elongatum*	-4.75
19	P_29-XM_7	*Paromalus flavicornis*	*Eledonoprius armatus*	-4.74
20	X_7-X_4	*Stictoleptura trisignata*	*Oligomerus brunneus*	-4.65
21	XM_13-XM_5	*Mycetophagus quadriguttatus*	*Dorcatoma agenjoi*	-4.64
22	P_29-XM_5	*Paromalus flavicornis*	*Dorcatoma agenjoi*	-4.63
23	X_7-P_1	*Stictoleptura trisignata*	*Abraeus perpusillus*	-4.58
24	DSA_18-SX_25	*Myolepta dubia*	*Probaticus anthracinus*	-4.55
25	P_15-P_9	*Gnathoncus communis*	*Colydium elongatum*	-4.48
26	XM_4-X_11	*Diplocoelus fagi*	*Xyleborus dryographus*	-4.39
27	XM_2-SX_11	*Cryptophagus dentatus*	*Cryptophagus reflexus*	-4.34
28	XM_3-P_15	*Cryptophagus scanicus*	*Gnathoncus communis*	-4.34
29	P_15-CSA_23	*Gnathoncus communis*	*Tenebrio punctipennis*	-4.29
30	CSA_15-P_15	*Dermestes undulatus*	*Gnathoncus communis*	-4.29
31	SX_21-SX_13	*Oryctes nasicornis*	*Dorcus parallelipipedus*	-4.24
32	XM_5-CSA_23	*Dorcatoma agenjoi*	*Tenebrio punctipennis*	-4.23
33	SX_2-XM_7	*Alocerus moesiacus*	*Eledonoprius armatus*	-4.23
34	P_9-CSA_23	*Colydium elongatum*	*Tenebrio punctipennis*	-4.22
35	XM_11-CSA_23	*Litargus connexus*	*Tenebrio punctipennis*	-4.18
36	XM_1-X_10	*Cryptophagus cylindrellus*	*Xyleborinus saxesenii*	-4.17
37	X_7-P_9	*Stictoleptura trisignata*	*Colydium elongatum*	-4.13
38	P_2-SX_29	*Ampedus aurilegulus*	*Pseudocistela ceramboides*	-4.12
39	P_15-XM_7	*Gnathoncus communis*	*Eledonoprius armatus*	-4.08

40	X_1-SX_27	*Cerambyx welensii*	*Protaetia mirifica*	-4.08
41	XM_7-CSA_23	*Eledonoprius armatus*	*Tenebrio punctipennis*	-4.03
42	CSA_11-DSA_9	*Cryptophagus saginatus*	*Ferdinandea aurea*	-4.01
43	DSA_17-SX_29	*Myolepta difformis*	*Pseudocistela ceramboides*	-3.93
44	P_29-XM_11	*Paromalus flavicornis*	*Litargus connexus*	-3.92
45	P_15-XM_11	*Gnathoncus communis*	*Litargus connexus*	-3.92
46	XM_4-DSA_21	*Diplocoelus fagi*	*Spilomyia digitata*	-3.92
47	P_20-CSA_18	*Ischnodes sanguinicollis*	*Limoniscus violaceus*	-3.92
48	P_29-DSA_16	*Paromalus flavicornis*	*Myathropa florea*	-3.92
49	SX_2-XM_11	*Alocerus moesiacus*	*Litargus connexus*	-3.88
50	SX_2-XM_5	*Alocerus moesiacus*	*Dorcatoma agenjoi*	-3.85
51	DSA_7-SX_17	*Criorhina floccosa*	*Melanotus dichrous*	-3.81
52	P_29-P_9	*Paromalus flavicornis*	*Colydium elongatum*	-3.81
53	P_29-XM_13	*Paromalus flavicornis*	*Mycetophagus quadriguttatus*	-3.73
54	P_33-SX_4	*Troglops furcatus*	*Anaspis regimbarti*	-3.71
55	XM_13-P_9	*Mycetophagus quadriguttatus*	*Colydium elongatum*	-3.69
56	SX_6-X_4	*Camptorhinus statua*	*Oligomerus brunneus*	-3.68
57	SX_26-SX_27	*Protaetia cuprea*	*Protaetia mirifica*	-3.66
58	DSA_14-DSA_18	*Mallota dusmeti*	*Myolepta dubia*	-3.65
59	DSA_5-SX_29	*Callicera spinolae*	*Pseudocistela ceramboides*	-3.65
60	P_1-X_4	*Abraeus perpusillus*	*Oligomerus brunneus*	-3.64
61	SX_27-P_12	*Protaetia mirifica*	*Dendrophilus punctatus*	-3.64

62	SX_11-P_13	*Cryptophagus reflexus*	*Ectamenogonus montandoni*	-3.63
63	SX_1-XM_16	*Aderus populneus*	*Symbiotes gibberosus*	-3.63
64	P_21-P_32	*Lacon punctatus*	*Procraerus tibialis*	-3.63
65	P_23-XM_13	*Margarinotus merdarius*	*Mycetophagus quadriguttatus*	-3.62
66	SX_15-SX_16	*Ischnomera xanthoderes*	*Isomira hispanica*	-3.62
67	X_4-SX_29	*Oligomerus brunneus*	*Pseudocistela ceramboides*	-3.61
68	XM_14-XM_5	*Orchesia micans*	*Dorcatoma agenjoi*	-3.59
69	X_7-SX_6	*Stictoleptura trisignata*	*Camptorhinus statua*	-3.59
70	P_15-P_16	*Gnathoncus communis*	*Gnathoncus nannetensis*	-3.58
71	P_15-XM_13	*Gnathoncus communis*	*Mycetophagus quadriguttatus*	-3.57
72	SX_18-SX_17	*Mycetochara linearis*	*Melanotus dichrous*	-3.56
73	P_33-SX_19	*Troglops furcatus*	*Mycetochara quadrimaculata*	-3.55
74	P_16-P_9	*Gnathoncus nannetensis*	*Colydium elongatum*	-3.54
75	SX_27-SX_11	*Protaetia mirifica*	*Cryptophagus reflexus*	-3.53
76	X_6-SX_3	*Rhyncolus reflexus*	*Anaspis (Anaspis) ruficollis*	-3.53
77	SX_15-SX_3	*Ischnomera xanthoderes*	*Anaspis (Anaspis) ruficollis*	-3.53
78	XM_3-P_29	*Cryptophagus scanicus*	*Paromalus flavicornis*	-3.53
79	CSA_10-XM_5	*Cryptophagus micaceus*	*Dorcatoma agenjoi*	-3.52
80	XM_13-CSA_23	*Mycetophagus quadriguttatus*	*Tenebrio punctipennis*	-3.52
81	SX_8-XM_2	*Cryptophagus aurelioi*	*Cryptophagus dentatus*	-3.52
82	P_14-P_1	*Elater ferrugineus*	*Abraeus perpusillus*	-3.51
83	CSA_10-P_29	*Cryptophagus micaceus*	*Paromalus flavicornis*	-3.50

84	XM_13-XM_7	*Mycetophagus quadriguttatus*	*Eledonoprius armatus*	-3.50
85	XM_5-DSA_16	*Dorcatoma agenjoi*	*Myathropa florea*	-3.47
86	P_32-SX_3	*Procraerus tibialis*	*Anaspis (Anaspis) ruficollis*	-3.43
87	SX_8-XM_7	*Cryptophagus aurelioi*	*Eledonoprius armatus*	-3.42
88	X_7-DSA_17	*Stictoleptura trisignata*	*Myolepta difformis*	-3.39
89	SX_1-P_1	*Aderus populneus*	*Abraeus perpusillus*	-3.38
90	P_18-SX_15	*Hypebaeus albifrons*	*Ischnomera xanthoderes*	-3.33
91	SX_27-P_23	*Protaetia mirifica*	*Margarinotus merdarius*	-3.31
92	SX_1-DSA_5	*Aderus populneus*	*Callicera spinolae*	-3.29
93	XM_11-XM_13	*Litargus connexus*	*Mycetophagus quadriguttatus*	-3.25
94	CSA_10-CSA_23	*Cryptophagus micaceus*	*Tenebrio punctipennis*	-3.25
95	SX_9-XM_7	*Cryptophagus jakowlewi*	*Eledonoprius armatus*	-3.24
96	SX_13-DSA_21	*Dorcus parallelipipedus*	*Spilomyia digitata*	-3.23
97	XM_16-P_32	*Symbiotes gibberosus*	*Procraerus tibialis*	-3.22
98	SX_2-XM_13	*Alocerus moesiacus*	*Mycetophagus quadriguttatus*	-3.18
99	SX_2-P_16	*Alocerus moesiacus*	*Gnathoncus nannetensis*	-3.18
100	SX_13-X_9	*Dorcus parallelipipedus*	*Xestobium rufovillosum*	-3.17
101	P_16-SX_25	*Gnathoncus nannetensis*	*Probaticus anthracinus*	-3.17
102	P_21-XM_16	*Lacon punctatus*	*Symbiotes gibberosus*	-3.16
103	CSA_10-XM_7	*Cryptophagus micaceus*	*Eledonoprius armatus*	-3.16
104	SX_26-P_32	*Protaetia cuprea*	*Procraerus tibialis*	-3.16
105	SX_6-X_11	*Camptorhinus statua*	*Xyleborus dryographus*	-3.14

106	SX_2-P_4	*Alocerus moesiacus*	*Anthocomus fenestratus*	-3.14
107	P_16-XM_7	*Gnathoncus nannetensis*	*Eledonoprius armatus*	-3.14
108	SX_8-XM_5	*Cryptophagus aurelioi*	*Dorcatoma agenjoi*	-3.14
109	P_7-DSA_18	*Brachygonus megerlei*	*Myolepta dubia*	-3.14
110	SX_15-X_6	*Ischnomera xanthoderes*	*Rhyncolus reflexus*	-3.13
111	P_19-SX_12	*Hypebaeus flavipes*	*Dendarus pectoralis*	-3.13
112	DSA_16-XM_7	*Myathropa florea*	*Eledonoprius armatus*	-3.12
113	X_1-XM_16	*Cerambyx welensii*	*Symbiotes gibberosus*	-3.12
114	P_4-CSA_6	*Anthocomus fenestratus*	*Attagenus incognitus*	-3.12
115	SX_6-XM_5	*Camptorhinus statua*	*Dorcatoma agenjoi*	-3.12
116	DSA_12-SX_16	*Ferdinandea ruficornis*	*Isomira hispanica*	-3.11
117	DSA_12-DSA_10	*Ferdinandea ruficornis*	*Ferdinandea cuprea*	-3.09
118	CSA_6-P_32	*Attagenus incognitus*	*Procraerus tibialis*	-3.09
119	XM_3-XM_5	*Cryptophagus scanicus*	*Dorcatoma agenjoi*	-3.09
120	SX_26-P_13	*Protaetia cuprea*	*Ectamenogonus montandoni*	-3.09
121	DSA_13-DSA_14	*Mallota cimbiciformis*	*Mallota dusmeti*	-3.08
122	X_12-P_29	*Xyleborus monographus*	*Paromalus flavicornis*	-3.08
123	P_26-DSA_7	*Megapenthes lugens*	*Criorhina floccosa*	-3.07
124	P_14-P_21	*Elater ferrugineus*	*Lacon punctatus*	-3.07
125	XM_4-XM_14	*Diplocoelus fagi*	*Orchesia micans*	-3.07
126	X_1-P_12	*Cerambyx welensii*	*Dendrophilus punctatus*	-3.06
127	DSA_12-X_9	*Ferdinandea ruficornis*	*Xestobium rufovillosum*	-3.06

128	SX_25-P_9	*Probaticus anthracinus*	*Colydium elongatum*	-3.03
129	CSA_20-SX_23	*Palorus depressus*	*Prionychus ater*	-3.02
130	X_7-SX_29	*Stictoleptura trisignata*	*Pseudocistela ceramboides*	-3.00
131	XM_7-XM_8	*Eledonoprius armatus*	*Endophloeus marcovichianus*	-2.99
132	SX_10 -SX_16	*Cryptophagus punctipennis*	*Isomira hispanica*	-2.98
133	SX_26-CSA_6	*Protaetia cuprea*	*Attagenus incognitus*	-2.97
134	X_1-P_32	*Cerambyx welensii*	*Procraerus tibialis*	-2.96
135	P_23-P_12	*Margarinotus merdarius*	*Dendrophilus punctatus*	-2.95
136	P_20-X_6	*Ischnodes sanguinicollis*	*Rhyncolus reflexus*	-2.94
137	DSA_7-DSA_5	*Criorhina floccosa*	*Callicera spinolae*	-2.93
138	P_21-X_6	*Lacon punctatus*	*Rhyncolus reflexus*	-2.92
139	X_7-DSA_5	*Stictoleptura trisignata*	*Callicera spinolae*	-2.92
140	SX_6-XM_7	*Camptorhinus statua*	*Eledonoprius armatus*	-2.92
141	DSA_13-DSA_18	*Mallota cimbiciformis*	*Myolepta dubia*	-2.92
142	XM_4-SX_6	*Diplocoelus fagi*	*Camptorhinus statua*	-2.91
143	SX_6-CSA_23	*Camptorhinus statua*	*Tenebrio punctipennis*	-2.90
144	X_1-P_13	*Cerambyx welensii*	*Ectamenogonus montandoni*	-2.90
145	SX_18-DSA_10	*Mycetochara linearis*	*Ferdinandea cuprea*	-2.90
146	X_12-XM_11	*Xyleborus monographus*	*Litargus connexus*	-2.90
147	SX_8-P_9	*Cryptophagus aurelioi*	*Colydium elongatum*	-2.86
148	P_18-SX_18	*Hypebaeus albifrons*	*Mycetochara linearis*	-2.86
149	SX_9-CSA_15	*Cryptophagus jakowlewi*	*Dermestes undulatus*	-2.85

150	P_9-XM_8	*Colydium elongatum*	*Endophloeus marcovichianus*	-2.85
151	X_10-CSA_22	*Xyleborinus saxesenii*	*Soronia oblonga*	-2.83
152	X_12-P_1	*Xyleborus monographus*	*Abraeus perpusillus*	-2.83
153	SX_9- SX_10	*Cryptophagus jakowlewi*	*Cryptophagus punctipennis*	-2.82
154	SX_21-SX_30	*Oryctes nasicornis*	*Scraptia testacea*	-2.82
155	SX_8-XM_11	*Cryptophagus aurelioi*	*Litargus connexus*	-2.81
156	XM_5-XM_8	*Dorcatoma agenjoi*	*Endophloeus marcovichianus*	-2.81
157	SX_30-SX_17	*Scraptia testacea*	*Melanotus dichrous*	-2.80
158	XM_4-SX_24	*Diplocoelus fagi*	*Prionychus fairmairei*	-2.80
159	XM_4-P_9	*Diplocoelus fagi*	*Colydium elongatum*	-2.78
160	XM_4-X_4	*Diplocoelus fagi*	*Oligomerus brunneus*	-2.78
161	DSA_18-XM_16	*Myolepta dubia*	*Symbiotes gibberosus*	-2.77
162	X_12-XM_5	*Xyleborus monographus*	*Dorcatoma agenjoi*	-2.77
163	XM_3-CSA_20	*Cryptophagus scanicus*	*Palorus depressus*	-2.76
164	P_26-DSA_5	*Megapenthes lugens*	*Callicera spinolae*	-2.74
165	SX_6-P_9	*Camptorhinus statua*	*Colydium elongatum*	-2.74
166	SX_8-XM_3	*Cryptophagus aurelioi*	*Cryptophagus scanicus*	-2.74
167	SX_9-XM_5	*Cryptophagus jakowlewi*	*Dorcatoma agenjoi*	-2.74
168	SX_9-SX_17	*Cryptophagus jakowlewi*	*Melanotus dichrous*	-2.73
169	XM_1-SX_9	*Cryptophagus cylindrellus*	*Cryptophagus jakowlewi*	-2.72
170	P_14-SX_3	*Elater ferrugineus*	*Anaspis (Anaspis) ruficollis*	-2.72
171	SX_2-CSA_6	*Alocerus moesiacus*	*Attagenus incognitus*	-2.72

172	X_7-DSA_7	*Stictoleptura trisignata*	*Criorhina floccosa*	-2.71
173	SX_21-CSA_22	*Oryctes nasicornis*	*Soronia oblonga*	-2.71
174	SX_1-DSA_17	*Aderus populneus*	*Myolepta difformis*	-2.70
175	XM_3-CSA_15	*Cryptophagus scanicus*	*Dermestes undulatus*	-2.70
176	SX_13-P_9	*Dorcus parallelipipedus*	*Colydium elongatum*	-2.70
177	SX_26-CSA_20	*Protaetia cuprea*	*Palorus depressus*	-2.67
178	SX_1-X_11	*Aderus populneus*	*Xyleborus dryographus*	-2.65
179	SX_30-X_6	*Scraptia testacea*	*Rhyncolus reflexus*	-2.65
180	XM_14-DSA_21	*Orchesia micans*	*Spilomyia digitata*	-2.65
181	X_1-CSA_6	*Cerambyx welensii*	*Attagenus incognitus*	-2.65
182	CSA_10-P_15	*Cryptophagus micaceus*	*Gnathoncus communis*	-2.64
183	X_7-P_26	*Stictoleptura trisignata*	*Megapenthes lugens*	-2.63
184	P_20-SX_12	*Ischnodes sanguinicollis*	*Dendarus pectoralis*	-2.62
185	SX_6-XM_11	*Camptorhinus statua*	*Litargus connexus*	-2.62
186	P_13-XM_16	*Ectamenogonus montandoni*	*Symbiotes gibberosus*	-2.62
187	P_23-DSA_5	*Margarinotus merdarius*	*Callicera spinolae*	-2.61
188	SX_2-XM_8	*Alocerus moesiacus*	*Endophloeus marcovichianus*	-2.61
189	SX_2-DSA_21	*Alocerus moesiacus*	*Spilomyia digitata*	-2.61
190	P_4-X_4	*Anthocomus fenestratus*	*Oligomerus brunneus*	-2.60
191	X_12-XM_7	*Xyleborus monographus*	*Eledonoprius armatus*	-2.60
192	X_1-SX_26	*Cerambyx welensii*	*Protaetia cuprea*	-2.59
193	XM_3-P_7	*Cryptophagus scanicus*	*Brachygonus megerlei*	-2.59

194	SX_6-DSA_17	*Camptorhinus statua*	*Myolepta difformis*	-2.58
195	P_16-XM_5	*Gnathoncus nannetensis*	*Dorcatoma agenjoi*	-2.58
196	P_14-XM_16	*Elater ferrugineus*	*Symbiotes gibberosus*	-2.58
197	CSA_20-P_19	*Palorus depressus*	*Hypebaeus flavipes*	-2.57
198	P_1-SX_29	*Abraeus perpusillus*	*Pseudocistela ceramboides*	-2.57
199	DSA_16-P_9	*Myathropa florea*	*Colydium elongatum*	-2.57
200	P_12-CSA_20	*Dendrophilus punctatus*	*Palorus depressus*	-2.57
201	SX_2-X_7	*Alocerus moesiacus*	*Stictoleptura trisignata*	-2.57
202	SX_9-CSA_11	*Cryptophagus jakowlewi*	*Cryptophagus saginatus*	-2.55
203	X_7-XM_11	*Stictoleptura trisignata*	*Litargus connexus*	-2.55
204	CSA_20-X_6	*Palorus depressus*	*Rhyncolus reflexus*	-2.55
205	DSA_16-CSA_23	*Myathropa florea*	*Tenebrio punctipennis*	-2.54
206	P_13-CSA_6	*Ectamenogonus montandoni*	*Attagenus incognitus*	-2.53
207	SX_26-XM_16	*Protaetia cuprea*	*Symbiotes gibberosus*	-2.53
208	SX_18-P_32	*Mycetochara linearis*	*Procraerus tibialis*	-2.53
209	SX_6-XM_14	*Camptorhinus statua*	*Orchesia micans*	-2.52
210	DSA_5-SX_19	*Callicera spinolae*	*Mycetochara quadrimaculata*	-2.51
211	SX_30-SX_16	*Scraptia testacea*	*Isomira hispanica*	-2.51
212	X_10-DSA_17	*Xyleborinus saxesenii*	*Myolepta difformis*	-2.49
213	X_12-P_9	*Xyleborus monographus*	*Colydium elongatum*	-2.49
214	SX_2-P_29	*Alocerus moesiacus*	*Paromalus flavicornis*	-2.49
215	CSA_15-CSA_16	*Dermestes undulatus*	*Epuraea fuscicollis*	-2.48

216	SX_6-XM_8	*Camptorhinus statua*	*Endophloeus marcovichianus*	-2.48
217	SX_9-P_29	*Cryptophagus jakowlewi*	*Paromalus flavicornis*	-2.47
218	SX_9-SX_16	*Cryptophagus jakowlewi*	*Isomira hispanica*	-2.47
219	P_21-P_26	*Lacon punctatus*	*Megapenthes lugens*	-2.46
220	SX_2-XM_14	*Alocerus moesiacus*	*Orchesia micans*	-2.46
221	CSA_21-XM_14	*Prionocyphon serricornis*	*Orchesia micans*	-2.46
222	SX_9-XM_11	*Cryptophagus jakowlewi*	*Litargus connexus*	-2.46
223	CSA_15-CSA_22	*Dermestes undulatus*	*Soronia oblonga*	-2.46
224	CSA_19-DSA_10	*Orphilus niger*	*Ferdinandea cuprea*	-2.44
225	P_21-P_4	*Lacon punctatus*	*Anthocomus fenestratus*	-2.42
226	SX_27-XM_16	*Protaetia mirifica*	*Symbiotes gibberosus*	-2.42
227	SX_27-XM_2	*Protaetia mirifica*	*Cryptophagus dentatus*	-2.42
228	SX_26-P_21	*Protaetia cuprea*	*Lacon punctatus*	-2.42
229	XM_3-XM_14	*Cryptophagus scanicus*	*Orchesia micans*	-2.42
230	CSA_10-P_9	*Cryptophagus micaceus*	*Colydium elongatum*	-2.41
231	XM_16-SX_23	*Symbiotes gibberosus*	*Prionychus ater*	-2.41
232	SX_26-P_12	*Protaetia cuprea*	*Dendrophilus punctatus*	-2.40
233	SX_15-P_32	*Ischnomera xanthoderes*	*Procraerus tibialis*	-2.40
234	P_32-SX_23	*Procraerus tibialis*	*Prionychus ater*	-2.40
235	SX_6-P_4	*Camptorhinus statua*	*Anthocomus fenestratus*	-2.40
236	SX_2-SX_6	*Alocerus moesiacus*	*Camptorhinus statua*	-2.39
237	SX_6-DSA_5	*Camptorhinus statua*	*Callicera spinolae*	-2.39

238	P_16-XM_11	*Gnathoncus nannetensis*	*Litargus connexus*	-2.38
239	SX_1-SX_29	*Aderus populneus*	*Pseudocistela ceramboides*	-2.38
240	XM_11-DSA_16	*Litargus connexus*	*Myathropa florea*	-2.38
241	XM_1-CSA_16	*Cryptophagus cylindrellus*	*Epuraea fuscicollis*	-2.37
242	P_21-P_23	*Lacon punctatus*	*Margarinotus merdarius*	-2.37
243	SX_6-P_33	*Camptorhinus statua*	*Troglops furcatus*	-2.36
244	SX_4-SX_24	*Anaspis regimbarti*	*Prionychus fairmairei*	-2.36
245	X_10-X_4	*Xyleborinus saxesenii*	*Oligomerus brunneus*	-2.36
246	SX_27-P_21	*Protaetia mirifica*	*Lacon punctatus*	-2.35
247	X_7-XM_15	*Stictoleptura trisignata*	*Rhamna semen*	-2.35
248	X_10-P_7	*Xyleborinus saxesenii*	*Brachygonus megerlei*	-2.35
249	CSA_16-CSA_22	*Epuraea fuscicollis*	*Soronia oblonga*	-2.34
250	SX_6-SX_5	*Camptorhinus statua*	*Camptorhinus simplex*	-2.33
251	P_21-P_13	*Lacon punctatus*	*Ectamenogonus montandoni*	-2.33
252	CSA_10-XM_11	*Cryptophagus micaceus*	*Litargus connexus*	-2.33
253	P_21-CSA_23	*Lacon punctatus*	*Tenebrio punctipennis*	-2.33
254	SX_8-SX_11	*Cryptophagus aurelioi*	*Cryptophagus reflexus*	-2.32
255	SX_2-XM_16	*Alocerus moesiacus*	*Symbiotes gibberosus*	-2.32
256	SX_15-DSA_10	*Ischnomera xanthoderes*	*Ferdinandea cuprea*	-2.32
257	X_1-SX_20	*Cerambyx welensii*	*Nalassus laevioctostriatus*	-2.32
258	DSA_21-P_9	*Spilomyia digitata*	*Colydium elongatum*	-2.32
259	SX_30-SX_3	*Scraptia testacea*	*Anaspis (Anaspis) ruficollis*	-2.31

260	SX_3-CSA_23	*Anaspis (Anaspis) ruficollis*	*Tenebrio punctipennis*	-2.31
261	SX_7-SX_17	*Cetonia aurataeformis*	*Melanotus dichrous*	-2.31
262	X_12-X_4	*Xyleborus monographus*	*Oligomerus brunneus*	-2.31
263	XM_1-CSA_22	*Cryptophagus cylindrellus*	*Soronia oblonga*	-2.30
264	P_21-SX_3	*Lacon punctatus*	*Anaspis (Anaspis) ruficollis*	-2.30
265	X_1-CSA_4	*Cerambyx welensii*	*Anthrenus minutus*	-2.29
266	XM_2-XM_3	*Cryptophagus dentatus*	*Cryptophagus scanicus*	-2.28
267	P_21-XM_13	*Lacon punctatus*	*Mycetophagus quadriguttatus*	-2.28
268	SX_6-DSA_21	*Camptorhinus statua*	*Spilomyia digitata*	-2.28
269	P_32-CSA_20	*Procraerus tibialis*	*Palorus depressus*	-2.28
270	SX_26-SX_17	*Protaetia cuprea*	*Melanotus dichrous*	-2.28
271	P_7-SX_25	*Brachygonus megerlei*	*Probaticus anthracinus*	-2.27
272	SX_1-XM_15	*Aderus populneus*	*Rhamna semen*	-2.26
273	P_7-CSA_22	*Brachygonus megerlei*	*Soronia oblonga*	-2.26
274	XM_3-XM_7	*Cryptophagus scanicus*	*Eledonoprius armatus*	-2.26
275	XM_4-SX_13	*Diplocoelus fagi*	*Dorcus parallelipipedus*	-2.26
276	SX_27-SX_25	*Protaetia mirifica*	*Probaticus anthracinus*	-2.25
277	P_14-P_7	*Elater ferrugineus*	*Brachygonus megerlei*	-2.25
278	X_11-P_33	*Xyleborus dryographus*	*Troglops furcatus*	-2.24
279	CSA_15-P_16	*Dermestes undulatus*	*Gnathoncus nannetensis*	-2.24
280	SX_26-SX_18	*Protaetia cuprea*	*Mycetochara linearis*	-2.23
281	X_12-XM_14	*Xyleborus monographus*	*Orchesia micans*	-2.23

282	X_12-DSA_21	*Xyleborus monographus*	*Spilomyia digitata*	-2.22
283	P_21-CSA_4	*Lacon punctatus*	*Anthrenus minutus*	-2.22
284	DSA_7-DSA_17	*Criorhina floccosa*	*Myolepta difformis*	-2.22
285	P_33-CSA_23	*Troglops furcatus*	*Tenebrio punctipennis*	-2.21
286	SX_9-P_15	*Cryptophagus jakowlewi*	*Gnathoncus communis*	-2.20
287	SX_13-DSA_9	*Dorcus parallelipipedus*	*Ferdinandea aurea*	-2.20
288	X_7-P_14	*Stictoleptura trisignata*	*Elater ferrugineus*	-2.19
289	SX_10 -DSA_7	*Cryptophagus punctipennis*	*Criorhina floccosa*	-2.18
290	X_1-P_21	*Cerambyx welensii*	*Lacon punctatus*	-2.18
291	XM_3-CSA_23	*Cryptophagus scanicus*	*Tenebrio punctipennis*	-2.18
292	P_7-SX_18	*Brachygonus megerlei*	*Mycetochara linearis*	-2.18
293	P_14-SX_18	*Elater ferrugineus*	*Mycetochara linearis*	-2.18
294	P_14-X_6	*Elater ferrugineus*	*Rhyncolus reflexus*	-2.16
295	X_7-XM_7	*Stictoleptura trisignata*	*Eledonoprius armatus*	-2.16
296	SX_26-X_6	*Protaetia cuprea*	*Rhyncolus reflexus*	-2.16
297	X_4-DSA_17	*Oligomerus brunneus*	*Myolepta difformis*	-2.15
298	SX_2-CSA_23	*Alocerus moesiacus*	*Tenebrio punctipennis*	-2.14
299	SX_3-DSA_10	*Anaspis (Anaspis) ruficollis*	*Ferdinandea cuprea*	-2.14
300	XM_16-P_12	*Symbiotes gibberosus*	*Dendrophilus punctatus*	-2.13
301	SX_11-P_7	*Cryptophagus reflexus*	*Brachygonus megerlei*	-2.13
302	XM_4-X_12	*Diplocoelus fagi*	*Xyleborus monographus*	-2.13
303	X_12-CSA_23	*Xyleborus monographus*	*Tenebrio punctipennis*	-2.13

304	P_15-DSA_16	*Gnathoncus communis*	*Myathropa florea*	-2.12
305	XM_4-XM_5	*Diplocoelus fagi*	*Dorcatoma agenjoi*	-2.12
306	P_21-SX_23	*Lacon punctatus*	*Prionychus ater*	-2.11
307	X_11-SX_5	*Xyleborus dryographus*	*Camptorhinus simplex*	-2.10
308	SX_11-CSA_20	*Cryptophagus reflexus*	*Palorus depressus*	-2.10
309	SX_17-SX_20	*Melanotus dichrous*	*Nalassus laevioctostriatus*	-2.10
310	P_2-DSA_5	*Ampedus aurilegulus*	*Callicera spinolae*	-2.10
311	XM_7-SX_25	*Eledonoprius armatus*	*Probaticus anthracinus*	-2.09
312	SX_2-SX_25	*Alocerus moesiacus*	*Probaticus anthracinus*	-2.09
313	P_7-P_23	*Brachygonus megerlei*	*Margarinotus merdarius*	-2.09
314	XM_3-XM_11	*Cryptophagus scanicus*	*Litargus connexus*	-2.08
315	P_4-XM_16	*Anthocomus fenestratus*	*Symbiotes gibberosus*	-2.08
316	P_14-P_32	*Elater ferrugineus*	*Procraerus tibialis*	-2.08
317	XM_2-P_13	*Cryptophagus dentatus*	*Ectamenogonus montandoni*	-2.08
318	P_4-P_9	*Anthocomus fenestratus*	*Colydium elongatum*	-2.07
319	X_4-XM_15	*Oligomerus brunneus*	*Rhamna semen*	-2.06
320	SX_21-SX_25	*Oryctes nasicornis*	*Probaticus anthracinus*	-2.06
321	P_13-P_12	*Ectamenogonus montandoni*	*Dendrophilus punctatus*	-2.06
322	P_32-CSA_4	*Procraerus tibialis*	*Anthrenus minutus*	-2.06
323	CSA_22-SX_4	*Soronia oblonga*	*Anaspis regimbarti*	-2.06
324	SX_7-DSA_21	*Cetonia aurataeformis*	*Spilomyia digitata*	-2.06
325	SX_18-CSA_20	*Mycetochara linearis*	*Palorus depressus*	-2.04

326	X_10-SX_4	*Xyleborinus saxesenii*	*Anaspis regimbarti*	-2.03
327	SX_6-SX_29	*Camptorhinus statua*	*Pseudocistela ceramboides*	-2.03
328	X_12-DSA_5	*Xyleborus monographus*	*Callicera spinolae*	-2.03
329	P_13-P_32	*Ectamenogonus montandoni*	*Procraerus tibialis*	-2.03
330	XM_14-P_9	*Orchesia micans*	*Colydium elongatum*	-2.02
331	XM_4-XM_8	*Diplocoelus fagi*	*Endophloeus marcovichianus*	-2.01
332	P_18-P_32	*Hypebaeus albifrons*	*Procraerus tibialis*	-2.01
333	P_18-SX_3	*Hypebaeus albifrons*	*Anaspis (Anaspis) ruficollis*	-2.01
334	X_1-P_7	*Cerambyx welensii*	*Brachygonus megerlei*	-2.00
335	SX_23-X_6	*Prionychus ater*	*Rhyncolus reflexus*	-2.00
336	P_14-XM_15	*Elater ferrugineus*	*Rhamna semen*	-2.00

Id	**Trophic guild couple**	**Pairs of species**		**B-C SES**
1	CSA_16-DSA_13	*Epuraea fuscicollis*	*Mallota cimbiciformis*	3.64
2	CSA_22-DSA_13	*Soronia oblonga*	*Mallota cimbiciformis*	3.45
3	X_12-DSA_13	*Xyleborus monographus*	*Mallota cimbiciformis*	3.36
4	CSA_21-DSA_13	*Prionocyphon serricornis*	*Mallota cimbiciformis*	3.30
5	X_12-CSA_16	*Xyleborus monographus*	*Epuraea fuscicollis*	3.18
6	CSA_16-DSA_14	*Epuraea fuscicollis*	*Mallota dusmeti*	3.09
7	SX_6-DSA_13	*Camptorhinus statua*	*Mallota cimbiciformis*	2.93
8	XM_3-DSA_13	*Cryptophagus scanicus*	*Mallota cimbiciformis*	2.92
9	SX_11-X_12	*Cryptophagus reflexus*	*Xyleborus monographus*	2.90

10	SX_7-X_12	*Cetonia aurataeformis*	*Xyleborus monographus*	2.90
11	CSA_16-DSA_16	*Epuraea fuscicollis*	*Myathropa florea*	2.90
12	X_1-CSA_21	*Cerambyx welensii*	*Prionocyphon serricornis*	2.90
13	SX_9-DSA_13	*Cryptophagus jakowlewi*	*Mallota cimbiciformis*	2.87
14	SX_7-CSA_21	*Cetonia aurataeformis*	*Prionocyphon serricornis*	2.80
15	CSA_22-DSA_14	*Soronia oblonga*	*Mallota dusmeti*	2.78
16	SX_11-CSA_21	*Cryptophagus reflexus*	*Prionocyphon serricornis*	2.75
17	SX_7-SX_11	*Cetonia aurataeformis*	*Cryptophagus reflexus*	2.75
18	SX_7-DSA_13	*Cetonia aurataeformis*	*Mallota cimbiciformis*	2.70
19	X_12-DSA_14	*Xyleborus monographus*	*Mallota dusmeti*	2.70
20	X_1-DSA_13	*Cerambyx welensii*	*Mallota cimbiciformis*	2.69
21	SX_7-CSA_16	*Cetonia aurataeformis*	*Epuraea fuscicollis*	2.68
22	SX_11-SX_6	*Cryptophagus reflexus*	*Camptorhinus statua*	2.67
23	DSA_13-SX_30	*Mallota cimbiciformis*	*Scraptia testacea*	2.65
24	CSA_21-CSA_16	*Prionocyphon serricornis*	*Epuraea fuscicollis*	2.65
25	SX_9-SX_11	*Cryptophagus jakowlewi*	*Cryptophagus reflexus*	2.60
26	SX_26-CSA_21	*Protaetia cuprea*	*Prionocyphon serricornis*	2.57
27	DSA_13-DSA_16	*Mallota cimbiciformis*	*Myathropa florea*	2.55
28	CSA_21-DSA_14	*Prionocyphon serricornis*	*Mallota dusmeti*	2.53
29	CSA_21-CSA_22	*Prionocyphon serricornis*	*Soronia oblonga*	2.52
30	SX_7-DSA_14	*Cetonia aurataeformis*	*Mallota dusmeti*	2.48
31	SX_11-DSA_13	*Cryptophagus reflexus*	*Mallota cimbiciformis*	2.48

32	SX_26-DSA_13	*Protaetia cuprea*	*Mallota cimbiciformis*	2.47
33	X_12-SX_30	*Xyleborus monographus*	*Scraptia testacea*	2.42
34	X_12-P_12	*Xyleborus monographus*	*Dendrophilus punctatus*	2.40
35	XM_3-DSA_14	*Cryptophagus scanicus*	*Mallota dusmeti*	2.38
36	CSA_21-SX_30	*Prionocyphon serricornis*	*Scraptia testacea*	2.38
37	X_1-X_12	*Cerambyx welensii*	*Xyleborus monographus*	2.33
38	X_1-SX_7	*Cerambyx welensii*	*Cetonia aurataeformis*	2.27
39	CSA_21-P_12	*Prionocyphon serricornis*	*Dendrophilus punctatus*	2.27
40	DSA_13-P_12	*Mallota cimbiciformis*	*Dendrophilus punctatus*	2.26
41	SX_9-DSA_14	*Cryptophagus jakowlewi*	*Mallota dusmeti*	2.26
42	X_12-CSA_21	*Xyleborus monographus*	*Prionocyphon serricornis*	2.24
43	SX_8-DSA_13	*Cryptophagus aurelioi*	*Mallota cimbiciformis*	2.23
44	SX_11-SX_30	*Cryptophagus reflexus*	*Scraptia testacea*	2.22
45	X_12-DSA_9	*Xyleborus monographus*	*Ferdinandea aurea*	2.22
46	X_12-CSA_22	*Xyleborus monographus*	*Soronia oblonga*	2.20
47	X_1-CSA_16	*Cerambyx welensii*	*Epuraea fuscicollis*	2.20
48	XM_2-DSA_13	*Cryptophagus dentatus*	*Mallota cimbiciformis*	2.18
49	P_2-DSA_13	*Ampedus aurilegulus*	*Mallota cimbiciformis*	2.18
50	P_20-DSA_13	*Ischnodes sanguinicollis*	*Mallota cimbiciformis*	2.17
51	CSA_16-DSA_9	*Epuraea fuscicollis*	*Ferdinandea aurea*	2.17
52	SX_26-X_12	*Protaetia cuprea*	*Xyleborus monographus*	2.16
53	X_12-P_13	*Xyleborus monographus*	*Ectamenogonus montandoni*	2.16

54	SX_13-DSA_13	*Dorcus parallelipipedus*	*Mallota cimbiciformis*	2.15
55	X_1-DSA_14	*Cerambyx welensii*	*Mallota dusmeti*	2.14
56	SX_6-CSA_16	*Camptorhinus statua*	*Epuraea fuscicollis*	2.14
57	CSA_10-DSA_13	*Cryptophagus micaceus*	*Mallota cimbiciformis*	2.12
58	SX_26-CSA_16	*Protaetia cuprea*	*Epuraea fuscicollis*	2.12
59	SX_26-CSA_10	*Protaetia cuprea*	*Cryptophagus micaceus*	2.12
60	P_20-CSA_16	*Ischnodes sanguinicollis*	*Epuraea fuscicollis*	2.12
61	DSA_13-CSA_23	*Mallota cimbiciformis*	*Tenebrio punctipennis*	2.11
62	SX_9-P_12	*Cryptophagus jakowlewi*	*Dendrophilus punctatus*	2.10
63	SX_6-DSA_14	*Camptorhinus statua*	*Mallota dusmeti*	2.10
64	X_1-CSA_10	*Cerambyx welensii*	*Cryptophagus micaceus*	2.09
65	P_29-CSA_16	*Paromalus flavicornis*	*Epuraea fuscicollis*	2.09
66	XM_13-CSA_16	*Mycetophagus quadriguttatus*	*Epuraea fuscicollis*	2.05
67	SX_6-P_12	*Camptorhinus statua*	*Dendrophilus punctatus*	2.04
68	DSA_13-SX_23	*Mallota cimbiciformis*	*Prionychus ater*	2.03
69	SX_11-DSA_14	*Cryptophagus reflexus*	*Mallota dusmeti*	2.02

Annex IV

Table A. - Non-random association patterns calculated by pairwise co-occurrence analysis applied to Cab. In the last column, a significant trend to aggregation or segregation between pair of species is indicated with the letter (A) or (S) respectively.

Id	Trophic guild couple	Pairs of species		B-C SES
1	DSA_5-DSA_17	*Callicera spinolae*	*Myolepta difformis*	-5.47 (A)
2	XM_5-XM_7	*Dorcatoma agenjoi*	*Eledonoprius armatus*	-5.07 (A)
3	XM_11-P_9	*Litargus connexus*	*Colydium elongatum*	-5.06 (A)
4	P_26-DSA_7	*Megapenthes lugens*	*Criorhina floccosa*	-4.86 (A)
5	XM_11-XM_7	*Litargus connexus*	*Eledonoprius armatus*	-4.84 (A)
6	P_1-XM_15	*Abraeus perpusillus*	*Rhamna semen*	-4.78 (A)
7	P_29-CSA_23	*Paromalus flavicornis*	*Tenebrio punctipennis*	-4.60 (A)
8	P_15-P_29	*Gnathoncus communis*	*Paromalus flavicornis*	-4.55 (A)
9	SX_8-XM_7	*Cryptophagus aurelioi*	*Eledonoprius armatus*	-4.54 (A)
10	P_29-XM_13	*Paromalus flavicornis*	*Mycetophagus quadriguttatus*	-4.52 (A)
11	XM_11-XM_5	*Litargus connexus*	*Dorcatoma agenjoi*	-4.49 (A)
12	XM_7-P_9	*Eledonoprius armatus*	*Colydium elongatum*	-4.34 (A)
13	P_18-SX_24	*Hypebaeus albifrons*	*Prionychus fairmairei*	-4.15 (A)
14	P_15-XM_13	*Gnathoncus communis*	*Mycetophagus quadriguttatus*	-4.14 (A)
15	XM_5-P_9	*Dorcatoma agenjoi*	*Colydium elongatum*	-4.13 (A)
16	SX_8-XM_5	*Cryptophagus aurelioi*	*Dorcatoma agenjoi*	-4.03 (A)
17	XM_13-XM_5	*Mycetophagus quadriguttatus*	*Dorcatoma agenjoi*	-4.03 (A)
18	XM_13-CSA_23	*Mycetophagus quadriguttatus*	*Tenebrio punctipennis*	-3.88 (A)
19	SX_21-DSA_9	*Oryctes nasicornis*	*Ferdinandea aurea*	-3.65 (A)
20	XM_4-X_11	*Diplocoelus fagi*	*Xyleborus dryographus*	-3.62 (A)
21	SX_8-XM_11	*Cryptophagus aurelioi*	*Litargus connexus*	-3.61 (A)
22	XM_3-P_15	*Cryptophagus scanicus*	*Gnathoncus communis*	-3.60 (A)
23	SX_8-P_9	*Cryptophagus aurelioi*	*Colydium elongatum*	-3.56 (A)
24	P_15-XM_5	*Gnathoncus communis*	*Dorcatoma agenjoi*	-3.51 (A)
25	P_14-P_1	*Elater ferrugineus*	*Abraeus perpusillus*	-3.50 (A)
26	P_29-XM_5	*Paromalus flavicornis*	*Dorcatoma agenjoi*	-3.46 (A)
27	P_16-P_9	*Gnathoncus nannetensis*	*Colydium elongatum*	-3.46 (A)
28	X_1-P_1	*Cerambyx welensii*	*Abraeus perpusillus*	-3.37 (A)
29	P_15-CSA_23	*Gnathoncus communis*	*Tenebrio punctipennis*	-3.29 (A)
30	X_1-XM_15	*Cerambyx welensii*	*Rhamna semen*	-3.28 (A)
31	P_14-XM_15	*Elater ferrugineus*	*Rhamna semen*	-3.24 (A)
32	X_7-DSA_7	*Stictoleptura trisignata*	*Criorhina floccosa*	-3.24 (A)
33	P_29-XM_7	*Paromalus flavicornis*	*Eledonoprius armatus*	-3.20 (A)
34	SX_21-SX_13	*Oryctes nasicornis*	*Dorcus parallelipipedus*	-3.20 (A)
35	SX_1-XM_15	*Aderus populneus*	*Rhamna semen*	-3.20 (A)
36	P_15-P_16	*Gnathoncus communis*	*Gnathoncus nannetensis*	-3.18 (A)
37	XM_13-P_9	*Mycetophagus quadriguttatus*	*Colydium elongatum*	-3.16 (A)
38	XM_3-P_29	*Cryptophagus scanicus*	*Paromalus flavicornis*	-3.16 (A)
39	P_16-SX_15	*Gnathoncus nannetensis*	*Ischnomera xanthoderes*	-3.15 (A)
40	XM_14-XM_8	*Orchesia micans*	*Endophloeus marcovichianus*	-3.15 (A)
41	SX_1-P_1	*Aderus populneus*	*Abraeus perpusillus*	-3.12 (A)
42	CSA_15-P_15	*Dermestes undulatus*	*Gnathoncus communis*	-3.05 (A)
43	P_23-DSA_5	*Margarinotus merdarius*	*Callicera spinolae*	-3.01 (A)
44	P_29-DSA_16	*Paromalus flavicornis*	*Myathropa florea*	-3.00 (A)
45	X_1-X_4	*Cerambyx welensii*	*Oligomerus brunneus*	-2.98 (A)
46	XM_5-CSA_23	*Dorcatoma agenjoi*	*Tenebrio punctipennis*	-2.98 (A)
47	P_21-P_33	*Spilomyia digitate*	*Troglops furcatus*	-2.97 (A)

48	XM_13-XM_7	*Mycetophagus quadriguttatus*	*Eledonoprius armatus*	-2.97 (A)
49	SX_21-SX_30	*Oryctes nasicornis*	*Scraptia testacea*	-2.95 (A)
50	SX_8-CSA_23	*Cryptophagus aurelioi*	*Tenebrio punctipennis*	-2.94 (A)
51	XM_11-XM_13	*Litargus connexus*	*Mycetophagus quadriguttatus*	-2.93 (A)
52	X_1-X_7	*Cerambyx welensii*	*Stictoleptura trisignata*	-2.89 (A)
53	X_11-P_23	*Xyleborus dryographus*	*Margarinotus merdarius*	-2.88 (A)
54	X_7-X_4	*Stictoleptura trisignata*	*Oligomerus brunneus*	-2.85 (A)
55	CSA_23-P_9	*Tenebrio punctipennis*	*Colydium elongatum*	-2.84 (A)
56	P_15-XM_7	*Gnathoncus communis*	*Eledonoprius armatus*	-2.83 (A)
57	P_15-P_9	*Gnathoncus communis*	*Colydium elongatum*	-2.83 (A)
58	X_7-P_18	*Stictoleptura trisignata*	*Hypebaeus albifrons*	-2.81 (A)
59	DSA_7-DSA_5	*Criorhina floccose*	*Callicera spinolae*	-2.80 (A)
60	SX_1-X_11	*Aderus populneus*	*Xyleborus dryographus*	-2.78 (A)
61	SX_6-X_4	*Camptorhinus statua*	*Oligomerus brunneus*	-2.76 (A)
62	SX_1-P_23	*Aderus populneus*	*Margarinotus merdarius*	-2.76 (A)
63	CSA_11-DSA_9	*Cryptophagus saginatus*	*Ferdinandea aurea*	-2.75 (A)
64	SX_1-DSA_5	*Aderus populneus*	*Callicera spinolae*	-2.75 (A)
65	SX_25-P_9	*Probaticus anthracinus*	*Colydium elongatum*	-2.74 (A)
66	XM_1-X_10	*Cryptophagus cylindrellus*	*Xyleborinus saxesenii*	-2.74 (A)
67	XM_7-CSA_23	*Eledonoprius armatus*	*Tenebrio punctipennis*	-2.74 (A)
68	P_21-P_23	*Spilomyia digitate*	*Margarinotus merdarius*	-2.73 (A)
69	X_7-P_1	*Stictoleptura trisignata*	*Abraeus perpusillus*	-2.73 (A)
70	P_2-SX_29	*Ampedus aurilegulus*	*Pseudocistela ceramboides*	-2.72 (A)
71	X_1-XM_13	*Cerambyx welensii*	*Mycetophagus quadriguttatus*	-2.68 (A)
72	X_7-P_9	*Stictoleptura trisignata*	*Colydium elongatum*	-2.66 (A)
73	X_1-XM_2	*Cerambyx welensii*	*Cryptophagus dentatus*	-2.64 (A)
74	P_16-XM_7	*Gnathoncus nannetensis*	*Eledonoprius armatus*	-2.63 (A)
75	XM_11-CSA_23	*Litargus connexus*	*Tenebrio punctipennis*	-2.63 (A)
76	P_18-P_33	*Hypebaeus albifrons*	*Troglops furcatus*	-2.62 (A)
77	P_15-XM_11	*Gnathoncus communis*	*Litargus connexus*	-2.61 (A)
78	X_1-P_14	*Cerambyx welensii*	*Elater ferrugineus*	-2.59 (A)
79	P_16-XM_5	*Gnathoncus nannetensis*	*Dorcatoma agenjoi*	-2.58 (A)
80	SX_8-P_29	*Cryptophagus aurelioi*	*Paromalus flavicornis*	-2.58 (A)
81	XM_4-DSA_21	*Diplocoelus fagi*	*Spilomyia digitata*	-2.56 (A)
82	P_29-XM_11	*Paromalus flavicornis*	*Litargus connexus*	-2.56 (A)
83	XM_5-DSA_16	*Dorcatoma agenjoi*	*Myathropa florea*	-2.56 (A)
84	X_7-SX_6	*Stictoleptura trisignata*	*Camptorhinus statua*	-2.54 (A)
85	P_29-P_9	*Paromalus flavicornis*	*Colydium elongatum*	-2.53 (A)
86	SX_8-SX_9	*Cryptophagus aurelioi*	*Cryptophagus jakowlewi*	-2.53 (A)
87	SX_9-XM_7	*Cryptophagus jakowlewi*	*Eledonoprius armatus*	-2.53 (A)
88	XM_2-P_4	*Cryptophagus dentatus*	*Anthocomus fenestratus*	-2.50 (A)
89	CSA_10-P_29	*Cryptophagus micaceus*	*Paromalus flavicornis*	-2.50 (A)
90	X_7-P_26	*Stictoleptura trisignata*	*Megapenthes lugens*	-2.50 (A)
91	SX_8-SX_6	*Cryptophagus aurelioi*	*Camptorhinus statua*	-2.48 (A)
92	XM_3-XM_5	*Cryptophagus scanicus*	*Dorcatoma agenjoi*	-2.47 (A)
93	SX_8-XM_13	*Cryptophagus aurelioi*	*Mycetophagus quadriguttatus*	-2.47 (A)
94	SX_9-CSA_11	*Cryptophagus jakowlewi*	*Cryptophagus saginatus*	-2.47 (A)
95	DSA_7-SX_19	*Criorhina floccose*	*Mycetochara quadrimaculata*	-2.44 (A)
96	X_11-P_21	*Xyleborus dryographus*	*Spilomyia digitata*	-2.44 (A)
97	SX_8-XM_3	*Cryptophagus aurelioi*	*Cryptophagus scanicus*	-2.42 (A)
98	DSA_17-SX_29	*Myolepta difformis*	*Pseudocistela ceramboides*	-2.42 (A)
99	SX_1-DSA_17	*Aderus populneus*	*Myolepta difformis*	-2.41 (A)
100	P_23-DSA_17	*Margarinotus merdarius*	*Myolepta difformis*	-2.41 (A)
101	X_1-SX_29	*Cerambyx welensii*	*Pseudocistela ceramboides*	-2.40 (A)
102	CSA_10-CSA_23	*Cryptophagus micaceus*	*Tenebrio punctipennis*	-2.35 (A)
103	P_1-X_4	*Abraeus perpusillus*	*Oligomerus brunneus*	-2.34 (A)
104	DSA_7-DSA_17	*Criorhina floccosa*	*Myolepta difformis*	-2.34 (A)
105	P_16-SX_25	*Gnathoncus nannetensis*	*Probaticus anthracinus*	-2.34 (A)

106	P_23-SX_18	*Margarinotus merdarius*	*Mycetochara linearis*	-2.33 (A)
107	DSA_16-XM_7	*Myathropa florea*	*Eledonoprius armatus*	-2.33 (A)
108	X_4-SX_18	*Oligomerus brunneus*	*Mycetochara linearis*	-2.32 (A)
109	XM_3-XM_13	*Cryptophagus scanicus*	*Mycetophagus quadriguttatus*	-2.32 (A)
110	X_7-XM_15	*Stictoleptura trisignata*	*Rhamna semen*	-2.30 (A)
111	SX_13-DSA_21	*Dorcus parallelipipedus*	*Spilomyia digitata*	-2.30 (A)
112	SX_9-P_16	*Cryptophagus jakowlewi*	*Gnathoncus nannetensis*	-2.30 (A)
113	P_18-SX_4	*Hypebaeus albifrons*	*Anaspis regimbarti*	-2.29 (A)
114	SX_7-DSA_13	*Cetonia aurataeformis*	*Mallota cimbiciformis*	-2.25 (A)
115	DSA_5-SX_29	*Callicera spinolae*	*Pseudocistela ceramboides*	-2.25 (A)
116	X_7-P_14	*Stictoleptura trisignata*	*Elater ferrugineus*	-2.25 (A)
117	X_10-P_18	*Xyleborinus saxesenii*	*Hypebaeus albifrons*	-2.25 (A)
118	P_16-XM_11	*Gnathoncus nannetensis*	*Litargus connexus*	-2.25 (A)
119	XM_4-SX_6	*Diplocoelus fagi*	*Camptorhinus statua*	-2.23 (A)
120	XM_3-P_16	*Cryptophagus scanicus*	*Gnathoncus nannetensis*	-2.22 (A)
121	SX_6-XM_5	*Camptorhinus statua*	*Dorcatoma agenjoi*	-2.21 (A)
122	X_7-DSA_17	*Stictoleptura trisignata*	*Myolepta difformis*	-2.21 (A)
123	SX_9-CSA_15	*Cryptophagus jakowlewi*	*Dermestes undulatus*	-2.20 (A)
124	DSA_16-CSA_23	*Myathropa florea*	*Tenebrio punctipennis*	-2.19 (A)
125	XM_2-X_4	*Cryptophagus dentatus*	*Oligomerus brunneus*	-2.19 (A)
126	SX_9-XM_3	*Cryptophagus jakowlewi*	*Cryptophagus scanicus*	-2.15 (A)
127	SX_6-XM_7	*Camptorhinus statua*	*Eledonoprius armatus*	-2.14 (A)
128	SX_6-DSA_7	*Camptorhinus statua*	*Criorhina floccosa*	-2.14 (A)
129	SX_8-P_15	*Cryptophagus aurelioi*	*Gnathoncus communis*	-2.13 (A)
130	P_16-XM_8	*Gnathoncus nannetensis*	*Endophloeus marcovichianus*	-2.12 (A)
131	SX_9-X_10	*Cryptophagus jakowlewi*	*Xyleborinus saxesenii*	-2.12 (A)
132	XM_3-CSA_15	*Cryptophagus scanicus*	*Dermestes undulatus*	-2.11 (A)
133	XM_13-DSA_16	*Mycetophagus quadriguttatus*	*Myathropa florea*	-2.10 (A)
134	P_33-SX_19	*Troglops furcatus*	*Mycetochara quadrimaculata*	-2.09 (A)
135	SX_8-P_16	*Cryptophagus aurelioi*	*Gnathoncus nannetensis*	-2.09 (A)
136	XM_2-SX_18	*Cryptophagus dentatus*	*Mycetochara linearis*	-2.08 (A)
137	XM_4-SX_18	*Diplocoelus fagi*	*Mycetochara linearis*	-2.08 (A)
138	SX_6-P_4	*Camptorhinus statua*	*Anthocomus fenestratus*	-2.07 (A)
139	XM_3-XM_14	*Cryptophagus scanicus*	*Orchesia micans*	-2.07 (A)
140	CSA_10-XM_5	*Cryptophagus micaceus*	*Dorcatoma agenjoi*	-2.05 (A)
141	XM_3-CSA_23	*Cryptophagus scanicus*	*Tenebrio punctipennis*	-2.05 (A)
142	CSA_15-P_16	*Dermestes undulatus*	*Gnathoncus nannetensis*	-2.04 (A)
143	SX_9-XM_5	*Cryptophagus jakowlewi*	*Dorcatoma agenjoi*	-2.03 (A)
144	XM_2-SX_30	*Cryptophagus dentatus*	*Scraptia testacea*	-2.02 (A)
145	SX_13-SX_25	*Dorcus parallelipipedus*	*Probaticus anthracinus*	-2.02 (A)
146	XM_14-XM_5	*Orchesia micans*	*Dorcatoma agenjoi*	-2.02 (A)
147	SX_6-P_23	*Camptorhinus statua*	*Margarinotus merdarius*	-2.00 (A)
148	XM_4-P_21	*Diplocoelus fagi*	*Spilomyia digitata*	-2.00 (A)
149	SX_21-SX_25	*Oryctes nasicornis*	*Probaticus anthracinus*	-2.00 (A)
150	X_12-CSA_16	*Xyleborus monographus*	*Epuraea fuscicollis*	3.88 (S)
151	SX_7-X_12	*Cetonia aurataeformis*	*Xyleborus monographus*	3.70 (S)
152	SX_7-CSA_21	*Cetonia aurataeformis*	*Prionocyphon serricornis*	3.44 (S)
153	X_12-CSA_21	*Xyleborus monographus*	*Prionocyphon serricornis*	3.34 (S)
154	CSA_21-CSA_16	*Prionocyphon serricornis*	*Epuraea fuscicollis*	3.34 (S)
155	CSA_21-CSA_22	*Prionocyphon serricornis*	*Soronia oblonga*	3.07 (S)
156	X_12-DSA_9	*Xyleborus monographus*	*Ferdinandea aurea*	3.04 (S)
157	X_12-CSA_22	*Xyleborus monographus*	*Soronia oblonga*	2.99 (S)
158	CSA_10-CSA_21	*Cryptophagus micaceus*	*Prionocyphon serricornis*	2.98 (S)
159	CSA_16-DSA_16	*Epuraea fuscicollis*	*Myathropa florea*	2.97 (S)
160	SX_7-CSA_16	*Cetonia aurataeformis*	*Epuraea fuscicollis*	2.89 (S)
161	CSA_21-DSA_9	*Prionocyphon serricornis*	*Ferdinandea aurea*	2.61 (S)
162	CSA_16-DSA_9	*Epuraea fuscicollis*	*Ferdinandea aurea*	2.53 (S)
163	CSA_10-CSA_22	*Cryptophagus micaceus*	*Soronia oblonga*	2.41 (S)

164	P_20-CSA_16	*Ischnodes sanguinicollis*	*Epuraea fuscicollis*	2.39 (S)
165	P_29-CSA_16	*Paromalus flavicornis*	*Epuraea fuscicollis*	2.37 (S)
166	SX_9-CSA_21	*Cryptophagus jakowlewi*	*Prionocyphon serricornis*	2.36 (S)
167	CSA_16-SX_25	*Epuraea fuscicollis*	*Probaticus anthracinus*	2.35 (S)
168	CSA_16-DSA_14	*Epuraea fuscicollis*	*Mallota dusmeti*	2.33 (S)
169	CSA_16-SX_29	*Epuraea fuscicollis*	*Pseudocistela ceramboides*	2.28 (S)
170	CSA_16-DSA_13	*Epuraea fuscicollis*	*Mallota cimbiciformis*	2.28 (S)
171	SX_7-P_15	*Cetonia aurataeformis*	*Gnathoncus communis*	2.27 (S)
172	P_29-CSA_22	*Paromalus flavicornis*	*Soronia oblonga*	2.25 (S)
173	XM_13-CSA_16	*Mycetophagus quadriguttatus*	*Epuraea fuscicollis*	2.23 (S)
174	CSA_11-X_12	*Cryptophagus saginatus*	*Xyleborus monographus*	2.22 (S)
175	X_12-P_20	*Xyleborus monographus*	*Ischnodes sanguinicollis*	2.22 (S)
176	SX_7-XM_3	*Cetonia aurataeformis*	*Cryptophagus scanicus*	2.21 (S)
177	CSA_22-DSA_16	*Soronia oblonga*	*Myathropa florea*	2.19 (S)
178	CSA_22-DSA_14	*Soronia oblonga*	*Mallota dusmeti*	2.17 (S)
179	CSA_22-SX_29	*Soronia oblonga*	*Pseudocistela ceramboides*	2.17 (S)
180	CSA_16-CSA_23	*Epuraea fuscicollis*	*Tenebrio punctipennis*	2.16 (S)
181	CSA_22-DSA_13	*Soronia oblonga*	*Mallota cimbiciformis*	2.15 (S)
182	SX_6-CSA_16	*Camptorhinus statua*	*Epuraea fuscicollis*	2.12 (S)
183	CSA_21-DSA_14	*Prionocyphon serricornis*	*Mallota dusmeti*	2.11 (S)
184	CSA_16-SX_19	*Epuraea fuscicollis*	*Mycetochara quadrimaculata*	2.10 (S)
185	SX_6-CSA_21	*Camptorhinus statua*	*Prionocyphon serricornis*	2.09 (S)
186	CSA_10-X_12	*Cryptophagus micaceus*	*Xyleborus monographus*	2.08 (S)
187	CSA_16-XM_8	*Epuraea fuscicollis*	*Endophloeus marcovichianus*	2.06 (S)
188	X_12-SX_21	*Xyleborus monographus*	*Oryctes nasicornis*	2.05 (S)
189	CSA_10-SX_29	*Cryptophagus micaceus*	*Pseudocistela ceramboides*	2.05 (S)
190	CSA_10-CSA_16	*Cryptophagus micaceus*	*Epuraea fuscicollis*	2.04 (S)
191	CSA_21-DSA_13	*Prionocyphon serricornis*	*Mallota cimbiciformis*	2.03 (S)
192	CSA_10-DSA_9	*Cryptophagus micaceus*	*Ferdinandea aurea*	2.03 (S)
193	P_20-CSA_21	*Ischnodes sanguinicollis*	*Prionocyphon serricornis*	2.01 (S)
194	P_2-CSA_16	*Ampedus aurilegulus*	*Epuraea fuscicollis*	2.00 (S)

Table B. - Non-random association patterns calculated by pairwise co-occurrence analysis applied to Camp. In the last column, a significant trend to aggregation or segregation between pair of species is indicated with the letter (A) or (S) respectively.

Id	Trophic guild couple	Pairs of species		B-C SES
1	SX_1-XM_16	*Aderus populneus*	*Symbiotes gibberosus*	-3.36 (A)
2	CSA_6-P_4	*Attagenus incognitus*	*Anthocomus fenestratus*	-2.75 (A)
3	CSA_10-DSA_18	*Cryptophagus micaceus*	*Myolepta dubia*	-2.74 (A)
4	X_10-SX_19	*Xyleborinus saxesenii*	*Mycetochara quadrimaculata*	-2.72 (A)
5	P_21-P_26	*Lacon punctatus*	*Megapenthes lugens*	-2.48 (A)
6	X_10-SX_13	*Xyleborinus saxesenii*	*Dorcus parallelipipedus*	-2.48 (A)
7	P_7-SX_18	*Brachygonus megerlei*	*Mycetochara linearis*	-2.39 (A)
8	P_23-XM_13	*Margarinotus merdarius*	*Mycetophagus quadriguttatus*	-2.39 (A)
9	SX_1-SX_13	*Aderus populneus*	*Dorcus parallelipipedus*	-2.39 (A)
10	P_32-XM_16	*Procraerus tibialis*	*Symbiotes gibberosus*	-2.37 (A)
11	P_21-P_32	*Lacon punctatus*	*Procraerus tibialis*	-2.37 (A)
12	P_21-XM_16	*Lacon punctatus*	*Symbiotes gibberosus*	-2.36 (A)
13	SX_7-CSA_11	*Cetonia aurataeformis*	*Cryptophagus saginatus*	-2.33 (A)
14	X_10-P_7	*Xyleborinus saxesenii*	*Brachygonus megerlei*	-2.31 (A)
15	SX_13-SX_19	*Dorcus parallelipipedus*	*Mycetochara quadrimaculata*	-2.27 (A)
16	CSA_10-P_14	*Cryptophagus micaceus*	*Elater ferrugineus*	-2.27 (A)
17	P_7-SX_19	*Brachygonus megerlei*	*Mycetochara quadrimaculata*	-2.20 (A)
18	XM_15-SX_23	*Rhamna semen*	*Prionychus ater*	-2.19 (A)
19	P_14-SX_19	*Elater ferrugineus*	*Mycetochara quadrimaculata*	-2.15 (A)
20	CSA_6-P_32	*Attagenus incognitus*	*Procraerus tibialis*	-2.11 (A)
21	P_26-XM_13	*Megapenthes lugens*	*Mycetophagus quadriguttatus*	-2.11 (A)
22	SX_27-P_13	*Protaetia mirifica*	*Ectamenogonus montandoni*	-2.09 (A)
23	X_10-CSA_20	*Xyleborinus saxesenii*	*Palorus depressus*	-2.09 (A)
24	SX_1-P_14	*Aderus populneus*	*Elater ferrugineus*	-2.08 (A)
25	X_12-SX_30	*Xyleborus monographus*	*Scraptia testacea*	-2.06 (A)
26	SX_1-P_32	*Aderus populneus*	*Procraerus tibialis*	-2.05 (A)
27	P_13-P_32	*Ectamenogonus montandoni*	*Procraerus tibialis*	-2.04 (A)
28	XM_16-P_4	*Symbiotes gibberosus*	*Anthocomus fenestratus*	-2.03 (A)
29	SX_11-DSA_13	*Cryptophagus reflexus*	*Mallota cimbiciformis*	4.70 (S)
30	X_1-DSA_13	*Cerambyx welensii*	*Mallota cimbiciformis*	4.47 (S)
31	CSA_16-DSA_13	*Epuraea fuscicollis*	*Mallota cimbiciformis*	4.41 (S)
32	XM_3-DSA_13	*Cryptophagus scanicus*	*Mallota cimbiciformis*	4.30 (S)
33	P_12-DSA_13	*Dendrophilus punctatus*	*Mallota cimbiciformis*	4.27 (S)
34	SX_26-DSA_13	*Protaetia cuprea*	*Mallota cimbiciformis*	4.27 (S)
35	XM_2-DSA_13	*Cryptophagus dentatus*	*Mallota cimbiciformis*	4.24 (S)
36	CSA_22-DSA_13	*Soronia oblonga*	*Mallota cimbiciformis*	3.92 (S)
37	SX_8-DSA_13	*Cryptophagus aurelioi*	*Mallota cimbiciformis*	3.83 (S)
38	P_13-DSA_13	*Ectamenogonus montandoni*	*Mallota cimbiciformis*	3.51 (S)
39	SX_11-DSA_14	*Cryptophagus reflexus*	*Mallota dusmeti*	3.47 (S)
40	X_1-DSA_14	*Cerambyx welensii*	*Mallota dusmeti*	3.25 (S)
41	XM_13-DSA_13	*Mycetophagus quadriguttatus*	*Mallota cimbiciformis*	3.16 (S)
42	CSA_16-DSA_14	*Epuraea fuscicollis*	*Mallota dusmeti*	3.07 (S)
43	SX_6-DSA_13	*Camptorhinus statua*	*Mallota cimbiciformis*	3.03 (S)
44	P_12-DSA_14	*Dendrophilus punctatus*	*Mallota dusmeti*	2.99 (S)
45	XM_3-DSA_14	*Cryptophagus scanicus*	*Mallota dusmeti*	2.97 (S)
46	SX_26-DSA_14	*Protaetia cuprea*	*Mallota dusmeti*	2.94 (S)
47	DSA_13-SX_23	*Mallota cimbiciformis*	*Prionychus ater*	2.92 (S)
48	XM_2-DSA_14	*Cryptophagus dentatus*	*Mallota dusmeti*	2.90 (S)
49	SX_7-DSA_13	*Cetonia aurataeformis*	*Mallota cimbiciformis*	2.85 (S)

50	XM_15-DSA_13	*Rhamna semen*	*Mallota cimbiciformis*	2.84 (S)
51	CSA_22-DSA_14	*Soronia oblonga*	*Mallota dusmeti*	2.78 (S)
52	SX_27-DSA_13	*Protaetia mirifica*	*Mallota cimbiciformis*	2.76 (S)
53	SX_8-DSA_14	*Cryptophagus aurelioi*	*Mallota dusmeti*	2.74 (S)
54	P_23-DSA_13	*Margarinotus merdarius*	*Mallota cimbiciformis*	2.71 (S)
55	P_13-DSA_14	*Ectamenogonus montandoni*	*Mallota dusmeti*	2.64 (S)
56	SX_11-SX_6	*Cryptophagus reflexus*	*Camptorhinus statua*	2.43 (S)
57	P_32-DSA_13	*Procraerus tibialis*	*Mallota cimbiciformis*	2.38 (S)
58	X_1-CSA_16	*Cerambyx welensii*	*Epuraea fuscicollis*	2.32 (S)
59	P_16-DSA_13	*Gnathoncus nannetensis*	*Mallota cimbiciformis*	2.29 (S)
60	DSA_13-DSA_16	*Mallota cimbiciformis*	*Myathropa florea*	2.28 (S)
61	DSA_14-SX_23	*Mallota dusmeti*	*Prionychus ater*	2.26 (S)
62	DSA_13-CSA_20	*Mallota cimbiciformis*	*Palorus depressus*	2.25 (S)
63	P_26-DSA_13	*Megapenthes lugens*	*Mallota cimbiciformis*	2.25 (S)
64	XM_3-SX_6	*Cryptophagus scanicus*	*Camptorhinus statua*	2.23 (S)
65	P_21-DSA_13	*Lacon punctatus*	*Mallota cimbiciformis*	2.21 (S)
66	SX_6-DSA_14	*Camptorhinus statua*	*Mallota dusmeti*	2.20 (S)
67	X_1-XM_3	*Cerambyx welensii*	*Cryptophagus scanicus*	2.20 (S)
68	SX_7-DSA_14	*Cetonia aurataeformis*	*Mallota dusmeti*	2.19 (S)
69	XM_2-XM_13	*Cryptophagus dentatus*	*Mycetophagus quadriguttatus*	2.18 (S)
70	SX_30-DSA_13	*Scraptia testacea*	*Mallota cimbiciformis*	2.16 (S)
71	XM_13-DSA_14	*Mycetophagus quadriguttatus*	*Mallota dusmeti*	2.14 (S)
72	XM_3-XM_15	*Cryptophagus scanicus*	*Rhamna semen*	2.14 (S)
73	XM_3-CSA_16	*Cryptophagus scanicus*	*Epuraea fuscicollis*	2.13 (S)
74	CSA_11-DSA_13	*Cryptophagus saginatus*	*Mallota cimbiciformis*	2.10 (S)
75	XM_15-DSA_14	*Rhamna semen*	*Mallota dusmeti*	2.07 (S)
76	P_4-DSA_13	*Anthocomus fenestratus*	*Mallota cimbiciformis*	2.00 (S)

Table C. - Non-random association patterns calculated by pairwise co-occurrence analysis applied to Quil. In the last column, a significant trend to aggregation or segregation between pair of species is indicated with the letter (A) or (S) respectively.

Id	Trophic guild couple	Pairs of species		B-C SES
1	P_21-CSA_23	*Lacon punctatus*	*Tenebrio punctipennis*	-4.15 (A)
2	P_29-CSA_20	*Paromalus flavicornis*	*Palorus depressus*	-3.66 (A)
3	SX_3-CSA_23	*Anaspis (Anaspis) ruficollis*	*Tenebrio punctipennis*	-3.49 (A)
4	P_32-CSA_23	*Procraerus tibialis*	*Tenebrio punctipennis*	-3.40 (A)
5	X_6-P_21	*Rhyncolus reflexus*	*Lacon punctatus*	-3.28 (A)
6	X_12-DSA_7	*Xyleborus monographus*	*Criorhina floccosa*	-3.03 (A)
7	CSA_18-SX_12	*Limoniscus violaceus*	*Dendarus pectoralis*	-2.98 (A)
8	SX_13-X_9	*Dorcus parallelipipedus*	*Xestobium rufovillosum*	-2.95 (A)
9	SX_13-CSA_20	*Dorcus parallelipipedus*	*Palorus depressus*	-2.88 (A)
10	X_12-P_29	*Xyleborus monographus*	*Paromalus flavicornis*	-2.84 (A)
11	P_29-SX_23	*Paromalus flavicornis*	*Prionychus ater*	-2.79 (A)
12	SX_8-P_14	*Cryptophagus aurelioi*	*Elater ferrugineus*	-2.76 (A)
13	XM_3-X_6	*Cryptophagus scanicus*	*Rhyncolus reflexus*	-2.75 (A)
14	X_6-P_29	*Rhyncolus reflexus*	*Paromalus flavicornis*	-2.75 (A)
15	X_12-CSA_20	*Xyleborus monographus*	*Palorus depressus*	-2.75 (A)
16	CSA_20-SX_23	*Palorus depressus*	*Prionychus ater*	-2.71 (A)
17	P_14-CSA_23	*Elater ferrugineus*	*Tenebrio punctipennis*	-2.70 (A)
18	P_20-CSA_18	*Ischnodes sanguinicollis*	*Limoniscus violaceus*	-2.69 (A)
19	CSA_21-DSA_16	*Prionocyphon serricornis*	*Myathropa florea*	-2.67 (A)
20	SX_17-DSA_7	*Melanotus dichrous*	*Criorhina floccosa*	-2.65 (A)
21	SX_10-DSA_7	*Cryptophagus punctipennis*	*Criorhina floccosa*	-2.63 (A)
22	P_26-CSA_22	*Megapenthes lugens*	*Soronia oblonga*	-2.59 (A)
23	SX_5-CSA_4	*Camptorhinus simplex*	*Anthrenus minutus*	-2.59 (A)
24	X_6-CSA_20	*Rhyncolus reflexus*	*Palorus depressus*	-2.52 (A)
25	P_2-CSA_22	*Ampedus aurilegulus*	*Soronia oblonga*	-2.52 (A)
26	SX_26-P_14	*Protaetia cuprea*	*Elater ferrugineus*	-2.48 (A)
27	CSA_18-CSA_16	*Limoniscus violaceus*	*Epuraea fuscicollis*	-2.46 (A)
28	SX_10-P_29	*Cryptophagus punctipennis*	*Paromalus flavicornis*	-2.45 (A)
29	SX_15-CSA_23	*Ischnomera xanthoderes*	*Tenebrio punctipennis*	-2.41 (A)
30	P_21-XM_13	*Lacon punctatus*	*Mycetophagus quadriguttatus*	-2.41 (A)
31	P_21-SX_15	*Lacon punctatus*	*Ischnomera xanthoderes*	-2.40 (A)
32	SX_10-SX_16	*Cryptophagus punctipennis*	*Isomira hispanica*	-2.39 (A)
33	P_19-CSA_20	*Hypebaeus flavipes*	*Palorus depressus*	-2.37 (A)
34	SX_8-XM_3	*Cryptophagus aurelioi*	*Cryptophagus scanicus*	-2.37 (A)
35	SX_26-P_29	*Protaetia cuprea*	*Paromalus flavicornis*	-2.35 (A)
36	P_21-P_32	*Lacon punctatus*	*Procraerus tibialis*	-2.35 (A)
37	P_21-SX_3	*Lacon punctatus*	*Anaspis (Anaspis) ruficollis*	-2.32 (A)
38	XM_3-P_20	*Cryptophagus scanicus*	*Ischnodes sanguinicollis*	-2.29 (A)
39	SX_6-CSA_22	*Camptorhinus statua*	*Soronia oblonga*	-2.28 (A)
40	SX_26-CSA_20	*Protaetia cuprea*	*Palorus depressus*	-2.28 (A)
41	SX_17-SX_18	*Melanotus dichrous*	*Mycetochara linearis*	-2.28 (A)
42	SX_8-P_20	*Cryptophagus aurelioi*	*Ischnodes sanguinicollis*	-2.27 (A)
43	SX_15-SX_16	*Ischnomera xanthoderes*	*Isomira hispanica*	-2.20 (A)
44	XM_3-P_29	*Cryptophagus scanicus*	*Paromalus flavicornis*	-2.17 (A)
45	CSA_4-P_21	*Anthrenus minutus*	*Lacon punctatus*	-2.16 (A)
46	SX_5-X_11	*Camptorhinus simplex*	*Xyleborus dryographus*	-2.16 (A)
47	SX_9-SX_10	*Cryptophagus jakowlewi*	*Cryptophagus punctipennis*	-2.14 (A)
48	P_29-DSA_7	*Paromalus flavicornis*	*Criorhina floccosa*	-2.08 (A)
49	X_9-DSA_12	*Xestobium rufovillosum*	*Ferdinandea ruficornis*	-2.07 (A)

50	DSA_12-SX_16	*Ferdinandea ruficornis*	*Isomira hispanica*	-2.06 (A)
51	SX_26-SX_8	*Protaetia cuprea*	*Cryptophagus aurelioi*	-2.06 (A)
52	XM_3-CSA_20	*Cryptophagus scanicus*	*Palorus depressus*	-2.06 (A)
53	SX_5-SX_6	*Camptorhinus simplex*	*Camptorhinus statua*	-2.05 (A)
54	SX_6-X_11	*Camptorhinus statua*	*Xyleborus dryographus*	-2.03 (A)
55	CSA_16-SX_12	*Epuraea fuscicollis*	*Dendarus pectoralis*	-2.03 (A)
56	P_2-SX_3	*Ampedus aurilegulus*	*Anaspis (Anaspis) ruficollis*	-2.03(A)
57	P_32-SX_3	*Procraerus tibialis*	*Anaspis (Anaspis) ruficollis*	-2.02 (A)
58	CSA_4-CSA_23	*Anthrenus minutus*	*Tenebrio punctipennis*	-2.01 (A)
59	P_19-CSA_22	*Hypebaeus flavipes*	*Soronia oblonga*	-2.01 (A)
60	P_26-P_19	*Megapenthes lugens*	*Hypebaeus flavipes*	-2.00 (A)
61	SX_7-SX_30	*Cetonia aurataeformis*	*Scraptia testacea*	2.62 (S)
62	SX_30-DSA_16	*Scraptia testacea*	*Myathropa florea*	2.44 (S)
63	SX_30-SX_12	*Scraptia testacea*	*Dendarus pectoralis*	2.16 (S)
64	P_20-SX_30	*Ischnodes sanguinicollis*	*Scraptia testacea*	2.08 (S)

Sección IV

Conclusiones

Conclusión General

Para el desarrollo total/ parcial de esta tesis, se tuvieron en cuenta datos de coleópteros y dípteros (sírfidos) saproxílicos provenientes de ecosistemas de bosque mediterráneo de diferentes espacios protegidos dentro de la Península Ibérica (Parque Nacional de “Cabañeros”, Reserva Biológica de “Campanarios de Azaba” y el Espacio Protegido “Sierra de las Quilamas”), recolectados mediante trampas de emergencia (Ricarte & Quinto, 2013a).

En los bosques del Mediterráneo ibérico, las oquedades arbóreas son los hábitats que actúan como importantes reservorios de diversidad de insectos saproxílicos (Ricarte et al., 2009; Marcos-García et al., 2010; Micó et al., 2011b; 2013a; Quinto et al., 2014), una de las comunidades de organismos más interesantes, diversas y amenazadas del continente europeo (Speight, 1989; Jonsell et al., 1998; Alexander, 2004; Ranius et al., 2005; Nieto & Alexander, 2010; Gouix et al., 2012). En el interior de cada oquedad, esta alta diversidad de insectos saproxílicos puede percibirse como una gran variedad de formas de vida de diferentes especies que se encuentran de algún modo ligadas, dando lugar a interacciones entre las especies en el interior de estos particulares medios (Quinto et al., 2014).

Los insectos saproxílicos incluyen algunas de las especies más amenazadas de extinción dentro del continente europeo (Nieto & Alexander, 2010; Radenkovic et al., 2013), no siendo una excepción de esta situación de vulnerabilidad la de alguna de sus poblaciones dentro de la península ibérica (Micó et al., 2011b; Ramírez-Hernández et al., 2014a) donde sus comunidades han sido gravemente afectadas durante los últimos años por las prácticas de manejo forestal no sostenible (Grove, 2002). Por este motivo, para las áreas forestales del mediterráneo ibérico, surge la necesidad de sentar las bases científicas y formular programas de gestión forestal adecuados, con el fin de preservar la entomofauna saproxílica mediante un correcto manejo de sus hábitats. En este sentido las oquedades arbóreas, muchas de ellas generadas a través del manejo tradicional de las podas a lo largo de la historia (Buse et al., 2008; Sirami et al., 2008; Ranius et al., 2009 a, b; Stokland et al., 2012; Sebek et al., 2012), son sistemas "multi-hábitat" que albergan y permiten el desarrollo de numerosas especies catalogadas con algún grado de amenaza (Dajoz, 1998; Ranius, 2002; Sverdrup-Thygeson, 2009; Micó et al., 2011b; Gouix et al., 2012; Gouix & Brustel, 2012; Ramírez-Hernández et al., 2014a).

Nuestros resultados ponen de manifiesto la importancia de tener en cuenta las relaciones interespecíficas de los organismos que conforman la comunidad entomológica saproxilica con el fin de poder comprender e interpretar la estructuración espacial de sus ensambles y analizar el papel que juegan estas interacciones en la conservación de esta biodiversidad. Es esta una perspectiva novedosa que ha permitido profundizar en el estudio de los ensambles formados por insectos saproxílicos (Coleópteros y Dípteros Syrphidae) ligados a las cavidades arbóreas de quercínas ibéricas (*Quercus* spp) (*ver trabajos de* Sección II y III). Las especies saproxílicas (coleópteros y dípteros sírfidos) conforman módulos cohesivos (*i.e.* agregaciones de especies), a lo largo de los distintos niveles formados por los gremios tróficos (Quinto et al., 2012), conformando complejas redes ecológicas conectadas a través de interacciones de especies insecto-insecto. Por todo ello es importante para la conservación de la comunidad entomológica saproxílica, centrar la atención en el estudio de especies clave que cumplen un papel fundamental en la organización de los ensambles al condicionar la presencia o ausencia de otras especies o gremios de especies que se desarrollan dentro de cada oquedad (*ej.* especies "ingenieros del ecosistema"). Ponemos de manifiesto también la importancia que tiene la microbiota dentro la oquedad como recurso trófico de las fases larvarias acuáticas de especies de sírfidos que como adultos, son visitantes florales asiduos de las flores de nuestros bosques mediterráneos.

Podemos concluir que para la conservación de las especies saproxílicas de los bosques del mediterráneo ibérico, debemos tener en cuenta la red de sus interacciones biológicas y los procesos funcionales en los que intervienen.

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Conclusiones

A continuación se resumen las principales conclusiones que podemos extraer de los trabajos de investigación presentados en la Sección II (a y b) y III de la presente tesis doctoral:

- **Sección II (a):** La actividad ejercida por coleópteros cetónidos como *Cetonia aurataeformis aurataeformis* Curti, 1913 *(*Coleoptera: Cetoniidae) en el interior de oquedades arbóreas de *Quercus rotundifolia* Lamarck, *Q. pyrenaica* Willdenow y *Fraxinus angustifolia* Vahl*,* puede considerarse como uno de los factores que, en mayor medida, determinan la presencia y desarrollo de las fases larvarias de sírfidos saprófagos como *Myathropa florea* (Linnaeus, 1758) (Diptera: Syrphidae).

- **Sección II (a):** Los sírfidos saproxílicos como *M. florea*, presentan un mejor desarrollo larvario y obtienen una eficacia biológica más alta cuando sus larvas acuáticas se desarrollan en sustratos enriquecidos con heces de larvas de coleópteros de Cetoniidae poniéndose de manifiesto por primera vez la existencia de interacciones de facilitación entre coleópteros saproxilófagos y dípteros (Syrphidae).

- **Sección II (a):** Considerando que los insectos saproxílicos (Coleoptera y Diptera: Syrphidae) son uno de los grupos taxonómicos más amenazados en el continente Europeo (*ver* Sección I), concluimos que resulta importante profundizar en el estudio de las relaciones intraespecíficas y en el papel que algunas de sus especies ejercen en el ecosistema con el fin de desarrollar adecuados programas de conservación de estas comunidades.

- **Sección II (b):** Los resultados muestran la existencia de interacciones entre sírfidos saproxílicos, cuyas larvas se desarrollan en el agua de las oquedades arbóreas y especies de bacterias del "grupo cereus" como son *Bacillus cereus* Franklandand Frankland, 1887, *Bacillus toyonensis* Jimenez et al. 2014 y *Lysinibacillus sphaericus* (Meyer and Neide 1904) Ahmed et al. 2007.

- **Sección II (b):** El modelo de estudio desarrollado con larvas del sírfido *Mallota dusmeti* Andreu, 1926, especie de distribución iberomagrebí y con categoría Vulnerable dentro de la península ibérica y la flora bacteriana presente en el medio líquido de la oquedad, han puesto de manifiesto por primera vez la presencia en el tracto digestivo del sírfido de algunas especies de microorganismos como *B. cereus* y *B. toyonensis*, también presentes en su medio de desarrollo, por lo que es posible que formen parte de su dieta.

- **Sección II (b):** El análisis también detectó la presencia de Enterobacterias: *Brenneria alni* (Surico et al. 1996) Hauben et al. 1999 y *Pectobacterium carotovorum* Jones 1901, en oquedades arbóreas de *Q. rotundifolia*. No obstante, estas bacterias no se encontraron en el tubo digestivo de las larvas saprófagas de *M. dusmeti*, siendo posible que estas dos especies de bacterias intervengan en los procesos de descomposición de los tejidos vegetales dentro de las oquedades.

- **Sección II (b):** En vista de que las larvas del sírfido saproxílico *M. dusmeti* son totalmente dependientes de oquedades con gran contenido de agua, y que a su vez estas oquedades son hábitats con alto contenido en materia orgánica donde se desarrollan las comunidades de microorganismos, se puede concluir que una de las acciones prioritarias de conservación debería ser el asegurar la protección de árboles maduros que mantienen depósitos de agua durante periodos prolongados y al tiempo evitar el uso de tratamientos químicos con fitosanitarios que puedan afectar negativamente la microbiota contenida en el agua de estas oquedades.

- **Sección III:** A nivel regional, especies consideradas como amenazadas o casi amenazadas estuvieron implicadas en 57 patrones individuales no aleatorios, de los cuáles 39 son agregaciones y 18 segregaciones. Además, 13 de estas agregaciones, estuvieron compuestas por especies consideradas como ingenieros del ecosistema (*Cerambyx welensii* Küster, 1846 y *Cetonia aurataeformis*).

- **Sección III:** En el Parque Nacional de Cabañeros, el análisis de coincidencia a nivel de matriz reveló un patrón general hacía la segregación de las especies, lo que podría indicar bien la existencia de dominancia de interacciones competitivas, o bien que esta segregación espacial sea causada por claras diferencias en los requerimientos biológicos de ocupación y del desarrollo larvario de las especies en la oquedad.

- **Sección III:** El análisis de coincidencia a nivel individual entre pares de especies, detectó que a nivel regional y local por cada tipo de bosque (Parque Nacional de “Cabañeros”; Reserva Natural de “Campanarios de Azaba” y Espacio protegido “Sierra de las Quilamas”) existe un porcentaje moderadamente bajo de patrones no aleatorios (agregación y segregación). Esto podría ser la consecuencia de una alta complejidad estructural de las oquedades arbóreas (en términos de diversidad de recursos tróficos ofrecidos por cada oquedad), lo cual incrementa una naturaleza estocástica de los patrones en general. Así mismo, esta estocasticidad puede ser la consecuencia de la alta variabilidad ambiental propia de las regiones de la Cuenca Mediterránea.

- **Sección III:** La diversidad (en términos de riqueza y abundancia) de especies que conforman los ensambles de insectos saproxílicos dentro de oquedades arbóreas, variaron significativamente según el tipo de bosque analizado, siendo por tanto muy bajo el porcentaje de los patrones no aleatorios (de agregación/o segregación) compartidos.

- **Sección III:** El análisis de coincidencia entre pares de especies, reveló que los patrones individuales no aleatorios de agregación son más numerosos, que patrones no aleatorios de segregación, y en su mayoría estas agregaciones estuvieron formadas por parejas de especies de coleópteros depredadores y especies coleópteros presa (pertenecientes a los gremios tróficos: xilomicetófagos y saproxilófagos).

- **Sección III:** El análisis de coincidencia entre pares de especies, reveló que los patrones no aleatorios de segregación, en su mayoría estuvieron formados por pares de especies que pertenecen a distintos gremios tróficos, lo que nos permite inferir que más que las interacciones de competencia, son las diferentes características de las oquedades arbóreas la fuerza que promueve la segregación espacial de las especies.

- **Sección III:** A nivel regional, el análisis de coincidencia aplicado en parejas individuales de especies, sugiere que ciertos patrones no aleatorios agregados podrían ser interpretados como interacciones de facilitación confirmando los resultados expuestos en la sección II (a).

- **Sección III:** Todos los hallazgos, basados en el uso de modelos nulos sin restricciones, sugieren que interacciones biológicas como la depredación y la facilitación, así como la segregación causada por la alta complejidad estructural de las oquedades arbóreas, actúan como los principales mecanismos que moldean la estructura de los ensambles formados por insectos saproxílicos (Coleoptera y Diptera: Syrphidae) dentro de las oquedades arbóreas.

- **Sección III:** En conclusión, para una conservación efectiva de los ensambles formados por insectos saproxílicos dentro de las oquedades arbóreas, es necesario tomar en cuenta la noción conjunta de alta heterogeneidad estructural dentro de las oquedades y la existencia de múltiples interacciones interespecíficas que se producen en estos microhábitats, poniendo especial atención en el papel que desempeñan especies ingenieros del ecosistema, especies amenazadas y casi amenazadas en estas interacciones biológicas.