

## COMMUNITY AND ECOSYSTEM ECOLOGY

# 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*.

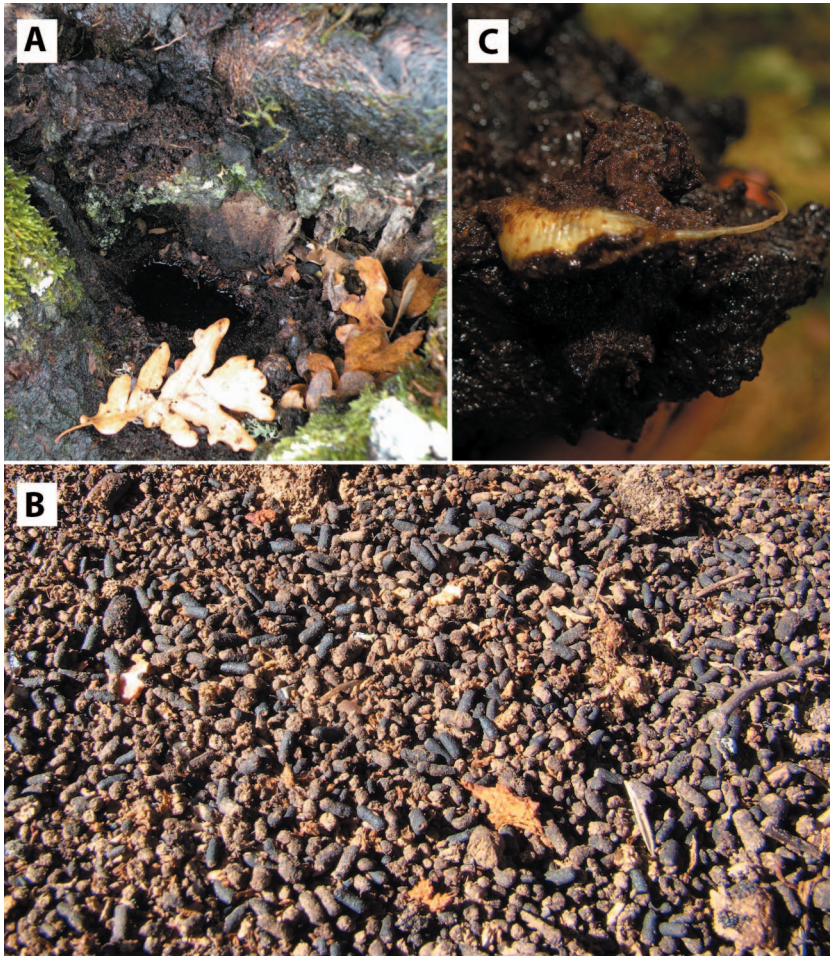
**KEY WORDS** Mediterranean forest, *Cetonia aurataeformis*, *Myathropa florea*, co-occurrence, ecosystem engineer

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). Brad-

shaw 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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**Fig. 1.** (A) The interior of a tree hollow with accumulated rain water and organic matter. (B) Cetoniid 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 cetoniid feces inside a tree hollow.

quis 2003, Diniz et al. 2012), gall makers (*Pemphigus betae* Doane, 1900; Waltz and Whitham 1997), leaf miners (*Phyllonorycter pastorella* Zellar, 1846; Johnson et al. 2002, Kagata and Ohgushi 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 (Connell and Slatyer 1997, Bronstein 2009).

One classic example of ecosystem engineer insects linked to deadwood is *Cerambyx cerdo* (L., 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 (Jönson 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 and Juliano 2006). Saproxylic Cetoniidae larvae develop inside tree hollows in Mediterranean forests, where they become abundant (Micó and Galante 2002, Ricarte et al. 2009, Micó et al. 2011). These cetoniid larvae transform large fragments of rotten wood and litter into feces that are richer than the original substrate (Murayama 1931; Micó et al. 2008, 2011; Fig. 1B). This enriched and thinner substrate could facilitate the occurrence of other saproxylic organisms, such as the species with filtering mouthparts (Rotheray and Gilbert 2011; Fig. 1C). Therefore, cetoniid larvae could also be considered as 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 or saproxylic insect (Coleoptera, Diptera: Syrphidae) food webs in the Cabañeros National Park, Spain. In

that study, we had reported that cetonid beetles and saprophagous Syrphidae (Diptera) co-occur in tree hollows in Mediterranean forests (Fig. 1). However, to the best of our knowledge, there are no studies that analyze either these spatiotemporal co-occurrences or 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.

### Materials and Methods

**Study Area.** The study was conducted from February 2009 to February 2010 in the Cabañeros National Park (39° 23' 47" N, 4° 29' 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 1,448 m. This zone belongs to the Mediterranean region, where the climate is characterized by a dry summer period, with annual rainfall ranging from 500 to 750 mm. The average annual temperature varies from 12.9 to 15.6°C, with maximum temperatures of 40°C in summer and minimum temperatures of -12°C in winter (Vaquero 1997).

**Field Experiment.** 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* Lam., 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 and Brustel 2012, 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 a 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 owing to their shape, size, and abundance (Fig. 1B).

To assess the effect of cetonid activity 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 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  $diam = \frac{P}{\pi}$  (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<sup>3</sup>), 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 semisphere and then  $Volum = \frac{2}{3}\pi r^3$  (cm<sup>3</sup>), 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 absence 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* (L., 1758), the most abundant syrphid species living in tree hollows in the study area (Quinto et al. 2012). The larvae of this species live in liquefied decaying vegetal matter (Hartley 1961). However, one of the most abundant cetonid species living inside tree hollows is *Cetonia aurataeformis* Curti, 1913 (Micó et al. 2011).

The laboratory experiment was conducted to assess the effect of the presence of feces of *C. aurataeformis* larvae on the life cycle and fitness of *M. florea*. In January 2011, we collected 60 third-instar larvae of *M. 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 the method by 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 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 (Fig. 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 (20 ± 1°C; 75 ± 10% relative humidity [RH]). The three different breeding media were tested using 20 larvae per treatment.

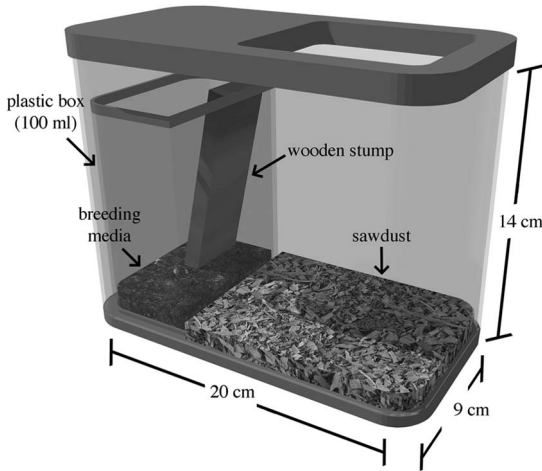


Fig. 2. Rearing box with breeding media where larvae of *M. florea* were placed until pupation. A plastic box containing the breeding media was placed inside a larger plastic box. We placed a wooden stump in the breeding media to enable the syrphid larvae to access the dry area to pupate.

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 *C. aurataeformis* larvae. This treatment consisted of 20 ml of detritus (*Q. pyrenaica* wood sawdust), 20 ml of feces of *C. aurataeformis* larvae, and 60 ml of purified water.

Treatment 3. Suboptimal 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 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 and 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; Dziock 2005, Amorós-Jiménez et al. 2012).

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 the study by Amorós-Jiménez et al. (2012). We registered the number of pupae that developed into adults 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 as a good indicator for adult fitness (Kingsolver and Pfennig 2004, Dziock 2005, Kingsolver and Huey 2008). Spe-

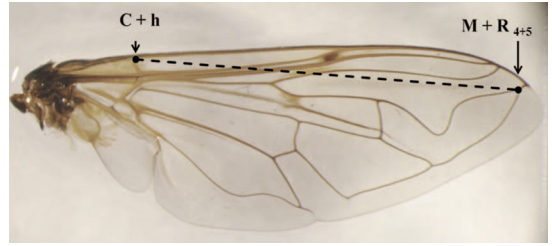


Fig. 3. Wing of *M. florea*. The distance between the two marked points is the shortest length between the junction of the costal vein (C) with the humeral cross vein (h) and the junction of R4 + 5 with the medial vein (M) (Dziock 2005).

cifically, 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) was measured (Dziock 2005; Fig. 3). Measurements were analyzed separately for each sex owing 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 Braak and 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).

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
<i>Brachyopa grunewaldensis</i> (Kassebeer, 2000)	11	S1
<i>Brachypalpoidea lentus</i> (Meigen, 1822)	2	S2
<i>Brachypalpus valgus</i> (Panzer, 1798)	4	S3
<i>Callicera aurata</i> (Rossi, 1790)	4	S4
<i>Callicera spinolae</i> Rondani, 1844	29	S5
<i>Ceriana vespiformis</i> (Latreille, 1804)	9	S6
<i>Criorhina floccosa</i> (Meigen, 1822)	8	S7
<i>Criorhina pachymera</i> Egger, 1858	4	S8
<i>Ferdinandea aurea</i> Rondani, 1844	24	S9
<i>Ferdinandea cuprea</i> (Scopoli, 1763)	3	S10
<i>Ferdinandea fumipennis</i> Kassebeer, 1999	1	S11
<i>Ferdinandea ruficornis</i> (F., 1775)	6	S12
<i>Mallota cimbiciformis</i> (Fallen, 1817)	33	S13
<i>Mallota dusmeti</i> Andréu, 1926	97	S14
<i>Mallota fuciformis</i> (F., 1794)	11	S15
<i>Milesia crabroniformis</i> (F., 1795)	1	S16
<i>Myathropa florea</i> (L., 1758)	203	S17
<i>Myolepta dubia</i> (F., 1805)	1	S19
<i>Myolepta obscura</i> Becher, 1882	4	S20
<i>Sphiximorpha subsessilis</i> (Illiger in Rossi, 1807)	1	S21
<i>Spilomyia digitata</i> (Rondani, 1865)	6	S22

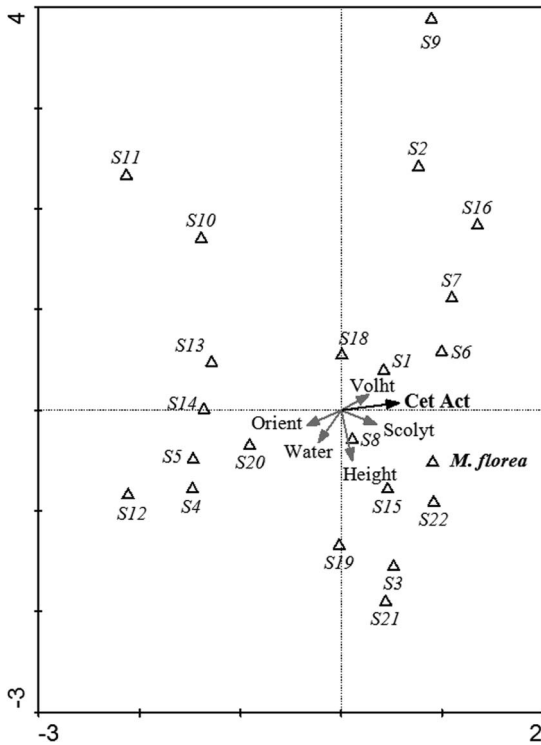


Fig. 4. CCA representation of the significant microenvironmental variables that affect the Syrphidae species distribution. The syrphid species other than *M. florea* labels (S17) can be found in Tables 2 and 3. Cet Act, Cetonid activity; Volth, tree hollow volume; Scolyt, presence of Scolytidae galleries;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

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

Results

**Influence of Cetonid Activity on Saprophagous Syrphidae Presence.** Just over 63.22% of the studied tree hollows exhibited evidence, presence, or both, of feces of *C. aurataeformis* larvae. The CCA showed that six microenvironmental variables influence Syrphidae species distribution (Fig. 4; Tables 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 Scolytidae galleries ( $F = 1.88$ ;  $P < 0.05$ ), presence of accumulated water ( $F = 1.65$ ;  $P < 0.05$ ), internal volume of hollow ( $F = 1.67$ ;  $P < 0.05$ ), and hollow orientation ( $F = 1.58$ ;  $P < 0.05$ ).

Table 2. Results of canonical correspondence analysis of syrphid larvae abundance as a function of the microenvironmental variables studied

Microenvironmental variables	F-ratio	P value
Cetonid activity (Cet Act)	2.55	0.002*
Height of hollow from the ground (Ht; 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 vol (Volth; cm <sup>3</sup> )	1.67	0.046*
Hollow opening area (Area; cm <sup>2</sup> )	1.19	0.504
Vertebrate presence (Verteb)	0.75	0.804
Organic matter vol (Volmo; cm <sup>3</sup> )	0.68	0.892
Diameter of trunk (diam; cm)	0.53	0.942

Asterisk indicates the microenvironmental factors that significantly explain a major percentage of variation ( $P < 0.05$ ) of the distribution of saprophagous syrphids in tree hollows.

The syrphid species most related to cetonid activity was *M. florea* (present in 35% of the tree hollows examined), followed by *Brachyopa grunewaldensis* (Kassebeer 2000) (13%), *Myolepta difformis* (Strobl, 1909) (10%), and *Spilomyia digitata* (Rondani, 1865) (7%).

Scolytidae 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 *Cr. pachymera*, *Mallota fuciformis* (F., 1794), *S. digitata*, and *Brachypalpus valgus* (Panzer, 1798). Finally, the species most influenced by the hollow volume was *B. grunewaldensis* (Fig. 4).

**Influence of Cetonid Feces on *M. florea* Larval Development and Adult Fitness.** The larval growth rate of *M. florea* for treatment 2 (enriched with cetonid feces) was significantly higher than that for the other two treatments ( $F = 7.50$ ;  $df = 2$ ;  $P < 0.01$ ). In addition, wing length average was also significantly

Table 3. Eigenvalues and correlation coefficients for axes 1 and 2, and canonical coefficients for each microenvironmental variable

CCA output	Canonical axes	
	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 Scolytidae galleries	0,517	-0,204
Presence of accumulated water	-0,338	-0,458
Internal vol of hollow	0,407	0,22
Hollow orientation	-0,507	-0,221

Asterisk indicates the highest eigenvalue corresponding to “Cetonid activity”.

Table 4. Metrics of the syrphid *M. 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	<i>P</i> = 0.0016*
Pupal wt (g)	0.1228 ± 0.0092	0.1316 ± 0.0064	0.1117 ± 0.0150	<i>P</i> = 0.4030
Median larval growth period (d)	26	23	33	<i>P</i> = 0.1089
Adult emergence rate (%)	65	80	60	<i>P</i> = 0.3679
Average wing length (mm)	4.48 ± 3.77	5.21 ± 3.52	2.28 ± 3.58	<i>P</i> = 0.0354*

Treatment 1, Optimal conditions for saprophagous syrphid larvae growth; Treatment 2, Substrate enriched with feces of *C. aurataeformis* larvae; Treatment 3, Suboptimal treatment (see details in Methods).

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

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 ( $\chi^2 = 4.43$ ;  $df = 2$ ;  $P > 0.05$ ; Table 4).

### Discussion

It has been suggested that several beetle species considered as ecosystem engineers (e.g., *C. cerdo* and *O. eremita*) could be important facilitation factors that determine higher species richness of saproxylic insects in tree hollows (Jönson et al. 2004, Ranius et al. 2005, Buse et al. 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 to understand the biodiversity hosted by tree hollows.

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

*M. florea* is a cosmopolitan saprophagous hoverfly (Speight and Castella 2011), whose distribution in the Iberian Peninsula is wide (Marcos-García 1985). The aquatic larvae of *M. 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 and 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 *M. florea*, which can extend to over a year in natural conditions (Rotheray and Gilbert 2011). This food enrichment provided by cetonid feces can lead to a lack of synchrony in the life cycle of *M. florea* at local scale (i.e., shortening the life cycle of *M. 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 saproxylic larvae population in tree hollows frequently consist of different sizes and instars (Rotheray and Gilbert 2011).

The laboratory experiment corroborates our field facilitation results, demonstrating that *M. florea* larvae had a higher growth rate when reared in an enriched substrate with *C. aurataeformis* 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 better flight capacity (Dziocck 2005). However, other studies on larval interspecific relations undertaken with *M. florea* and three other common insects (two Nematocera and one Coleoptera species) that live 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 owing to the attractiveness for elective oviposition exerted on gravid syrphid females by tree hollows enriched with organic matter (Speight and Castella 2011). 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 *C. aurataeformis*, act as ecosystem engineers within tree hollows, favoring the establishment, survival, and fitness of *M. 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 and 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 and Gilbert 2011) that require deep hollows to survive the

long drought periods that are characteristic of the Mediterranean climate. These horizontal hollows constitute a suitable habitat for the development of large *M. florea* larvae (Schmidl et al. 2008). The preference of this species for tree hollows with a greater volume of water, as observed in *My. obscura* and *Ma. 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 *Cr. pachymera*, *Ma. fuciformis*, and *Br. valgus* tend to occupy higher tree hollows, which is consistent with their adult habits. These are primarily arboreal, flying high, and descending to flowering understorey trees to feed (Speight and Castella 2011).

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

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