J Insect Conserv (2015) 19:141–153
DOI 10.1007/s10841-015-9754-9

ORIGINAL PAPER

What can physical, biotic and chemical features of a tree hollow tell us about their associated diversity?

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Received: 9 October 2014 / Accepted: 6 January 2015 / Published online: 10 January 2015
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Abstract Tree hollows are keystone structures for saproxylic fauna and host numerous endangered species. However, not all tree hollows are equal. Many variables including physical, biotic and chemical ones, can characterise a tree hollow, however, the information that these could provide about the saproxylic diversity they harbour has been poorly explored. We studied the beetle assemblages of 111 *Quercus* species tree hollows in four protected areas of the Iberian Peninsula. Three physical variables related to tree hollow structure, and two biotic ones (presence of Cetoniidae and *Cerambyx* species recognised as ecosystem engineers) were measured in each hollow to explore their relative effect on beetle assemblages. Moreover, we analysed the chemical composition of the wood mould in 34 of the hollows, in order to relate beetle diversity with hollow quality. All the environmental variables analysed (physical and biological) showed a significant influence on saproxylic beetle assemblages that varied depending on the species. Furthermore, the presence of ecosystem engineers affected both physical and chemical features. Although wood mould volume, and both biotic variables could act as beetle diversity surrogate, we enhance the presence of Cetoniidae and *Cerambyx* activity (both easily observable in the field) as indicator variables, even more if both co-occur as each affect to different assemblages. Finally, assimilable carbon and phosphorous contents could act as indicator for past and present beetle activity inside the cavity that could become a useful tool in functional diversity studies. However, an extension of this work to other taxonomic groups would be desirable.

Keywords Ecosystem engineers · Diversity surrogate · Mediterranean forests · *Quercus* species · Red-list species · Substrate quality

Introduction

One of the most complex communities in terrestrial environments depends on the diverse range of microhabitats offered by dead wood (Winter and Möller 2008; Stokland et al. 2012). The complexity of this saproxylic assemblage is given not only by the high number of species (Dajoz 2000; Grove 2002; Stokland et al. 2012), where insects in general and beetles in particular are the best represented taxa, but also by the coexistence of several types of interactions among them and with woody substrates (Quinto et al. 2012). Many efforts have been made to search for biodiversity indicators that could simplify the complicated task of species identification in the huge saproxylic assemblage for conservation purposes (see Müller et al. 2014).

Trees with hollows have been recognised as keystone structures for saproxylic beetles in European forests. In particular, hollow trees with mould are more diverse functionally and phylogenetically, and they are richer in red-listed species

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Electronic supplementary material The online version of this article (doi:10.1007/s10841-015-9754-9) contains supplementary material, which is available to authorized users.

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than other saproxylic microhabitats (Alexander 2008; Nieto and Alexander 2010; Müller and Bütler 2010; Müller et al. 2014). The importance of tree hollows (in both Temperate and Mediterranean forests) that host rich saproxylic assemblages is indisputable, and they have been considered per se as diversity umbrellas for conservation management (Müller et al. 2014; Sirami et al. 2008; Quinto et al. 2014). However, not all cavities are equal (Quinto et al. 2014); many variables can characterise a tree hollow, including physical, biotic and chemical ones, which make each tree hollow unique in space and time. Nevertheless, the independent effects of these kinds of variables on saproxylic diversity inhabiting the hollows have not yet been established, and their possible value as a diversity surrogate has been poorly explored. A key question then is what tree hollow features can tell us about the biodiversity they harbour, and to what extent they can be used as biodiversity predictors.

It is known that large cavities with wood mould are exceptionally long—lasting and stable dead—wood microhabitats (Müller et al. 2014), and that large hollow sizes and high wood mould volumes are both features that, in general, favour invertebrate diversity (see Sebek et al. 2013; Quinto et al. 2014). Nevertheless, at the same time, organisms that inhabit hollows contribute to enlarging the cavity as well as increasing the wood mould volume (Siitonen 2012). In this way, fungi and invertebrates, together with physical break down and abiotic factors, play a decisive role in the development of these cavities and they could also drive the chemical transformation of the hollow substrate (Ranius 2002a; Jönsson et al. 2004; Micó et al. 2011; Siitonen 2012). Focusing on beetles, whose larvae often dominate the community in terms of biomass (Siitonen 2012), there are good examples of the functional importance of tree hollow inhabitants; under the concept of ecosystem engineers, Buse et al. (2008) showed that the great Capricorn (*Cerambyx cerdo*) alters its own habitat to create favourable habitat conditions for other threatened beetle species. Actually, *Cerambyx* larvae create extensive galleries (Palm 1959; Martín et al. 2005), which act as entrances and habitats for other species (Buse et al. 2008).

Larvae of many Cetonids (Cetoniidae) are also among the known functionally important beetles in cavities; they live deep in wood mould and consume the decaying walls of cavities (Ranius 2002a, b; Siitonen 2012). They expand the cavity with their action and produce a large quantity of frass (larval faeces), and also increase wood mould volume. Therefore, larval activity modifies two important features of the cavity (tree cavity size and substrate volume) and, moreover, they alter the chemical composition of wood mould, as the faeces they produce are rich in nitrogen (N) and phosphorous (P) (Jönsson et al. 2004; Micó et al. 2011). As regards this data, it seems difficult to depict the thin line that delimits the boundaries of the effects of physical, biotic and chemical variables on tree hollow assemblages.

Although the positive effect of the presence of tree hollows with wood mould on saproxylic assemblages is well-known (see references above), until now there have been few empirical studies relating wood mould volume and species richness (see Ranius and Nilsson (1997) and Ranius and Wilander (2000)). Similarly, despite the relevance of species interactions and functionality on assemblage diversity (Tanahashi and Togashi 2009; Kadowaki 2010; Quinto et al. 2012), very few studies have analysed the importance of the named ecosystem engineers in saproxylic communities (see Ranius 2002a; Buse et al. 2008; Victorsson 2012; Sánchez-Galván et al. 2014). Moreover, although it is known that quality (as far as we are concerned, substrate chemical composition) affects saproxylic diversity (Jönsson et al. 2004; Saint-Germain et al. 2007; Lachat et al. 2013; Gossner et al. 2013), there is still a great lack of studies of the relationship between tree wood mould quality and their associated beetle biota.

Regarding all these previous data, the main aim of this study was to analyse first to what extent physical, biotic (presence of ecosystem engineers) and chemical features (wood mould quality) of tree hollows can explain the saproxylic beetle diversity they harbour, and second which is the best diversity surrogate (powerful and easy to measure) for conservation purposes. The study was carried out in oak tree hollows from four protected areas in the Mediterranean region of the Iberian Peninsula, where tree hollows are one of the most important microhabitats for saproxylic fauna (see Quinto et al. 2014; Ramírez-Hernández et al. 2014; Sirami et al. 2008). First we explored the effect of physical and biotic variables on saproxylic beetle species, and then looked for correlation with beetle richness and abundance, paying special attention to the role of ecosystem engineers in tree hollow assemblages. We also wanted to know whether wood mould volume inside cavities went hand in hand with quality, and if the presence of the ecosystem engineers also affected quantity and quality features. We finally tested what wood mould chemical composition revealed from its associated fauna and to what extent it could be an indicator of the activity of hollow-inhabiting beetles.

By answering all these questions we expect to elucidate what combination of measurable tree hollow variables could be used as a saproxylic hollow diversity surrogate and to provide a framework for conservation management.

Materials and methods

Study area

Fieldwork was carried out in four protected areas in the Mediterranean region of the Iberian Peninsula (Table 1); Cabañeros National Park, a protected area of 40,856 ha located in central Spain with altitudes varying between 560 and 1,448 m. The park has extensive areas of well-preserved Mediterranean landscape with various woodland types, where *Quercus* species (*Q. rotundifolia* and *Q. pyrenaica*) are the most representative (see Quinto et al. 2012; Micó et al. 2013 for more details). “Campanarios de Azaba” Biological Reserve (LIFE/E/NAT/000762), a protected cultural landscape of 522 ha, altitude about 800 m in the western Iberian Peninsula, dominated by *Q. rotundifolia* and *Q. pyrenaica* (see Ramírez-Hernández et al. 2014 for more details). “Sierra de Batuecas-Peña de Francia” Natural Park, a protected natural area of 31,801 ha, altitude between 500 and 1,700 m in the western Iberian Peninsula, where the most extensive forests are dominated by *Q. rotundifolia*, with isolated trees of *Q. suber* and pine plantations. “Sierra de las Quilamas” Natural Area (SCI by Habitat Directive (92/43/EEC)) with an extension of 11,100 ha, altitude between 600 and 1,400 in the western Iberian Peninsula, whose forest habitats are dominated by *Q. pyrenaica*.

Beetle sampling and species identification

One hundred and eleven emergence traps were used for collecting beetles inhabiting tree hollows (Table 1). Emergence traps consist of a black acrylic mesh that covers and seals the tree hollow, and a catcher pot containing ethylene-glycol or propylene-glycol as preservative is attached to the mesh (Gouix and Brustel 2011; Quinto et al. 2013). Traps were placed on tree hollows of *Quercus* species (*Q. rotundifolia* and *Q. pyrenaica*). Tree hollows were selected to represent real heterogeneity and abundance of tree hollows in each stand. Traps were replaced monthly from May to November in all stands; the stands in Cabañeros National Park were surveyed in 2009, those in the Biological Reserve “Campanarios de Azaba” in 2010 and the ones in “Sierra de Batuecas-Peña de Francia” Natural Park and “Sierra de las Quilamas” Natural Area in 2012.

Nomenclature is according to the Fauna Europaea (http://www.faunaeur.org/), Bouchard et al. (2011) and the Catalogues of Palaearctic Coleoptera (Löbl and Smetana 2004, 2006, 2007, 2008). Several specialists in saproxylic beetles collaborated in species identification (see acknowledgments). The specimens are deposited in the Entomological Collection of the University of Alicante (CEUA).

Characterising tree hollows: physical and biotic variables

We measured three physical variables, all of them continuous, related to tree hollow structure and two biotic ones (both categorical) consisting of the presence of species recognised as “ecosystem engineers” due to their ability to transform the tree hollow microhabitat (Buse et al. 2008; Jönsson et al. 2004; Micó et al. 2011). These variables were measured for 111 tree hollows belonging to the four protected areas surveyed. Measurements were taken as follows:

Physical

- Hollow volume (HOVol): this was estimated by considering the volume as a hypothetical cylinder using the equation $= \pi r^2 h$, where r was the maximum radius of the cavity, and h the maximum height. Maximum height was measured using a calibrated rod.
- Wood mould volume (WMVol): Wood mould contained in each tree hollow was defined as a loose material of fine wood fragments (colonised mainly by brown rot fungi), insect frass, and remains of invertebrates and insect nests (Jönsson et al. 2004). Wood mould volume was estimated by considering this volume as a hypothetical cylinder using the equation $= \pi r^2 h$, where r was the radius of the upper level of wood mould, and h the height (depth) of the wood mould in the hollow. Depth was measured using a calibrated rod.
- Hollow height (HOHeigh): The hollow height to ground was measured as the distance from the lower part of the hollow opening to the ground.

Biotic

- Presence of Cetoniidae larval activity (CET): We recorded the presence of cetonid faeces in the tree

Table 1 Sampling sites and sampling design

Locality	Coordinates	Tree species	N° ET
Sierra de las Quilamas Natural Area	N40 35.642 W6 03.201	*Q. pyrenaica*	18
Batuecas-Peña de Francia Natural Park	N40 27.291 W6 08.088	*Q. rotundifolia*	23
Cabañeros National Park	N39 21.161 W4 21.516	*Q. rotundifolia*	28
		Q. pyrenaica	21
Campanarios de Azaba Biological Reserve	N40 30.221 W6 48.098	*Q. rotundifolia*	13
		Q. pyrenaica	8

ET, emergence trap

hollow before trap installation and/or the presence of cetonid species emerging from the hollow. The faeces were easily distinguishable from the rest of the substrate due to their shape, size, and abundance (Sánchez-Galván et al. 2014).

- Presence of *Cerambyx* activity (*CER*): We recorded the presence of *Cerambyx* galleries in the tree hollow before trap installation and/or the presence of *Cerambyx* species emerging from the hollow.

Chemical analysis

We analysed the chemical composition of wood mould contained in 34 tree hollows belonging to "Sierra de Batuecas-Peña de Francia" Natural Park and "Sierra de las Quilamas" Natural Area.

A quantity of up to one litre of wood mould contained in the 34-surveyed tree hollows was taken after 1 year of beetle sampling (May 2013). Then, samples were taken to the laboratory to analyse elemental composition [Nitrogen (N), Carbon (C)], and phosphorous (P) contents and assimilable carbon (C_a), so that we could relate beetle-emerging from a tree hollow throughout a whole year with the wood mould chemical composition from the same hollow.

Samples were ground and dried at 60 °C, then elemental composition (total C and N) was analysed in a Carlo Erba CHNS-O EA1108 apparatus, and content in P was determined using colorimetry with phosphomolybdovanadate at 460 nm (Kitson and Mellon 1944). Carbon (C), Nitrogen (N) and Phosphorus (P) are essential components that organisms require to achieve synthesis of metabolites (proteins, carbohydrates, nucleic acids, etc.). Furthermore, C is consumed during respiration processes. Moreover, from all C content we determined the percentage of assimilable organic carbon (C_a) using the Walkley–Black chromic acid wet oxidation method (Walkley and Black 1934). The analysis of C_a allowed the less complex components (organic structures) to be quantified. These degrade easily during mineralisation as a result of the transformation of the complex structures of plant residues (lignin and cellulose) by organisms. We also calculated C/N and C/P in order to show the relative mineralisation of C compared to N or P, respectively, both items are directly related to preferential consumption of C versus N or P by organisms.

Data analysis

A generalized linear model (GLM) was used to examine the relationships between abundance and species richness and the physical and biological variables. We used quasipoisson error distribution to construct the model and checked for overdispersion of the data (Crawley 2007). GLM was carried out using R 6.1. (Crawley 2007; R Development Core Team 2012).

Canonical correspondence analysis (CCA) was used in order to examine relationships between each saproxylic beetle species and physical and biological variables (Ter Braak 1986). Global permutation tests (carried out by Monte Carlo tests with 499 permutations under the full model) were performed to judge the statistical significance of the relationship between species and microhabitat variables. CCA analyses were carried out using Canoco for Windows (Version 4.5, Ter Braak and Šmilauer 2002).

We looked for significant differences in diversity (species richness and abundance) between traps where the presence of Cetoniidae species (and/or their larval faeces) or *Cerambyx* species (and/or their larval galleries) were confirmed and those where these species were not present, in order to investigate the possible effect of biotic factors (ecosystem engineers) on the tree hollow saproxylic assemblages. We also analysed whether the presence of these species influenced the wood mould volume contained in the cavity or the wood mould chemical contents. Due to the absence of normality in the data, we used the Kruskal–Wallis test and Bonferroni post hoc tests to compare wood mould volumes and chemical components between traps with presence or absence of these species. Kruskal–Wallis tests were done with STATISTICA (StatSoft 2007).

We used Spearman rank correlation coefficients to test whether quantity (wood mould volume) and quality (wood mould chemical composition) were correlated. Then, we analysed the relationship between the species richness and abundance found in hollows and both the quantity and quality of the wood mould they harboured. Quantity was evaluated as the volume of wood mould inside the hollow; all 111 tree hollows of the whole study were used for this analysis. Quality was considered as a surrogate for the chemical composition of this wood mould; data from 34 hollows were used in this case (see "chemical analysis" in methods). Spearman rank correlations were performed using SigmaPlot 11.0 (Systat Software, San Jose, CA).

Results

Influence of physical and biotic variables

A total of 2,697 individuals belonging to 133 species and 34 beetle families were identified (Table 2).

Hollow volume and wood mould volume were positive and significantly correlated (Spearman rank correlation coefficient: $\rho = 0.82$, $p < 0.01$). Attending to the focus of this paper, we selected the wood mould among the correlated variable to be included in the GLM and CCA.

The GLM of the effect of physical and biological variables on community distribution found significant influence of both biological variables and wood mould volume on species richness and of hollow height and Cetoniidae larval activity on abundance (Table 3).

Moreover, the global permutation tests of the CCA based on the sum of all canonical eigenvalues indicated a significant relationship between the selected variables and the species distribution ($F = 1.826$, $p < 0.01$). The first two axes account for 68.9 % of the variance (Fig. 1). Many species, such as *Stenohelops montanus* (Tenebrionidae) and the Trogossitidae *Tenebroides maroccanus*, seem to be highly influenced by tree hollow height. In the group of species influenced by height all trophic habits were represented, where 60 % were saprophagous (Dermestidae) and saproxylophagous (Cetoniidae, Curculionidae and Tenebrionidae) and 30 % were predators. The presence of ecosystem engineers, such as *Cerambyx* affected a wide group of saproxylic species (Fig. 1). However, in this case 50 % were predators and 28 % were saproxylophagous–saprophagous (see species in Table 2); we highlight species such as the Near Threatened *Elater ferrugineus* and *Ectamenogonus montandoni* (both elaterids) or the Vulnerable cetonid *Protaetia mirifica*, all favoured by the presence of *Cerambyx* galleries. Another wide group of species was highly favoured by cetonid faeces' presence and by wood mould volume (Fig. 1). In this case trophic habit percentages were inverted, with saproxylophagous-saprophagous as the most common habit (53 %), followed by predators (34 %). The Endangered species *Limoniscus violaceus* (species included in Habitat Directive) was one of the species positively affected by both these variables.

Beetle species richness and abundance varied significantly between hollows with presence of ecosystem engineers and those without, both for Cetoniidae (K–W: species richness $H = 13.68$, $N = 111$, $p < 0.01$; abundance, $H = 9.58$, $N = 111$, $p < 0.01$) and for *Cerambyx* (K–W: species richness $H = 9.21$, $N = 111$, $p < 0.01$; abundance, $H = 5.86$, $N = 111$, $p < 0.05$). Post hoc tests showed that tree hollows where larval activity of Cetoniidae and *Cerambyx* species was present contained higher diversity of saproxylic beetles than those where these species were absent (Fig. 2). In addition, wood mould volume varied significantly between hollows with presence of those species and those without, both for Cetoniidae (K–W: $H = 11.27$, $N = 111$, $p < 0.01$) and for *Cerambyx* (K–W: $H = 9.27$, $N = 111$, $p < 0.01$). Post hoc tests showed that the tree hollows with presence of these species contained higher wood mould volume (Fig. 2). Regarding the effect of the ecosystem engineer species on chemical composition of tree hollows, we found that cavities with *Cerambyx* presence were significantly richer in C and C_a (Table 4) than those without *Cerambyx*.

Wood mould quantity versus quality

The first question we wanted to address was whether wood mould quantity goes hand in hand with quality. Phosphorous and C/P were the only chemical variables that significantly correlated with wood mould volume; this correlation of wood mould was positive with P and subsequently negative with the C/P ratio (see Table 5).

As stated above, wood mould quantity influence beetle assemblage (Table 3; Fig. 1). In addition, Spearman rank correlations coefficients showed significant and positive relationships between the wood mould volumes contained inside the tree hollows and the number of hosted species and individuals (species richness: $\rho = 0.4$, $p < 0.01$; abundance: $\rho = 0.35$, $p < 0.01$). Regarding wood mould quality, the relationship with species richness and abundance varied depending on the chemical variable analysed (Table 5). This last result is based on 417 individuals belonging to 66 species from 34 tree hollows. Higher beetle richness and abundance were related to higher amounts of C_a and P. And although the same occurred with C and N, these positive correlations were not significant. On the contrary, a negative correlation with richness and abundance was found for C/P and C/N. However, only the C/P ratio was significant (Table 5).

Discussion

Trunk hollows with wood mould are unique and highly complex microhabitats (Ranius 2002b; Müller et al. 2014; Quinto et al. 2014) that harbour very specialised insect fauna. Our results provide evidence that physical, biotic and chemical features of hollows could provide valuable information about the beetle diversity they harbour, and the biotic variables (presence of ecosystem engineers) may greatly affect the other two kinds of variables.

Both, physical and biological variables have shown a significant influence on species diversity (Table 3). Moreover, another interesting point is that the physical variables together with biotic ones (presence of ecosystem engineers) were able to explain about 65 % of the variance of beetle species abundance (Fig. 1). These results represent higher values of explanation compared with other studies on saproxylic organisms including only physical variables (see Taylor and Ranius 2014; Ramírez-Hernández et al. 2014). Regarding species composition, both physical variables (HOheight and WMVol) influenced two different beetle assemblages (Fig. 1); influence of height has been demonstrated before for several saproxylic beetle species

Table 2 Families, species, abundance and corresponding numbers in CCA diagrams

CCA No	Specie	Family	Family	Specie	No ind.	CCA No
1	*Abraeus perpusillus*	His	Ade	*Aderus populneus*	12	2
2	*Aderus populneus*	Ade		*Cnopus minor*	1	27
3	*Ahasverus advena*	Sil		*Otolelus neglectus*	5	93
4	*Alocerus moesiacus*	Cer	Biph	*Diplocoelus fagi*	12	51
5	*Ampedus aurilegulus*	Ela	Bup	*Eurythyrea quercus*	1	60
6	*Amphotis marginata*	Nit	Cer	*Alocerus moesiacus*	19	4
7	*Anaspis ruficollis*	Scr		*Cerambyx welensii*	69	23
8	*Anaspis regimbarti*	Scr		*Stictoleptura fontenayi*	1	120
9	*Anthocomus fenestratus*	Mal		*Stictoleptura trisignata*	34	121
10	*Anthrenus angustefasciatus*	Der		*Trichoferus fasciculatus*	1	126
11	*Anthrenus festivus*	Der	Cet	*Cetonia aurataeformis*	208	24
12	*Anthrenus minutus*	Der		*Protaetia cuprea*	67	107
13	*Anthrenus pimpinellae*	Der		*Protaetia mirifica*	8	108
14	*Anthrenus verbasci*	Der		*Protaetia opaca*	8	109
15	*Aplocnemus nigricornis*	Das	Cii	*Cis pygmaeus*	1	25
16	*Atomaria pusilla*	Cry		*Cis striatulus*	1	26
17	*Attagenus incognitus*	Der	Cle	*Opilo domesticus*	6	88
18	*Attagenus schaefferi*	Der	Cry	*Atomaria pusilla*	1	16
19	*Attagenus trifasciatus*	Der		*Cryptophagus aurelioi*	32	32
20	*Axinotarsus marginalis*	Mal		*Cryptophagus cylindrellus*	4	33
21	*Camptorhinus simplex*	Cur		*Cryptophagus dentatus*	23	34
22	*Camptorhinus statua*	Cur		*Cryptophagus denticulatus*	1	35
23	*Cerambyx welensii*	Cer		*Cryptophagus distinguendus*	1	36
24	*Cetonia aurataeformis*	Cet		*Cryptophagus jakowlewi*	187	37
25	*Cis pygmaeus*	Cii		*Cryptophagus micaceus*	76	38
26	*Cis striatulus*	Cii		*Cryptophagus populi*	1	39
27	*Cnopus minor*	Ade		*Cryptophagus pubescens*	6	40
28	*Colobicus hirtus*	Zoph		*Cryptophagus punctipennis*	10	41
29	*Colydium elongatum*	Zophe		*Cryptophagus saginatus*	19	42
30	*Corticeus fasciatus*	Ten		*Cryptophagus scanicus*	101	43
31	*Cryptolestes ferrugineus*	Lae	Cur	*Camptorhinus simplex*	4	21
32	*Cryptophagus aurelioi*	Cry		*Camptorhinus statua*	102	22
33	*Cryptophagus cylindrellus*	Cry		*Gasterocercus hispanicus*	2	61
34	*Cryptophagus dentatus*	Cry		*Rhyncolus reflexus*	6	113
35	*Cryptophagus denticulatus*	Cry	Pla	*Platypus cylindrus*	1	98
36	*Cryptophagus distinguendus*	Cry	Sco	*Xyleborinus saxesenii*	17	131
37	*Cryptophagus jakowlewi*	Cry		*Xyleborus dryographus*	6	132
38	*Cryptophagus micaceus*	Cry		*Xyleborus monographus*	206	133
39	*Cryptophagus populi*	Cry	Das	*Aplocnemus nigricornis*	1	15
40	*Cryptophagus pubescens*	Cry		*Dasytes pauperculus*	1	44
41	*Cryptophagus punctipennis*	Cry		*Mauroania bourgeoisi*	2	76
42	*Cryptophagus saginatus*	Cry	Der	*Anthrenus angustefasciatus*	4	10
43	*Cryptophagus scanicus*	Cry		*Anthrenus festivus*	1	11
44	*Dasytes pauperculus*	Das		*Anthrenus minutus*	6	12
45	*Dendarus pectoralis*	Ten		*Anthrenus pimpinellae*	1	13
46	*Dendrophilus punctatus*	His		*Anthrenus verbasci*	2	14
47	*Dermestes bicolor*	Der		*Attagenus incognitus*	13	17
48	*Dermestes frischii*	Der		*Attagenus schaefferi*	1	18

Table 2 continued

CCA No	Specie	Family	Family	Specie	No ind.	CCA No
49	*Dermestes hispanicus*	Der		*Attagenus trifasciatus*	5	19
50	*Dermestes undulatus*	Der		*Dermestes bicolor*	1	47
51	*Diplocoelus fagi*	Biph		*Dermestes frischii*	1	48
52	*Dorcatoma agenjoi*	Dor		*Dermestes hispanicus*	1	49
53	*Dorcus parallelipipedus*	Luc		*Dermestes undulatus*	18	50
54	*Ectamenogonus montandoni*	Ela		*Orphilus niger*	4	90
55	*Elater ferrugineus*	Ela	Dyn	*Oryctes nasicornis*	7	91
56	*Elathous platiai*	Ela	Ela	*Ampedus aurilegulus*	28	5
57	*Eledonoprius armatus*	Ten		*Ectamenogonus montandoni*	22	54
58	*Endophloeus marcovichianus*	Zoph		*Elater ferrugineus*	47	55
59	*Epuraea fuscicollis*	Nit		*Elathous platiai*	1	56
60	*Eurythyrea quercus*	Bup		*Ischnodes sanguinicollis*	39	68
61	*Gasterocercus hispanicus*	Cur		*Lacon punctatus*	13	71
62	*Gnathoncus communis*	His		*Limoniscus violaceus*	4	72
63	*Gnathoncus nannetensis*	His		*Megapenthes lugens*	12	77
64	*Hemicoelus nitidus*	Anob		*Melanotus dichrous*	4	78
65	*Hetaerius ferrugineus*	His		*Melanotus villosus*	1	79
66	*Hypebaeus albifrons*	Mal		*Procraerus tibialis*	17	106
67	*Hypebaeus flavipes*	Mal	End	*Mycetaea hirta*	5	81
68	*Ischnodes sanguinicollis*	Ela		*Symbiotes gibberosus*	15	122
69	*Ischnomera xanthoderes*	Oed	Euc	*Nycteus meridionalis*	1	86
70	*Isomira hispanica*	Alle	Hel	*Prionocyphon serricornis*	87	101
71	*Lacon punctatus*	Ela	His	*Abraeus perpusillus*	13	1
72	*Limoniscus violaceus*	Ela		*Dendrophilus punctatus*	30	46
73	*Litargus balteatus*	Myc		*Gnathoncus communis*	22	62
74	*Litargus connexus*	Myc		*Gnathoncus nannetensis*	10	63
75	*Margarinotus merdarius*	His		*Hetaerius ferrugineus*	1	65
76	*Mauroania bourgeoisi*	Das		*Margarinotus merdarius*	28	75
77	*Megapenthes lugens*	Ela		*Merohister ariasi*	12	80
78	*Melanotus dichrous*	Ela		*Paromalus flavicornis*	25	95
79	*Melanotus villosus*	Ela		*Platylomalus gardineri*	1	97
80	*Merohister ariasi*	His		*Platysoma filiforme*	1	99
81	*Mycetaea hirta*	End		*Plegaderus caesus*	1	100
82	*Mycetochara linearis*	Alle	Lae	*Cryptolestes ferrugineus*	4	31
83	*Mycetochara quadrimaculata*	Alle		*Placonotus testaceus*	1	96
84	*Mycetophagus quadriguttatus*	Myc	Luc	*Dorcus parallelipipedus*	46	53
85	*Nalassus laevioctostriatus*	Ten	Mal	*Anthocomus fenestratus*	26	9
86	*Nycteus meridionalis*	Euc		*Axinotarsus marginalis*	8	20
87	*Oligomerus brunneus*	Anob		*Hypebaeus albifrons*	6	66
88	*Opilo domesticus*	Cler		*Hypebaeus flavipes*	2	67
89	*Orchesia micans*	Mel		*Troglops furcatus*	43	127
90	*Orphilus niger*	Der	Mel	*Orchesia micans*	6	89
91	*Oryctes nasicornis*	Dyn	Mon	*Rhizophagus unicolor*	1	112
92	*Oryzaephilus surinamensis*	Sil	Myc	*Litargus balteatus*	1	73
93	*Otolelus neglectus*	Ade		*Litargus connexus*	8	74
94	*Palorus depressus*	Ten		*Mycetophagus quadriguttatus*	44	84
95	*Paromalus flavicornis*	His	Nit	*Amphotis marginata*	1	6
96	*Placonotus testaceus*	Lae		*Epuraea fuscicollis*	143	59

Table 2 continued

CCA No	Specie	Family	Family	Specie	No ind.	CCA No
97	*Platylomalus gardineri*	His		*Soronia oblonga*	133	116
98	*Platypus cylindrus*	Pla	Oed	*Ischnomera xanthoderes*	22	69
99	*Platysoma filiforme*	His	Anob	*Hemicoelus nitidus*	2	64
100	*Plegaderus caesus*	His		*Oligomerus brunneus*	14	87
101	*Prionocyphon serricornis*	Hel		*Xestobium rufovillosum*	3	130
102	*Prionychus ater*	Alle	Dor	*Dorcatoma agenjoi*	13	52
103	*Prionychus fairmairei*	Alle		*Stagetus elongatus*	2	117
104	*Probaticus anthracinus*	Ten	Mes	*Rhamna semen*	36	111
105	*Probaticus granulatus*	Ten	Scr	*Anaspis ruficollis*	6	7
106	*Procraerus tibialis*	Ela		*Anaspis regimbarti*	12	8
107	*Protaetia cuprea*	Cet		*Scraptia testacea*	64	114
108	*Protaetia mirifica*	Cet	Scy	*Scydmaenus cornutus*	2	115
109	*Protaetia opaca*	Cet		*Stenichnus collaris*	3	118
110	*Pseudocistela ceramboides*	Alle	Sil	*Ahasverus advena*	1	3
111	*Rhamna semen*	Mes		*Oryzaephilus surinamensis*	3	92
112	*Rhizophagus unicolor*	Mon		*Uleiota planata*	2	129
113	*Rhyncolus reflexus*	Cur	Ten	*Corticeus fasciatus*	1	30
114	*Scraptia testacea*	Scr		*Dendarus pectoralis*	10	45
115	*Scydmaenus cornutus*	Scy		*Eledonoprius armatus*	7	57
116	*Soronia oblonga*	Nit		*Nalassus laevioctostriatus*	6	85
117	*Stagetus elongatus*	Dor		*Palorus depressus*	11	94
118	*Stenichnus collaris*	Scy		*Probaticus anthracinus*	26	104
119	*Stenohelops montanus*	Ten		*Probaticus granulatus*	1	105
120	*Stictoleptura fontenayi*	Cer		*Stenohelops montanus*	1	119
121	*Stictoleptura trisignata*	Cer		*Tenebrio punctipennis*	34	124
122	*Symbiotes gibberosus*	End	Alle	*Isomira hispanica*	10	70
123	*Temnochila caerulea*	Trogo		*Mycetochara linearis*	16	82
124	*Tenebrio punctipennis*	Ten		*Mycetochara quadrimaculata*	60	83
125	*Tenebroides maroccanus*	Trogo		*Prionychus ater*	28	102
126	*Trichoferus fasciculatus*	Cer		*Prionychus fairmairei*	10	103
127	*Troglops furcatus*	Mala		*Pseudocistela ceramboides*	25	110
128	*Trox scaber*	Trogi	Trogi	*Trox scaber*	2	128
129	*Uleiota planata*	Sil	Trogo	*Temnochila caerulea*	2	123
130	*Xestobium rufovillosum*	Anob		*Tenebroides maroccanus*	2	125
131	*Xyleborinus saxesenii*	Sco	Zoph	*Colobicus hirtus*	1	28
132	*Xyleborus dryographus*	Sco		*Colydium elongatum*	5	29
133	*Xyleborus monographus*	Sco		*Endophloeus marcovichianus*	12	58

Columns are ordered in two different ways to facilitate the data search

Ade (Aderidae), Biph (Biphyllidae), Bup (Buprestidae), Cer (Cerambycidae), Cet (Cetoniidae), Cii (Ciidae), Cle (Cleridae), Cry (Cryptophagidae), Cur (Curculionidae), Pla (Curculionidae: Platypodinae), Sco (Curculionidae: Scolytinae), Das (Dasytidae), Der (Dermestidae), Dyn (Dynastidae), Ela (Elateridae), End (Endomychidae), Euc (Eucinetidae), Hel (Helodidae/Scirtidae), His (Histeridae), Lae (Laemophloeidae), Luc (Lucanidae), Mal (Malachiidae), Mel (Melandryidae), Mon (Monotomidae: Rhizophaginae), Myc (Mycetophagidae), Nit (Nitidulidae), Oed (Oedemeridae), Anob (Ptinidae: Anobiinae), Dor (Ptinidae: Dorcatominae), Mes (Ptinidae: Mesocoleopodinae), Scr (Scraptiidae), Scy (Scydmaenidae), Sil (Silvanidae), Ten (Tenebrionidae), Alle (Tenebrionidae: Alleculinae), Trogi (Trogidae), Trogo (Trogositidae), Zoph (Zopheridae: Colydiinae)

(Ranius 2002b, Quinto et al. 2014) and for some saproxylic mites (Taylor and Ranius 2014). A first explanation could be related to differences in the microclimate at different heights that may influence the decay of wood (Ranius 2002b). Another possible explanation is that bird nests are more frequent at greater heights (Nilsson 1984) and some

Table 3 Results from the GLM analyses about the effect of physical and biological variables on community distribution

Variable	Abundance			Species richness		
	df	x^2	*p* value	*df*	x^2	*p* value
Height	1	162.02	**0.04**	1	5.879	0.24
OMVol	1	126.96	0.06	1	66.390	**<0.001**
CET	1	165.12	**0.03**	1	35.221	**<0.01**
CER	1	124.81	0.07	1	33.981	**<0.01**

Significant differences in bold

Height, Height of the hollow; WMVol, wood mould volumen; CET, presence of Cetoniidae larval activity; *CER*, presence of *Cerambyx* larval activity

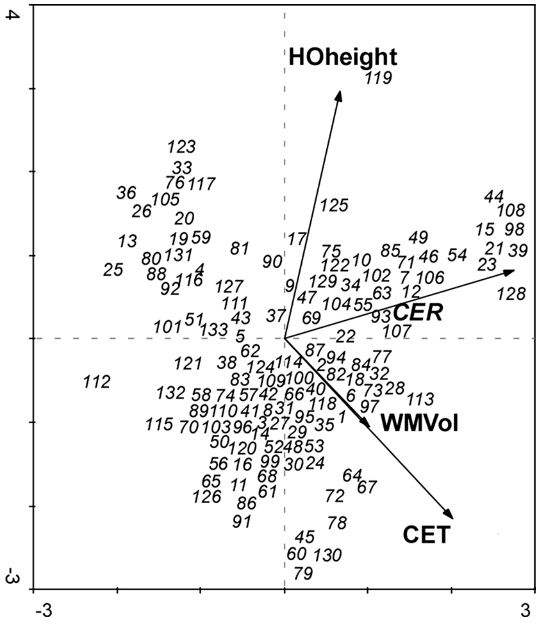

Fig. 1 Canonical correspondence analysis (CCA) ordination diagram showing the distribution of species with respect to the environmental variables (*arrows*). Height: Height of the hollow, *CER*: presence of *Cerambyx* species activity (larval galleries) in the hollow, CET: presence Cetoniidae activity (larval feces) in the hollow, WMVol: Wood mould volume. Species represented by each number are shown in Table 2

species may prefer hollows containing nests, as the nutrient content might be higher. And a third possibility is that wood mould composition varies in its percentage of soil and litter, depending on distance to the ground (Taylor and Ranius 2014). Trophic habits of the assemblage most influenced by hollow height could help us to confirm the previous hypotheses, and although all trophic habits were represented, most of the species (60 %) influenced by hollow height were highly dependent on substrate features, such as saprophagous and saproxylophagous beetles. Among them, 30 % of the species were saprophagous (Dermestids), which some of them, are known to be associated with vertebrate and invertebrate nests (Snyder et al. 1984); 30 % were saproxylophagous (belonging to Cetoniidae, Curculionidae and Tenebrionidae), for which decaying-state wood and amount of litter should be important. Finally, another 30 % were predators, which are expected to be more influenced by the presence of prey as well as other abiotic variables, such as humidity (Dajoz 2000). In agreement with Taylor and Ranius (2014), the effect of hollow height on saproxylic assemblages seems to be related to changes in qualitative features of wood mould due to the hollow's height.

Continuing with physical variables, wood mould accumulated in tree hollows provides a continuous supply of dead wood to a wide spectrum of saproxylic (dead wood dependent) invertebrates and fungi that constitute a large part of woodland biodiversity (Speight 1989; Stokland et al. 2012). In general, it is said that larger volumes of wood mould maintain higher saproxylic diversity, however, empiric correlations are scarce and normally refer to endangered species (Ranius and Nilsson 1997; Ranius and Wilander 2000). Here, we demonstrate that wood mould volume affects beetle richness (Table 3) and that is important for a large beetle assemblage (Fig. 1). Moreover, this physical variable seems to be closely related to the presence of Cetoniidae activity (Fig. 1); in fact, cavities with presence of this ecosystem engineer species were richer in wood mould than those where the species was absent (Fig. 2). Cetoniidae larvae feed on the walls and also on accumulated litter, producing a high quantity of frass that remains in the cavity for a long time (Micó and Galante 2003; Micó et al. 2011), which increases the volume of substrate inside the cavity. Beetle assemblages influenced by volume of wood mould with presence of cetonid faeces (WMVol + CET) were mainly substrate dependent, such as saprophagous and saproxylophagous (53 %), followed by predators (34 %). Among the group of species most influenced by WMVol + CET, we found the endangered hollow specialist *Limoniscus violaceus*, which is known to inhabit large cavities (Gouix et al. 2012). In addition, *Limoniscus* larvae seem to prefer organically-rich wood mould, which has been enriched partly by nutrients derived from dead animals (Gouix et al. 2012) and, as we shall discuss below, nutrients derived from cetonid faeces could also favour this endangered species, enhancing yet again the importance of species interactions on biodiversity (see Sánchez-Galván et al. 2014).

The presence of Cetoniidae is not the only biotic factor affecting physical variables; in fact, the action of *Cerambyx* larvae also increases the amount of dead wood on the trees (Buse et al. 2008). Our results show that hollows with presence of *Cerambyx* species also hosted greater wood

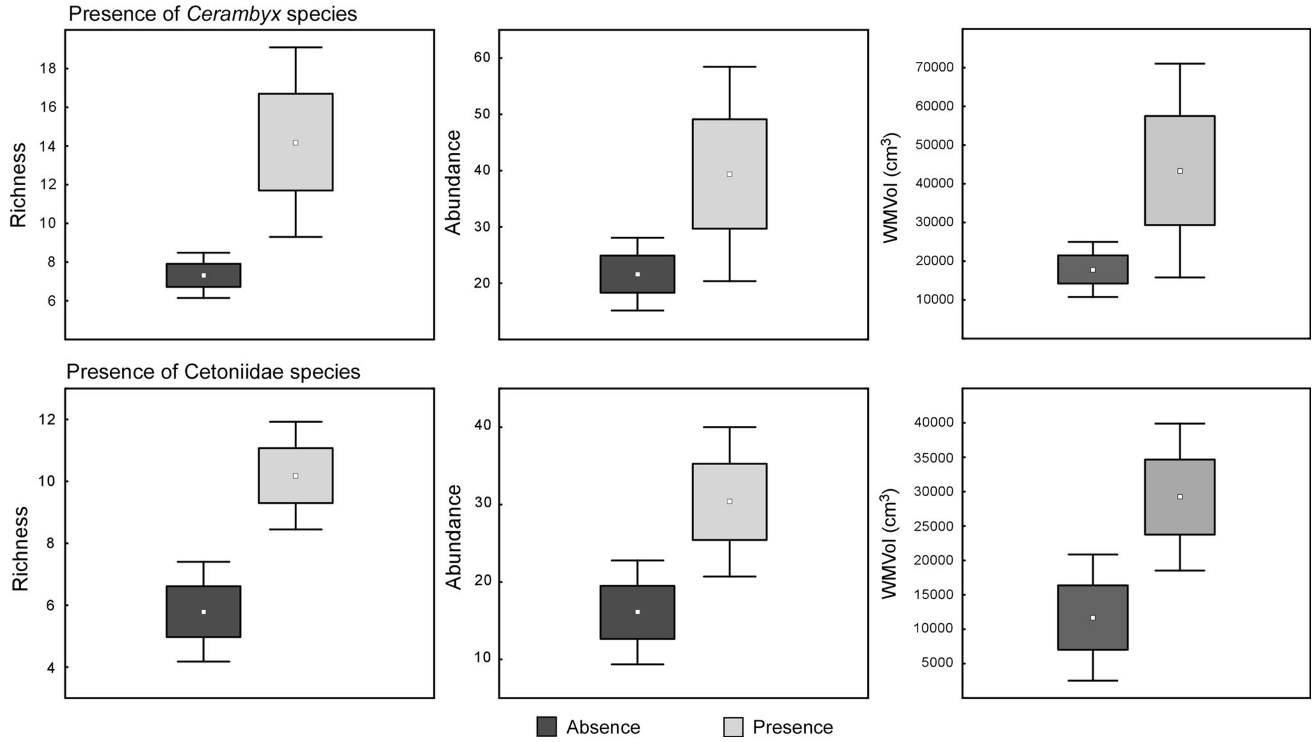

Fig. 2 Comparisons of species richness, abundance and wood mould volume between hollows with presence or absence of *Cerambyx* activity and Cetoniidae activity based on Kruskal–Wallis and subsequent posthoc test. *Square* mean; *box* mean ± SE; *bars* mean ± 1.95 × SE

Table 4 Differences in chemical variables between tree hollows with presence or absence of facilitator species based on Krukal–Wallis test

Chemical variable	CET	*CER*
C	$H = 0.12$, $No = 34$, $p > 0.05$	**$H = 7.79$, $N = 34$, $p < 0.05$**
C_a	$H = 0.01$, $No = 34$, $p > 0.05$	**$H = 4.12$, $N = 34$, $p < 0.05$**
P	$H = 1.17$, $No = 34$, $p > 0.05$	$H = 1.51$, $N = 34$, $p > 0.05$
N	$H = 0.78$, $No = 34$, $p > 0.05$	$H = 0.77$, $N = 34$, $p > 0.05$
C/N	$H = 0.59$, $No = 34$, $p > 0.05$	$H = 0.02$, $N = 34$, $p > 0.05$
C/P	$H = 2.59$, $No = 34$, $p > 0.05$	$H = 0.28$, $N = 34$, $p > 0.05$

Significant differences in bold

H, Kruskal–Wallis index; No, number of samples; C, total carbon; C_a, assimilable carbon; P, phosphorous; N, nitrogen; CET, presence of Cetoniidae larval activity; *CER*, presence of *Cerambyx* larval activity

mould volume (Fig. 2), however, although *Cerambyx* species affects species richness also (Table 3), the beetle assemblage affected by this biotic variable was very different to that affected by WMVol + CET (see Fig. 1). The most striking fact was that trophic habit percentages were inverted in this case, with predators being 50 % of the species, and only 28 % saproxylophagous-saprophagous. In this way, the beetle assemblage associated with the presence of *Cerambyx* was dominated by predators (i.e. *Procaerus tibialis*, or the Near Threatened *E. ferrugineus* and *E. montandoni*), which, in agreement with Buse et al. (2008), probably use *Cerambyx* galleries for hunting. Moreover, *Cerambyx* galleries may act as entrances and habitats for saprophagous and saproxylophagous species, such as the Vulnerable cetonid *Protaetia mirifica*, as has also been demonstrated previously for the Cetonid *Osmoderma eremita*, or for some Tenebrionids (Palm 1959; Buse et al. 2008).

The studied biotic agents are not only able to modify the substrate physically, previous studies showed that the cetonid larvae modify it chemically by feeding; cetonid larval faeces have been demonstrated to be richer in N and P than the substrate they feed on (Jönsson et al. 2004; Micó et al. 2011). Moreover, Sánchez-Galván et al. (2014) showed that a substrate enriched with cetonid larval faeces improved the development and fitness of the saproxylic

Table 5 Spearman rank correlations coefficients and significance for pairwise comparisons of chemical variables with species richness and abundance and wood mould volume

Chemical variable	Species richness	Abundance	WMVol
C	$\rho = 0.12$, $p > 0.05$	$\rho = 0.23$, $p > 0.05$	$\rho = 0.11$, $p > 0.05$
C_a	$\boldsymbol{\rho = 0.41, p < 0.05}$	$\boldsymbol{\rho = 0.46, p < 0.05}$	$\rho = 0.32$, $p > 0.05$
P	$\boldsymbol{\rho = 0.49, p < 0.05}$	$\boldsymbol{\rho = 0.41, p < 0.05}$	$\boldsymbol{\rho = 0.48, p < 0.05}$
C/P	$\boldsymbol{\rho = -0.39, p < 0.05}$	$\rho = -0.33$, $p > 0.05$	$\boldsymbol{\rho = -0.43, p < 0.05}$
N	$\rho = 0.27$, $p > 0.05$	$\rho = 0.28$, $p > 0.05$	$\rho = 0.24$, $p > 0.05$
C/N	$\rho = -0.13$, $p > 0.05$	$\rho = -0.2$, $p > 0.05$	$\rho = -0.2$, $p > 0.05$

Significant values in bold

C, Total carbon; C_a, assimilable carbon P, Phosphorous; N, Nitrogen. WMVol, Wood mould volume

syrphid (Diptera: Syrphidae) *Myathropa florea* (L.) However, although it has been demonstrated that faeces are richer in nutrients than substrate when analysed separately, tree hollows with presence of faeces were not always significantly richer in nutrients than those without (see Table 4). The effect of faeces' accumulations concentrating nutrients inside tree hollows probably becomes blurred within the effect of decomposer organisms, such as other invertebrates, fungi and bacteria, which are the principal wood decomposers (Stokland et al. 2012). It sounds reasonable that, although cetonid larvae modify the substrate chemically, producing a residue richer in nutrients than the original substrate and with an organic structure that is easier to decompose for other organisms (Micó et al. 2011), it cannot explain the chemical composition of the tree hollow wood mould by itself.

Physical modification of tree hollows by *Cerambyx* larvae is clear, and a physiological modification of trees has been suspected (see Buse et al. 2008); both actions could explain that cavities with *Cerambyx* were richer than those without (Fig. 2). Moreover, a chemical transformation of the substrate could also be deduced by the fact that hollows with *Cerambyx* presence were significantly richer in C and C_a (see Table 4) than those without *Cerambyx*. A suitable explanation is that *Cerambyx* galleries are powder-filled as a result of a mechanical action of larvae that disrupts the "lignin barrier" by grinding the wood very finely, consequently favouring mechano-biochemical decomposition of solid wood (Kirk and Cowling 1984).

We confirm that both biotic elements considered here behave as ecosystem engineers that act as facilitator species [see also Buse et al. (2008) and Sánchez-Galván et al. (2014)], and although their presence is associated, in general, with higher species richness (Fig. 2), each one affects a different beetle assemblage that included hollow-dependent endangered species in both cases (Fig. 1).

By examining wood mould quality in depth, we found that some can give us valuable information about their associated beetle diversity. In this way, P and C_a content were positively correlated with both beetle richness and abundance (Table 5), allowing us to deduce that both chemical elements could, to some extent, indicate the beetle activity inside the hollow. Among the total content in C, a higher proportion of C_a in hollows with more beetles is a clear consequence of a higher activity of decomposition in the tree hollow, as stated above. This higher activity of decomposition seems to be related to direct and/or indirect effect of beetle assemblage.

Tree hollows are very special microhabitats where many organisms, not only beetles, are able to fix atmospheric N (see Jönsson et al. 2004; Micó et al. 2011), which could mean that vegetal decomposition here is more limited by P than by N. Moreover, P is much less soluble than N and does not have gas forms (Juárez and Sánchez 1996), therefore it is feasible that P concentrates in hollows over time, and this could also explain that higher wood mould volume also had a higher P content (see Table 5).

We can conclude that physical, biotic and chemical features characterising a tree hollow are all informative. However, these variables are not totally independent, and biotic ones affect both physical and chemical features to some extent, in a direct or in an indirect way. These results should encourage us to investigate more about interspecific interactions in tree hollows and species functionality as a key point.

In agreement with other studies (i.e. Ranius and Nilsson 1997; Ranius and Wilander 2000; Quinto et al. 2014), we show that wood mould volume could act as a good surrogate for saproxylic beetle diversity; in addition, our results show that presence of Cetoniidae faeces or *Cerambyx* galleries (both easily observable in the field) could be used also as good diversity indicator in tree hollows, even more if both biotic elements co-occur as each affect to different assemblages (Fig. 1). Finally, the performance of chemical analysis to measure C_a and P contents as a possible surrogate for beetle activity could become a useful tool in functional diversity studies and consequently for conservation in the future. However, chemical correlation with beetle diversity is still weak and many other organisms should be acting directly or indirectly on substrate quality, for this reason an extension of this work to other forest types and other taxonomic groups, including fungi, would be desirable to confirm our results with beetles as indicator of saproxilic quality.

Acknowledgments We are very grateful to the staff of the four protected areas for their help during the study. We would also like to thank all our colleagues for their invaluable help with the taxonomy and biology of the studied groups: H Brustel, L Chékir, M Kadej, P Leblanc, JL Lencina, G Liberti, MJ López, T Noblecourt, JC Otero, O Rose, F Soldati, A Verdugo, P Vien, A Viñolas, JL Zapata. Ana Paola Falcó for the statistical Support. Kate Burke helped with the English grammar. Financial support was provided by “Ministerio de Ciencia e Innovación” (CGL2011-23658), “Ministerio de Economia y Competitividad (CGL2012-31669)” and by “Generalitat Valenciana” (PROMETEO/2013/03412 Project).

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