

Saproxylic Beetle Assemblage Selection as Determining Factor of Species Distributional Patterns: Implications for Conservation

A. García-López,^{1,2} E. Galante² and E. Micó²

¹Laboratorio de Ecología de Ambientes Fragmentados, Universidad de Chile. Av. Santa Rosa 11735, La Pintana, Santiago, Chile,

²Centro Iberoamericano de la Biodiversidad (CIBIO), Universidad de Alicante, Spain (alejandra.garcia@ua.es; galante@ua.es; e.mico@ua.es) and ³Corresponding author, e-mail: alejandra.garcia@ua.es; e.mico@ua.es

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Abstract

The knowledge of the distributional patterns of saproxylic beetles is essential for conservation biology due to the relevance of this fauna in the maintenance of ecological processes and the endangerment of species. The complex community of saproxylic beetles is shaped by different assemblages that are composed of species linked by the microhabitats they use. We evaluate how different the species distribution patterns that are obtained can be, depending on the analyzed assemblage and to what extent these can affect conservation decisions. Beetles were sampled using hollow emergence and window traps in three protected areas of the Iberian Peninsula. Species richness, composition, and diversity turnover were analyzed for each sampling method and showed high variation depending on the analyzed assemblage. Beta diversity was clearly higher among forests for the assemblage captured using window traps. This method collects flying insects from different tree microhabitats and its captures are influenced by the forest structuring. Within forests, the assemblages captured by hollow emergence traps, which collect the fauna linked to tree hollows, showed the largest turnover of species, as they are influenced by the characteristics of each cavity. Moreover, the selection of the forest showing the highest species richness strongly depended on the studied assemblage. This study demonstrates that differences in the studied assemblages (group of species co-occurring in the same habitat) can also lead to significant differences in the identified patterns of species distribution and diversity turnover. This fact will be necessary to take into consideration when making decisions about conservation and management.

Key words: hollow emergence trap assemblage, *Quercus pyrenaica*, species composition, species richness, window trap assemblage.

The understanding of the distributional patterns of saproxylic species is considered an important challenge for conservation biology (Stokland *et al.* 2012, Grove 2002). Saproxylic beetles are one of the main components of forest fauna due to their high diversity and because they are involved in important ecosystem services, such as breaking down deadwood and recycling nutrients (Dajoz 1998, Buse *et al.* 2009, Micó *et al.* 2011, Stokland *et al.* 2012, Ulyshen 2012). At the same time, they are one of the most threatened animal assemblages in European forests (Speight 1989, Nieto and Alexander 2010). They constitute a complex community formed by many species that show different trophic habits depending on different microhabitats and that interact among themselves and with the substrate in different ways (Boulanger *et al.* 2010, Andersson *et al.* 2012, Quinto *et al.* 2012, Gutowski *et al.* 2014).

This saproxylic beetle community is complex, as many species are specific to some microhabitats (Siitonen 2001, Ranius 2002,

McGeoch *et al.* 2007, Winter and Möller 2008, Brunet and Isacson 2009, Stokland *et al.* 2012), some have low dispersal ability (Thomas 2000, Ranius and Hedin 2001, Ewers and Didham 2006), and some others are small and cryptic (Bouget *et al.* 2008); this makes the collection of samplings of the whole community challenging in practice. As a consequence, most studies have been focused on some specific assemblages that depend on one or a few microhabitats (Alinvi *et al.* 2007, Brunet and Isacson 2009, Horak and Pavlicek 2013, Müller *et al.* 2013a). The chosen sampling method is ultimately the factor that defines the sampled assemblage since, depending on its characteristics, it will capture species coming from different microhabitats (Quinto *et al.* 2013, Redolfi *et al.* 2014) and it is known that distinct saproxylic microhabitats harbor assemblages that vary in species composition (Hjältén *et al.* 2012, Stokland *et al.* 2012). In this regard, several studies had already revealed that different sampling methods capture different saproxylic beetle

species (García-López *et al.* 2010, Ferro *et al.* 2012, Quinto *et al.* 2013). However, the influence of these compositional differences on the obtained data about the species distribution and the diversity turnover patterns has not been analyzed. In this regard, the objective of this study is not to compare the diversity among different study areas or the effectiveness of different types of traps, but to compare the pattern of species distribution resulting from different species assemblages through the study areas. Taking into account that depending on the characteristics of the microhabitats, the related assemblages will also vary in the environmental requirements of species and in their dispersal ability, we can predict that not only the species captured by each sampling method will be different, but their distributional patterns (beta diversity) within and among forests will differ, as well. This is a poorly explored issue that could be critical, as its results could change not only our ideas about the distribution of this essential fauna in forests, but also the information that we consider is required in order to be able to reach conclusions about management and conservation of forests based on saproxylic beetles (Gibb *et al.* 2013). Moreover, the different distributional patterns of assemblages could act as proxies of the microhabitat diversity distributions, a key aspect in forest conservation and management (Winter and Möller 2008, Gossner *et al.* 2013b, Müller *et al.* 2013b).

In this study, two sampling methods commonly used for capturing saproxylic beetles, window traps (henceforth WT) and hollow emergence traps (henceforth ET), were selected to compare the distributions among different forests of the saproxylic assemblages sampled by each one of them. WT (see 'Materials and Methods' section for a description of the trap) are an interception sampling method that efficiently reflect beetle diversity at the stand level (Bouget *et al.* 2008, Sverdrup-Thygeson and Birkemoe 2009, Heikkala *et al.* 2015) mainly catches flying adults (Saint-Germain *et al.* 2006, Alinvi *et al.* 2007) arriving from a wide range of woody resources within the woodland environment such as dead wood on the ground (e.g., snags, logs) and from microhabitats of the trees (e.g., decaying branches, bark, or tree hollows) (Ranius and Jansson 2002, Sverdrup-Thygeson and Birkemoe 2009). Hollow ET are considered a highly effective method to capture species linked to tree hollows as the main microhabitat (Goux and Brustel 2012, Quinto *et al.* 2013). They allow recording saproxylic species shortly after their emergence from immature stages and provide accurate information about the species inhabiting these microhabitats (see 'Materials and Methods' section for a description of the trap) (Bouget and Brustel 2009, Quinto *et al.* 2013). The compositional differences of these two assemblages (WT and ET assemblage) have been proved; Quinto *et al.* (2013) and Coccia *et al.* (2014) found that in the same forest areas, a high number of species appeared to be exclusively associated with one type of trap. This underlies the fact that these two assemblages exhibit a particular associated diversity and constitute separate entities. However, as mentioned, the influence of these compositional differences on the diversity distribution of this fauna has not been studied.

Hollow trees provide long-lasting resources and a stable abiotic environment (Chiari *et al.* 2012, Müller *et al.* 2013a), and saproxylic species adapted to them appear to have low dispersal propensity as compared with species associated with other microhabitats as snags, logs, bark, dying branches, etc. (Stokland *et al.* 2012). This fact, along with the mentioned bias of WT related to flying adults, suggests that species belonging to the assemblages captured by WT are expected to show larger dispersions than those from the assemblage captured by ET. In this context, we might predict that diversity associated with ET will show higher differences among forests

than that associated with WT, whose species will be more widely distributed. However, it also could be possible that tree hollow variables affecting species distribution (i.e., hollow height, hollow volume, wood mold volume) are more homogeneous than those influencing species from WT assemblage (e.g., density of trees, diversity and volume of dead wood, and canopy and brushwood coverage). This would lead to the opposite pattern in which assemblages inhabiting tree hollows from different forests will be more similar than those under the influence of the forest variables. Finally, a third scenario could be that in which both mentioned possibilities were true and their effects were balanced, producing similar diversity patterns among both assemblages.

The objective of this study is to determine whether differences in the studied assemblages can lead to deep differences among the identified patterns of species distribution and diversity turnover (beta diversity). Regarding this, the following questions are raised: 1) Are the species from ET assemblages and WT assemblages distributed among forests following similar diversity patterns? 2) If any differences are found, to what extent can they affect the associated conservation management decisions?

Materials and Methods

Study Area

Fieldwork was carried out in Mediterranean forests dominated by *Quercus pyrenaica* Willd. and located in three protected areas of the Iberian Peninsula, as representative of the Mediterranean woodlands and its heterogeneity. The tree species *Q. pyrenaica* is a western Mediterranean and Atlantic species, located from south-western France to northern Morocco (DGCN 2006). The significant surface occupied by *Q. pyrenaica* and the threats these forests face (risk of fire and degradation caused by the progressive abandonment of the traditional management) highlight the need to increase the understanding of these stand dynamics (Corcuera *et al.* 2006, Salomón *et al.* 2013).

The Biological Reserve 'Campanarios de Azaba' (henceforth *Camp*) (LIFE/E/NAT/000762) is located in the southwest of the Salamanca province in western Spain (40° 29' 60" N, 6° 46' 50" W). The reserve has 522 ha, and its altitude is 800 m. The average annual precipitation is 563 mm, and temperatures range from -3 to 35°C (annual average around 12°C) (Llorente-Pinto 2011). The landscape is a typical 'dehesa', characterized by the presence of scattered trees in savannah-like open woodland (Ramírez-Hernández *et al.* 2014), and it is dominated by *Q. pyrenaica* and *Quercus rotundifolia* Lam coexisting with some individuals of *Quercus faginea* Lam (Sánchez-Martínez *et al.* 2013). This ecosystem is included in the Habitat Directive (Annex I 6310) and also in the Natura 2000 network (www.natura.org), due to its high value at a European level as a cultural landscape and also as a biodiversity reservoir (Díaz *et al.* 1997). The study area has been a private protected reserve since 2009 (www.fnyh.org/proyectos-life/reserva-campanarios-azaba/) and has recently been cataloged as the first entomological reserve in Spain (www.entomologica.es).

Cabañeros National Park (henceforth *Cab*) is located in central Spain (Ciudad Real province) (39° 23' 470" N, 4° 29' 140" W). The altitude varies from 560 to 1,448 m. The annual rainfall is varied between 750 and 500 mm. The average annual temperature ranges from 12.9 to 15.6°C, and the average monthly temperature fluctuates between 3.9 and 23.8°C (Vaquero 1997). The park features 40,856 ha of well-preserved Mediterranean ecosystems including a diverse range of woodlands (Vaquero 1997). *Q. pyrenaica*

stands appear scattered through the park, with a total extension of 634 ha. Signs of ancient pollard activity are not noticeable.

Sierra de las Quilamas Natural Area (henceforth *Quil*) is located in the south of the Salamanca province in western Spain (6° 05' 15" W, 40° 30' 10" N). The area has an extension of 11,100 ha and an altitude between 600 and 1,400 m. The average annual temperature is ~13.7°C, and the average monthly temperature fluctuates between 5.2 and 24.5°C. The average annual precipitation is 126 mm. It appears in the proposal of Sites of Community Importance (92/43/CEE, code ES4150108-Quilamas). *Q. pyrenaica* is the dominant tree species. It is mixed with *Erica* spp. (L.) and *Arbutus unedo* (L.) in the lower parts exposed to sunlight and with *Castanea sativa* Mill. and *Ilex aquifolium* (L.) in the shady parts of the hillsides. Former management of pollarding is reflected in the presence of tree hollows, although no management is currently performed.

Beetle Sampling and Species Identification

Adults of saproxylic insects were sampled using hollow ET and WT, all of them placed on *Q. pyrenaica* trees. Each ET consisted of a black acrylic mesh that completely seals the tree hollow and a catcher pot attached to the mesh (Gouix and Brustel 2012). Each WT consisted of two transparent sheets lying over a funnel and a collection container (Bouget *et al.* 2008). Traps were hung from live trees at 1.5–2 m above the ground. In both types of traps, ethylene glycol or propylene glycol was used as a preservative. A total of 59 ET and 43 WT distributed in the three selected sites were used (Table 1). Selected stands are at similar altitudes (*Quil*: 1,100 m, *Cab*: 800 m, *Camp*: 800 m) and have similar tree mean diameter (*Quil*: 65.74 cm, *Cab*: 63.78 cm, *Camp*: 61.18 cm) to avoid biased data for comparison. Traps were checked monthly for 7 months in the case of ET and for 8 months in the case of WT (Table 1). The selection of the sampling period used for each type of trap looked to maximize the sampling coverages, to include the months when the maximum levels of diversity are found.

Nomenclature is according to Fauna Europaea (<http://www.fauna-eu.org/>), Bouchard *et al.* (2011), and the Catalogue of Palaearctic Coleoptera (Löbl and Smetana 2004, 2006, 2007, 2008, 2010). We had the support of European specialists in saproxylic beetles for species identification (see 'Acknowledgments' section). The specimens were deposited in the Entomological Collection of the University of Alicante (Spain).

Data Analysis

Inventory completeness was calculated as the percentage of observed species for each sampling site and for the entire study with respect to the number of species predicted by the estimators ACE and Chao1, by using EstimateS 7.5.0 (Colwell 2005). The non-parametric estimators ACE and Chao1 are highly accurate independently of the degree of data aggregation, and satisfy the requirements for a robust estimator (Hortal *et al.* 2006).

In order to investigate the patterns of beta diversity (turnover in species composition) among sites and trap assemblages, the Jaccard index of similarity was calculated as an inverse measured of this turnover (Jaccard 1912, Magurran 1988). Using the resulting similarity matrix, we carried out ordinations of samples using non-metric multidimensional scaling (NMDS) and an analysis of similarity (ANOSIM) (Faith *et al.* 1987) to test the significance of the differences. ANOSIM is a non-parametric method producing a permutation statistic R, which is an absolute measure of distance between the groups. Positive and large values (up to 1) of R indicate low similarity between groups, while low values (to 0) indicate high similarity

Table 1. Number of traps and sampling period in each one of the three selected locations

Site	ET		WT	
	Nº of traps	Period of sampling	Nº of traps	Period of sampling
<i>Quil</i>	27	May–Nov 2012	17	Feb–Sep 2013
<i>Cab</i>	22	May–Nov 2009	14	Feb–Sep 2005
<i>Camp</i>	10	May–Nov 2010	12	Feb–Sep 2011

ET, hollow emergence trap; WT, window trap; *Quil*, Sierra de las Quilamas Natural Area; *Cab*, Cabañeros National Park; *Camp*, Biological Reserve 'Campanarios de Azaba'.

between groups. The significance level is calculated by permutations of sites among groups (Sackmann 2006). The permutation statistic R was used to compare the degree of similarity among assemblages. The values of the Jaccard index between traps within the same forest were also used to calculate the percentage of these comparisons in each site that showed composition similarity values lower than 20%. This allowed us to check whether assemblages captured by ET in a single site (data from each ET, ergo linked to a particular tree hollow) differed more among themselves than each sample of WT assemblages within a forest (data from each WT). Analysis of similarity, ANOSIM, and NMDS were performed with PRIMER (Clarke and Gorley 2006).

We analyzed the existence of significant differences in species richness among sites, attending to the data of the saproxylic assemblages captured by WT on one hand and the data of the saproxylic assemblages captured by ET on the other hand. Due to the lack of normality in the data, we used the Kruskal-Wallis test and Bonferroni post hoc tests to compare the species richness between sites. Kruskal-Wallis tests were done with STATISTICA (StatSoft, Inc. 2007).

Results

A total of 7,781 individuals belonging to 53 families, 186 genera, and 290 species were collected (Supp Table 1 [online only]). The number of species and individuals varied at each site and for each assemblage (Table 2). For the WT assemblages, *Quil* was the site showing the highest number of species (196) and individuals (2,961), while *Cab* showed the lowest number of individuals (826) and *Camp* showed the lowest number of species (92) (Table 2). In the case of the ET assemblages, *Cab* was the site showing the highest number of species (89) and individuals (1,244), and *Camp* showed the lowest number of species (59) and individuals (440) (Table 2). In all cases, the species richness estimators (ACE, Chao1) for the sampling sites suggested quite reliable inventories (Table 2).

Results from ANOSIM showed that species composition varied significantly among the studied areas for both assemblages, with these differences being higher for the WT assemblages ($R = 0.628$, $P < 0.001$) than for the ET assemblages ($R = 0.298$, $P < 0.001$). This pattern is confirmed in the pairwise tests, where differences between WT assemblages were higher than those between ET assemblages (Table 3). Moreover, these differences in composition among areas were always significant in the case of the WT assemblages, but not in the case of ET assemblages, where analysis of ANOSIM did not find any significant differences between the closest sites *Quil* and *Camp* (Table 3).

These results are supported by the NMDS where, in addition to a clear separation of the fauna from the two analyzed assemblages,

Table 2. Observed species richness (Sobs), abundance, number of singletons (observed species represented by a single individual) and doubletons (observed species represented by two individuals) and percentages of inventory completeness for each site and assemblage

Assemblage sampled by WT						
Site	Sobs	Abundance	Singletons	Doubletons	ACE (%)	Chao 1 (%)
Total	261	5,581	69	38	78	81
<i>Quil</i>	196	2,961	61	24	74	73
<i>Cab</i>	108	826	41	19	70	72
<i>Camp</i>	92	1,794	27	15	79	81
Assemblage sampled by ET						
Total	134	2,200	36	19	77	81
<i>Quil</i>	64	516	13	10	91	90
<i>Cab</i>	89	1,244	25	12	78	79
<i>Camp</i>	59	440	16	9	84	83

ET, hollow emergence trap; WT, window trap; *Quil*, Sierra de las Quilamas Natural Area; *Cab*, Cabañeros National Park; *Camp*, Biological Reserve 'Campanarios de Azaba'.

Table 3. Values of permutation statistic R and significance from the pairwise tests of ANOSIM analysis among sites assemblages

Pairwise test	Assemblage sampled by WT		Assemblage sampled by ET	
	Statistic R	P-value	Statistic R	P-value
<i>Quil-Camp</i>	0.537	<0.05	0.108	0.92
<i>Quil-Cab</i>	0.619	<0.05	0.346	<0.05
<i>Camp-Cab</i>	0.755	<0.05	0.437	<0.05

Significant values in bold. *Quil*, Sierra de las Quilamas Natural Area; *Cab*, Cabañeros National Park; *Camp*, Biological Reserve 'Campanarios de Azaba'.

the higher differences among the three selected WT assemblages than among the three ET assemblages are clearly evident (Fig. 1).

We found important differences between assemblages when we observed the values of the Jaccard index between traps within the same site when looking for similarities lower than 20%. Although the number of traps with low similarity varied depending on the site in both types of assemblage, the percentages were much lower for the WT assemblages (*Quil*: 41.18%, *Cab*: 26.37%, *Camp*: 18.18%) than for the ET assemblages (*Quil*: 87.18%, *Cab*: 67.96%, *Camp*: 51.11%).

Beetle species richness varied significantly between sites, both for the WT assemblages and for the ET assemblages (K-W: WT assemblages $H = 10.5$, $n = 43$, $P < 0.05$; ET assemblages $H = 19.2$, $n = 59$, $P < 0.05$). Noteworthy is that post hoc tests showed that the pattern of species richness among sites varied significantly depending on the analyzed assemblage (Fig. 2). Although *Quil* appeared to be the poorest site in number of species regarding the ET assemblages, it was the richest regarding the data from the WT assemblages.

Discussion

This study shows that the results about saproxylic beetle species distribution in which we base important decisions on conservation and forest management could be masked by the assemblage that we are analyzing. The results here highlight the deep differences of

saproxylic beetle diversity distribution obtained by two commonly used methods, window traps and hollow emergence traps. Both composition and species richness of the studied group depend on the analyzed trap assemblage and, therefore, so do the detected patterns of diversity turnover (beta diversity) (Figs. 1 and 2).

Beta diversity is considered one of the most important parameters in the understanding of diversity and in conservation (Crist *et al.* 2003, Hirao *et al.* 2007, Müller and Gofner 2010), and saproxylic beetles are not an exception. Many studies have emphasized the importance of compositional heterogeneity among sites for total biodiversity in this group and the value of its knowledge as essential for conservation purposes (Gossner *et al.* 2013a, Micó *et al.* 2013, Müller *et al.* 2013b). The present results have shown that the values of diversity turnover (in this study measured as change in species composition) may be highly different depending on the sampling method used, since it acts in a selective way on the biology of the species.

Due to the high stability of tree hollows as microhabitats, inhabiting saproxylic species seem to have lower dispersions than those associated with other microhabitats such as snags, logs, etc. (Stokland *et al.* 2012). Fauna inhabiting tree hollows include even non-flying beetles, with very low dispersal ability. This fact would lead us to predict higher differences among forests for this fauna than for the species that are part of the assemblages captured by WT. However, the opposite pattern has been found (Fig. 1), and results show closer similarities for the ET assemblages among forests than those for the WT assemblages. This, together with the lower similarity values within forests for ET assemblages, could be explained by the strong relationship of these species to the microvariables of the tree hollow (Quinto *et al.* 2014, Micó *et al.* 2015). Factors affecting this assemblage, such as the height of the tree hollow and the organic matter volume contained within it (Quinto *et al.* 2014, Micó *et al.* 2015), vary from one cavity to another, with consequent modification of the associated fauna. When we compare ET assemblages among different sites, the similarity increases because the set of tree hollows from each site presents cavities with similar characteristics.

In contrast, WT assemblages clearly showed a lower similarity among sites, and their identity in regard to the type of forest is higher (Fig. 1). In these assemblages, species are related to a wide range of woody resources that are spread within the woodland environment (Saint-Germain *et al.* 2006, Alinvi *et al.* 2007). These resources are closely linked to the characteristics of forests (e.g., tree density, dominant tree species, shrub coverage, decaying wood density and diversity, type and intensity of management, etc.), and therefore, they are maintained relatively homogeneous within a forest while showing higher variations among them.

Additionally, it could be expected that, due to the fact that WT captured species arriving from a wide range of woody microhabitats, the presence of species appearing occasionally and showing low abundances in WT assemblages was more likely (Bouget *et al.* 2009) than in ET assemblages, and this could also contribute to the higher turnover among forests of the former. However, according to the number of singletons and doubletons for each type of trap (observed species represented by a single individual or two individuals in the sample) (Colwell and Coddington 1994) (Table 2), we found that the percentages that these species represent of the total fauna sampled by each method are almost the same in both cases (WT: singletons 26.4%, doubletons 14.5%, ET: singletons 26.9%, doubletons 14.2%). This fact allows us to conclude that this does not seem to be a decisive factor in the emerged pattern.

The high differences between ET and WT assemblages do not only affect the beta diversity patterns. Species richness values showed a striking result (Fig. 2) where the poorest forest according

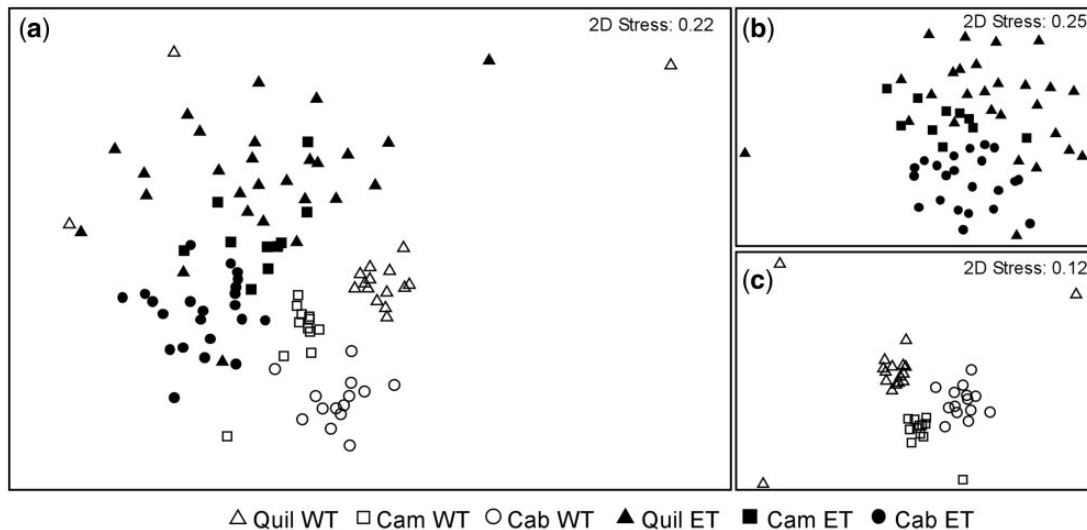


Fig. 1. NMDS ordination of sampling sites and assemblages as defined by Jaccard distances (a) Data from WT assemblages and ET assemblages together, (b) Data from ET assemblages, (c) Data from WT assemblages Squares, traps from *Cam*; circles, traps from *Cab*; triangles, traps from *Quil* *Quil*, Sierra de las Quilamas Natural Area; *Cab*, Cabañeros National Park; *Camp*, Biological Reserve 'Campanarios de Azaba'.

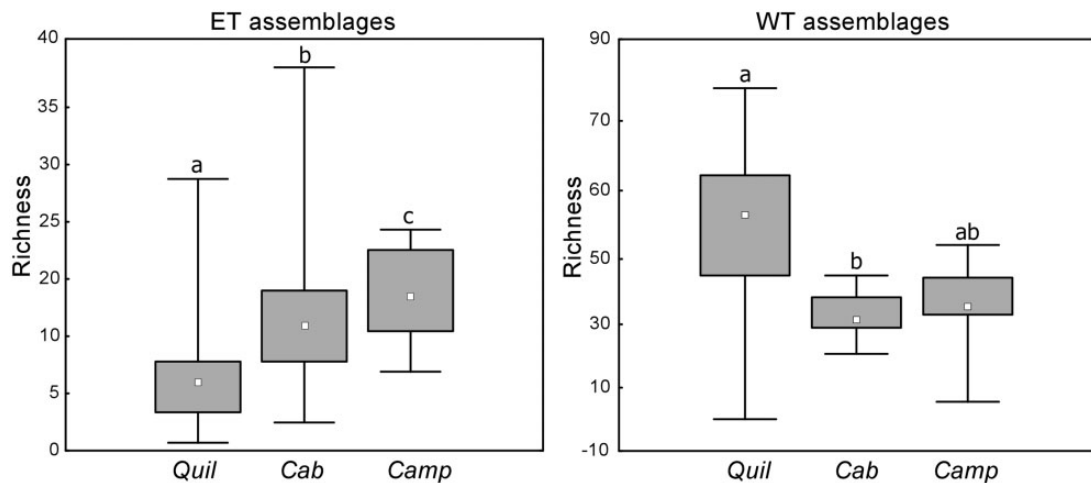


Fig. 2. Comparisons of species richness of saproxylic beetles between sites based on Kruskal-Wallis and subsequent post hoc test. Square, median; box, quartiles; bars, range. Sites with different letter indicate significant differences in the value of species richness. *Quil*, Sierra de las Quilamas Natural Area; *Cab*, Cabañeros National Park; *Camp*, Biological Reserve 'Campanarios de Azaba'.

to data from ET assemblages (*Quil*) becomes the richest one when the WT assemblages are analyzed. This points out that in different forest sites, different microhabitats are driving the local saproxylic beetle diversity.

There are many studies on saproxylic beetles in which only one of the sampling methods analyzed here is employed (i.e., Müller and Goßner 2010, Bouget *et al.* 2013, Horak and Pavlicek 2013, Lassaue *et al.* 2013, Micó *et al.* 2013, Quinto *et al.* 2014). The use of a single sampling method does not invalidate these works, but in view of the results presented here, it seems important to take into consideration the possible associated bias and its consequences on the reported conclusions.

In a wide and valuable study about the importance of micro- and macrohabitats on the diversity of saproxylic beetles, Hjältén *et al.* (2012) concluded that there are no diversity differences between reserves and mature managed forests. Consequently, they postulate that the studied managed stands maintain mostly complete

assemblages of saproxylic beetles. As this study is based on data from ET assemblages, it would be interesting to determine whether that pattern would be the same if WT assemblages were under study. We have found that WT assemblages tend to differ among themselves much more than ET assemblages and, therefore, significant differences could have appeared if WT had been considered.

The opposite scenario can be found in the study by Micó *et al.* (2013). In this case, the authors used data from WT assemblages to investigate the saproxylic beetle diversity distribution of a protected area characterized by its woodland habitats' heterogeneity. They found a high species turnover among forests, concluding that woodland heterogeneity (highly affected by woodland composition) seems to be the driving force for saproxylic beetle diversity in the studied area.

Implications for Biodiversity Monitoring and Conservation.

The fact that different saproxylic assemblages and their related sampling methods, can yield information about composition and

richness that is highly different results a widely known issue. The contribution of this study is to demonstrate that differences in the studied assemblages can also lead to significant differences in the identified patterns of species distribution and diversity turnover. In this way, we can find high or low beta diversity among sites depending on the particular assemblage we are analyzing, as well as being able to identify a sampling site as the richest or the poorest in number of species depending on the selected assemblage. These data are crucial to assess conservation requirements, especially taking into account that saproxylic beetles are a target group for forest conservation (Bouget and Brustel 2009). In addition, further studies should explore to what extent the information obtained from the analysis of these differences among saproxylic beetle assemblages (captured by ET, WT, and others) could be correlated with the spatial distribution of the microhabitat diversity.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Insect Science* online.

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