

Diversity distribution of saproxylic beetles in Chilean Mediterranean forests: influence of spatiotemporal heterogeneity and perturbation

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Abstract Mediterranean ecosystems have been recognized as a priority for biodiversity conservation due to their high levels of species richness and endemism. In South America, these environments are restricted to central Chile and represent a biodiversity hotspot. The study of saproxylic beetles in this area is an unexplored topic, despite the ecological role they play in these ecosystems and their potential usefulness for monitoring the degree of forest conservation. We investigated the diversity distribution of trophic guilds of saproxylic beetles in Chilean Mediterranean forests, to identify the main environmental variables that influence their distribution. We also analyzed seasonal dynamics as a key factor influencing insect communities and the effect of human disturbance on their diversity and composition. We identified characteristic species of perturbation degree as bioindicators for habitat monitoring. A total of 40 window traps were used

to survey three Mediterranean forest types in the Río Clarillo National Reserve and the adjacent non-protected areas. We found that the diversity, abundance and composition of saproxylic beetles varied significantly spatiotemporally among the studied forest types and among perturbation degrees, showing different patterns depending on the trophic guild. Results indicated that conservation decisions should include the preservation of a larger range of different vegetation types and the nearby zones that have suffered low levels of disturbance or fragmentation and where actions promoting the presence of old native trees would have a significant conservation value.

Keywords Diversity turnover · Indicator species · Saproxylic trophic guilds · True diversity · Río Clarillo

Introduction

The Mediterranean-climate regions of the world occupy <5% of the Earth's surface and harbour almost 20% of the known vascular plant species (Cowling et al. 1996; Heywood 1993). However, Mediterranean ecosystems have become one of the most threatened biomes because of a long history of human activities (Armesto et al. 2007; Naveh and Dan 1973; Ramírez-Hernández et al. 2014a; Underwood et al. 2009), and they have been recognized as being of priority importance for biodiversity conservation (Myers et al. 2000; Sala et al. 2000). In South America, Mediterranean environments are confined to a narrow area approximately 1000 km long in north-central Chile (30°–36° S) (Arroyo et al. 1995, 1999; Cowling et al. 1996). A number of studies in this region have underlined its geographic isolation and its high levels of biological diversity and endemism (Arroyo et al. 1995, 1999; Arroyo and Cavieres 1997; Villagrán 1995),

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being considered an important biodiversity hotspot (Arroyo et al. 1999; Myers 1990; Myers et al. 2000). Because of its small area relative to other Mediterranean regions, human impacts have been especially serious in Chilean Mediterranean ecosystems (Armesto et al. 2007; Arroyo et al. 1995; 1999; Donoso and Lara 1995). The conservation of their associated diversity is extremely challenging as <1% of the currently protected areas in Chile are located within the Mediterranean region (Sierralta et al. 2011).

The understanding of the distribution of saproxylic insect diversity constitutes a major challenge for conservation strategies in forest ecosystems (Stokland et al. 2012). These species are considered key organisms due to their high diversity (Stokland et al. 2012) and because they are involved in important ecosystem services, such as breaking down deadwood and recycling nutrients (Dajoz 1998; Micó et al. 2011; Stokland et al. 2012; Thompson and Rotheray 1998). Coleoptera, in particular, is considered one of the most diverse saproxylic taxa (Bouget and Brustel 2009; Dajoz 2000; Grove 2002; Schlaghamersky 2003). Moreover, they include representatives of several trophic guilds e.g. predators, saproxylophagous/saprophagous, xylomycetophagous, xylophagous and commensals (Bouget et al. 2005; Speight 1989), showing a wide range of biological requirements.

Recently interest in the investigation of saproxylic beetles in several countries has produced an increasing number of studies about the factors that influence their diversity (Buse et al. 2010; Lachat et al. 2012; Micó et al. 2015; Müller et al. 2013; Quinto et al. 2014, 2015; Ranius and Jansson 2000; Redolfi De Zan et al. 2014; Sebek et al. 2012; Stokland et al. 2012). A strong relationship between the diversity turnover of the group and the spatial heterogeneity of the landscape (related to the variation in environmental characteristics of the forest) has been established, being particularly crucial in Mediterranean areas (Buse et al. 2010; Micó et al. 2013; Ramírez-Hernández et al. 2014a; Ricarte et al. 2009, 2011). Additionally, Mediterranean biodiversity has been demonstrated to be both shaped and threatened by a long history of human activities in these areas including clearcutting, fire and land conversion for agriculture or raising cattle (Armesto et al. 2007; Arroyo et al. 1999; Donoso and Lara 1995). As a result, understanding the effect of anthropic perturbations on species communities is fundamental as a first step towards developing an adequate strategy for the conservation of this biodiversity.

In spite of their potential usefulness for monitoring the degree of forest conservation, the study of saproxylic insects in Chile is presently an unexplored issue. Some authors have pointed out the importance of deadwood and its decomposition in the maintenance of the Chilean forests (Carmona et al. 2002; Schlegel and Donoso 2008), but little attention has been devoted to the saproxylic fauna that participates in the process. In this sense, Mediterranean forests are not an exception. Until now, there has been no study

providing information about the diversity of saproxylic beetles in the Mediterranean forests of Chile, despite the fact that the similarities with other Mediterranean areas point to an important richness and value of its saproxylic fauna.

In view of this background, we conduct the first systematic study about the diversity of saproxylic beetles in Chilean Mediterranean forests to identify the main environmental variables that influence the distribution of the assemblage and their trophic guilds and to investigate the effect that human disturbances have on the diversity and composition of the assemblages. We incorporate the analysis of seasonal dynamics as a key factor influencing insect communities that usually receives little attention, often being set aside by spatial analysis established on short sampling periods (Sobek et al. 2009).

Our aim is to provide a useful tool for the conservation and management of the forests in the Mediterranean region of South America. In particular, we addressed the following questions: (1) How do saproxylic assemblage and saproxylic trophic guilds' diversity and composition patterns vary spatially and temporally in the Chilean Mediterranean forests? (2) Which environmental variables influence saproxylic assemblage and trophic guild species distribution? (3) To what degree does human modification of the area affect the diversity and composition of the assemblage? (4) Which beetle species can be considered as bioindicators of perturbation in these Mediterranean areas?

Methods

Study group

We used the classification of five trophic guilds described by Bouget et al. (2005) and Speight (1989): predators, saproxylophagous/saprophagous, xylomycetophagous, xylophagous and commensals. Identification was carried out with the help of the entomological collections of the Instituto de Entomología (IEUMCE, Universidad Metropolitana de Ciencias de la Educación) and of the Museo Nacional de Historia Natural of Santiago, Chile (MNHC). We also had the support of specialized bibliographies (Arias et al. 2008; Solervicens 2014; Elgueta and Arriagada 1989) and expert taxonomists (see "Acknowledgments") for the species identification and guild assignment.

Specimens were deposited in the entomological collections of the Laboratorio de Ecología de Ambientes Fragmentados (LEAF, Universidad de Chile), IEUMCE, and MNHC.

Study area

The Río Clarillo National Reserve (henceforth Reserve) was created by the Agriculture Ministry in 1982 (CONAF 1996)

and is located in the central region of Chile (33°46′00″S, 70°27′00″W), being entirely related to the basin of the Clarillo river. It has an extent of 13,085 ha and its altitude ranges from 860 to 3057 m (Niemeyer et al. 2002). The reserve has a Mediterranean climate with a significant seasonal oscillation, both in precipitation and in monthly average temperature (Niemeyer et al. 2002). It includes an important area of sclerophyllous scrub and forest, considered one of the most characteristic vegetation formations of the Mediterranean areas (Gajardo 1994; Quézel 2004).

Sampling method

Beetles were sampled using window traps, consisting of transparent cross vanes (75 cm long, 42 cm width) lying over a funnel and a collection container with preserving liquid (Bouget et al. 2008). The preserving liquid was a solution of salt and water at 10% with a few drops of an odourless detergent that allows the drowning of the insects and that serves an antibiotic role (Valladares 2000). This sampling method is the most frequently used technique for catching active flying saproxylic beetles (Barbalat 1995; Grove 2000; Martikainen et al. 2000; Okland 1996). The window traps sample individuals coming from the surroundings of the trap (Bouget et al. 2008; Sverdrup-Thygeson and Birke-moe 2009). These traps record a saproxylic assemblage linked to a wide range of woody resources of the tree such as decaying aerial branches, bark, or tree hollows, but also to deadwood on the ground (Alinvi et al. 2007; Hyvärinen et al. 2006; Quinto et al. 2013; Ranius and Jansson 2002; Saint-Germain et al. 2006; Sverdrup-Thygeson and Birke-moe 2009). Traps were always hung close to the trunk (<30 cm apart) and at a height of 1.5–2 m above the ground (Jonsell 2011; Sirami et al. 2008; Sverdrup-Thygeson et al. 2010). All selected trees were alive.

Spatiotemporal variation and environmental characteristics

In order to analyze the patterns of diversity distribution and the related environmental variables, three types of forest were selected: peumo forest (P), quillay forest (Q) and radial forest (R). These associations represent three sclerophyllous forest types that appear widely represented in the Reserve (Solervicens 2014). The names of these associations have been given using the common name of the dominant tree species present: peumo (*Cryptocarya alba* (Molina) Looser, Lauraceae), quillay (*Quillaja saponaria* Molina, Quillajaceae) and radial (*Lomatia hirsuta* Diels ex Macbr., Proteaceae).

For the analysis of diversity among types of forest inside the Reserve, three stands of peumo forest, three stands of quillay forest and three stands of radial forest were selected

and three traps were placed in each stand (a total of 27 traps, nine per type of forest). All traps were installed on a tree belonging to the dominant species of each forest (peumo, quillay or radial). Traps were checked monthly for 12 months: from February 2014 to January 2015. For this analysis we used a wide range of categorical and continuous ecological variables able to drive saproxylic communities at the stand and tree scale.

Stand variables

The area where stand variables were measured was a 20 m radius circumference around each trap, consisting of approximately 0.1 ha plots, which are sufficiently large to avoid unrealistically high estimates but small enough to capture small-scale variation (Müller et al. 2008, 2010; Okland et al. 1996). The variables evaluated were:

- Mean tree diameter (*MeanDiam*): continuous. We measured the tree circumference at 1.30 cm, and applied the equation $diam = P/\pi$ (cm), where P is the mean perimeter of all the trees in the sampling plot where variables were measured.
- Tree and shrub coverage (*TreeCov* and *ShrubCov*): continuous. Percentages of tree and shrub coverage were estimated by eye for each sampling plot as in Ramírez-Hernández et al. (2014a).
- Tree density (*TreeDens*): continuous. Total number of trees in each sampling plot was counted and the data were extrapolated to give the value per hectare.
- Deadwood volume: continuous. We measured the volume of total deadwood (*WoodVol*) and each stage of decomposition (*Wood1*, *Wood2*, *Wood3*), including all pieces of deadwood with a diameter $P \geq 5$ cm found in each sampling plot. Wood decay was estimated in three classes: (1) wood hard, bark firmly attached to the stem, impossible to penetrate with a knife, (2) bark more or less gone, wood soft, able to partly penetrate with a knife, (3) knife penetrates the wood without resistance, bark loose and mostly gone (modified from Franc et al. 2007).

Tree variables

Tree variables were measured for the selected tree where the trap was placed. The variables evaluated were:

- Tree diameter (*Diam*): continuous. We measured the tree circumference at 1.30 cm, and applied the equation $diam = P/\pi$ (cm), where P is the perimeter of the selected tree.
- Presence of hollows (*Hol*): categorical. We looked for the presence of hollows (with >5 cm aperture) in

the selected tree as these microhabitats are considered keystone structures for saproxylic beetles (Chiari et al. 2012; Dajoz 2000; Müller et al. 2013; Ramírez-Hernández et al. 2014a).

- Presence of dead parts (*DeadP*): categorical. Presence of dead branches or dead trunk parts representing >25% of the tree.
- Presence of damage (*Dam*): categorical. Presence of damage on trunk or branches: patches with bark loss of at least 5×5 cm mainly caused by felling or natural falling.

Human disturbance

To study the effect of anthropogenic perturbation on saproxylic beetle diversity, traps were distributed along a distance gradient (12.24 km long) from trees located in the Reserve to areas affected by human perturbation. In these areas, a massive logging of native trees has been carried out to develop activities such as farming, cattle raising or creation of urban areas. The intensity of these perturbations increases as we move away from the Reserve.

To analyze the effect of the degree of human perturbation on the saproxylic community, 13 traps separated by at least 600 m were placed along a distance gradient (12.24 km) from within the Reserve to disturbed areas (Fig. 1). In this case, all traps were placed on quillay trees in order to avoid possible effects from diversity coming from the tree species where the traps were hung (Micó et al. 2013). Quillay's selection was based on being the native tree species

with more specimens present on these disturbed areas. Traps were checked monthly for 4 months, from September 2014 to January 2015, coinciding with the spring season when the diversity of the group is high (Estrada and Solervicens 2004).

In order to carry out this part of the analysis, traps were grouped according to the perturbation characteristics of the surroundings (distance to the Reserve and coverage of native vegetation). Four traps (1–4 in Fig. 1) were placed in an area under a perturbation degree 1 (0–2.18 km from the Reserve). Three of these traps were in the Reserve and one was outside but adjacent and still surrounded by native and undisturbed vegetation. Four other traps (5–8 in Fig. 1) were in an area under a perturbation degree 2 (5.2–6.5 km). These traps were placed in a moderately urbanized zone where, although perturbation was evident (presence of buildings, roads, and considerable part of the land surface dedicated to agricultural and cattle raising), there was an important percentage of the area (≈50%) still covered by dense and native vegetation (5–8 in Fig. 1). The area of perturbation degree 3 (8–12.24 km) was sampled by five traps (9–13 in Fig. 1) placed in completely altered areas where all the surfaces were covered by anthropogenic infrastructures (buildings, roads, agriculture fields, cattle raising areas) and where we found only scattered trees mainly of exotic species.

Data analysis

All the analyses were performed for the entire saproxylic assemblage captured and for each trophic guild separately to explore whether the diversity distribution patterns changed

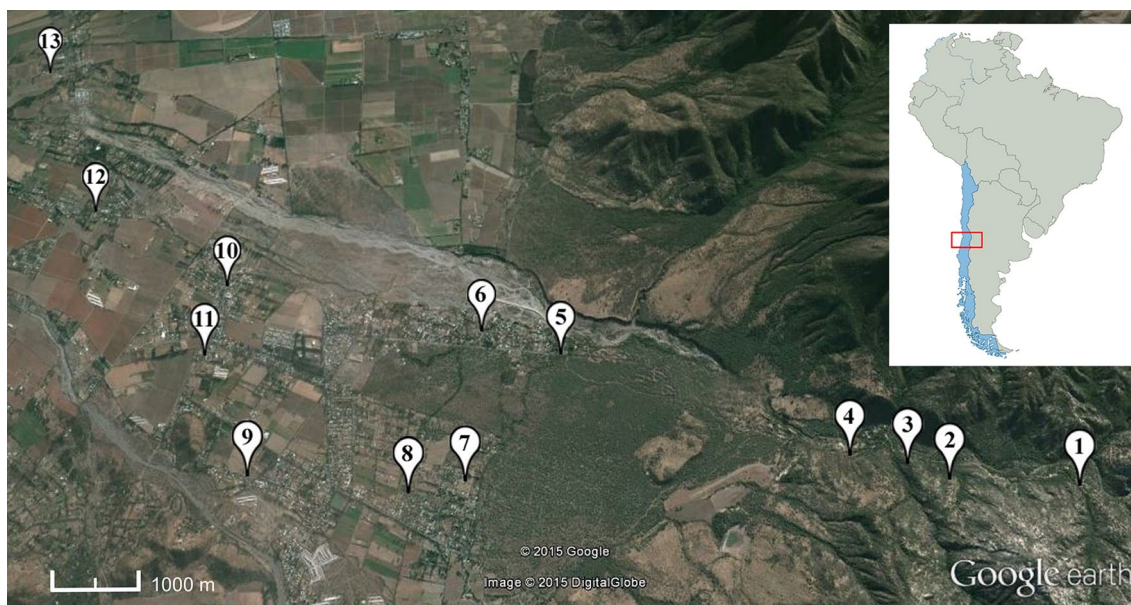


Fig. 1 The distribution of traps used to assess the impact of degree of human disturbance on the saproxylic beetle community. Image from Google Earth

depending on the biology of the species. The seasons considered for the analyses are those present in Mediterranean ecosystems and which are found in the study area: spring (September, October, November), summer (December, January, February), autumn (March, April, May) and winter (June, July, August).

Generalized linear models (GLM) were used to detect differences in the overall abundance of beetles among forest types, seasons, and perturbation degrees; traps were nested within sites. We checked the data distribution (random, aggregate or angular distributions) in order to apply the appropriate data transformation for the analysis. We used a Poisson error or quasi-Poisson distribution to construct the models and checked for overdispersion of the data (Crawley 2007). Transformations and generalized models were carried out using R 3.2.1 (Crawley 2007; R Development Core Team 2015).

Completeness of the saproxylic species inventory per forest type, season, and perturbation degree was evaluated as the percentage of observed species in relation to the number of species predicted by the sample coverage estimator suggested by Chao and Jost (2012), which is a less biased estimator of sample completeness:

$$C_n = 1 - \frac{f_1}{n} \left| \frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right|$$

where f_1 and f_2 are the number of singletons and doubletons in the sample, respectively, and n is the number of individuals. To detect differences in species diversity among forest types, seasons and perturbation degrees, we calculated the number of effective species for each one using the actual number of species counted. We used the measure of true diversity of order $q=2$ (D^2) that is the inverse Simpson concentration index, which can be interpreted as the effective number of ‘dominant’ species (Alencar et al. 2015; Chao and Shen 2003; Hsieh and Linsenmair 2012; Jost 2006, 2010; Magurran 1988). We calculated it using the minimum variance unbiased estimator (MVUE) (Benítez-Malvido et al. 2016; Chao and Jost 2015; Moreno et al. 2011). Sample coverage and true diversity metrics were calculated using the SPADE software (Chao and Shen 2010).

To assess the partitioning of the variability of species composition of each guild between types of forest, season and degree of perturbation, we used the Bray-Curtis index among them (Anderson 2001). Differences were analyzed with a permutational multivariate analysis of variance, as a non-parametric alternative to the multivariate analysis of variance (Anderson and Walsh 2013) after 999 permutations of residuals under the reduced model. Also, we performed ordinations of samples using nonmetric multidimensional scaling (NMDS) for type of forest, season and perturbation degree. Analyses and graphs were done in PRIMER v6.1

(Clarke and Gorley 2009). After permutation tests, pairwise tests were applied to determine differences in habitat pairs. Significant differences were set at $P \leq 0.05$.

We performed linear multiple regressions to detect the relationships between the environmental explanatory variables of forests and the species richness and abundance (Carbó-Ramírez and Zuria 2011; Kleinbaum et al. 1998; Quinto et al. 2014). We checked normality of the variables using a Kolmogorov–Smirnov test. Data were square root transformed only for data that did not pass normality. We used forward selection techniques in order to find the most accounted subset of explanatory variables for abundance and richness patterns and to avoid over-parameterization (Carbó-Ramírez and Zuria 2011; Quinto et al. 2014). The residuals of the final models obtained with linear multiple regressions revealed no obvious suggestions of non-normality or collinearity (Kleinbaum et al. 1998). Statistical analysis was performed using SigmaStat, version 3.5 (Systat Software 2006).

Indicator response of saproxylic species

We calculated the indicator value (IndVal; Dufrene and Legendre 1997) using the indicpecies package (De Cáceres and Legendre 2009) in R software R 3.2.1 (Crawley 2007; R Development Core Team 2015). The IndVal combines measurements of habitat fidelity (frequency within that habitat type) and specificity (uniqueness to a particular site) to identify the characteristic species of each category of perturbation. These species could be useful bioindicators for habitat quality and have valuable applications in the monitoring of habitat integrity (McGeoch et al. 2002). The IndVal index is highest when all the individuals of a species are found under a single habitat condition, and when that species occurs in all samples of that group. Finally, the statistical significance of association was analyzed using a permutation test between pairs of species and for groups of perturbation degrees using the multipatt function (De Cáceres et al. 2010, 2012).

Results

Saproxylic guild characterisation

We identified 156 species and 3083 individuals belonging to 34 families of saproxylic beetle (Online Resources 1 and 2). Guilds were composed of xylophagous: 78 species and 887 individuals; xylomycetophagous: 15 species and 261 individuals; saprophagous: 20 species and 588 individuals; predators: 40 species and 1286 individuals; commensals: three species and 61 individuals. Commensals were not included in the study of each separate guild because the low number of species did not allow the proper development of the analyses.

Species abundance patterns

Data from the number of individuals captured for each forest type, season and perturbation degree are shown in Table 2. Overall, the results of general models indicated differences in the abundance of beetles among forest types ($\chi^2=80.62$, $df=2$, $P<0.001$), seasons ($\chi^2=421.7$, $df=3$, $P<0.001$), and trophic guilds ($\chi^2=155$, $df=3$, $P<0.001$). We also detected differences among perturbation degrees in beetle abundance ($\chi^2=356$, $df=2$, $P<0.001$) and trophic guilds ($\chi^2=532$, $df=3$, $P<0.001$).

Species diversity and composition

Results on the completeness of the saproxylic species inventory showed that a large proportion of the species present in each forest type, season, and perturbation degree was recorded (sample coverage >90%; Table 1). All results on diversity values and composition similarity are presented in Tables 1 and 2, respectively. Figure 2 displays the NMDS showing the differences in similarity within forest types, seasons and disturbance degrees.

Table 2 Turnover of species composition of each guild between habitats based on the Bray-Curtis similarity index

| | % of similarity | | | | |
|-----------------------------|-------------------|-------------|-------------|-------------|-------------|
| | Entire assemblage | P | S | XM | X |
| Pair of forest types | | | | | |
| Q–P | 47.5 | 40.8 | 71.3 | 57.7 | 33.6 |
| Q–R | 33.9 | 39 | 43.6 | 56.4 | 41.6 |
| P–R | 42.7 | 35.2 | 46.9 | 37.3 | 24.3 |
| Pair of seasons | | | | | |
| Au–Sp | 23.9 | 15.5 | 5.2 | 70 | 24.3 |
| Au–Su | 16 | 10.6 | 4.1 | 28.1 | 28.7 |
| Au–Wi | 47.3 | 39 | 40 | 60.3 | 33 |
| Sp–Su | 39.4 | 45.3 | 48.9 | 35.8 | 26.7 |
| Sp–Wi | 19 | 6.3 | 6.7 | 64.1 | 18.3 |
| Su–Wi | 9 | 3.9 | 2.1 | 34.4 | 9.3 |
| Pair of perturbation degree | | | | | |
| 1–2 | 30.8 | 21 | 41.3 | 66.6 | 43.2 |
| 1–3 | 26.4 | 13.4 | 40.8 | 44 | 43.2 |
| 2–3 | 39.8 | 20.2 | 62.6 | 51.2 | 40.2 |

Comparisons that showed significant differences in pairwise tests are given in bold

Table 1 Estimates for forest type, season and perturbation degree of species richness (S), abundance (Ind), completeness of the sample coverage estimator (Cn), true diversity of order 2 (D^2) for the complete assemblage and for each guild

| Trophic guilds | Estimators | Forest type | | | Season | | | | Perturbation degree | | |
|-------------------|------------|-------------|-------|-------|--------|-------|-------|-------|---------------------|-------|-------|
| | | P | Q | R | Au | Wi | Sp | Su | 1 | 2 | 3 |
| Entire assemblage | S | 84 | 89 | 74 | 38 | 29 | 83 | 88 | 70 | 60 | 56 |
| | Ind | 603 | 846 | 399 | 155 | 128 | 747 | 818 | 678 | 335 | 223 |
| | Cn | 95 | 96 | 93 | 92 | 91 | 97 | 96 | 96 | 94 | 90 |
| | D^2 | 39.82 | 44.05 | 38.64 | 20.19 | 10.16 | 19.29 | 18.09 | 19.29 | 31.15 | 43.04 |
| Predators | S | 22 | 27 | 21 | 9 | 3 | 25 | 23 | 22 | 14 | 11 |
| | Ind | 192 | 356 | 115 | 32 | 9 | 277 | 345 | 435 | 145 | 43 |
| | Cn | 98 | 97 | 93 | 94 | 89 | 97 | 98 | 98 | 97 | 91 |
| | D^2 | 5.93 | 8.3 | 8.65 | 7.75 | 3 | 7.91 | 7.5 | 3.5 | 3.66 | 6.63 |
| Saprophagous | S | 10 | 13 | 10 | 4 | 3 | 9 | 14 | 11 | 13 | 9 |
| | Ind | 137 | 149 | 60 | 10 | 5 | 144 | 187 | 143 | 46 | 53 |
| | Cn | 96 | 99 | 97 | 90 | 60 | 99 | 98 | 99 | 89 | 96 |
| | D^2 | 2.14 | 3.97 | 4.98 | 5 | 3.33 | 4.43 | 2.05 | 4.34 | 5.34 | 6.34 |
| Xylomycetophagous | S | 15 | 12 | 8 | 11 | 11 | 12 | 10 | 8 | 6 | 6 |
| | Ind | 76 | 118 | 48 | 64 | 72 | 56 | 50 | 23 | 16 | 27 |
| | Cn | 93 | 97 | 96 | 94 | 93 | 95 | 90 | 83 | 87 | 89 |
| | D^2 | 6.62 | 5.47 | 5.03 | 6.5 | 4.01 | 6.66 | 4.04 | 5.88 | 6 | 3.05 |
| Xylophagous | S | 35 | 35 | 32 | 14 | 12 | 34 | 38 | 25 | 26 | 26 |
| | Ind | 184 | 215 | 172 | 49 | 42 | 264 | 216 | 67 | 118 | 81 |
| | Cn | 92 | 94 | 92 | 88 | 90 | 95 | 93 | 84 | 93 | 86 |
| | D^2 | 11.08 | 15.39 | 3.94 | 5.65 | 5.77 | 4.91 | 14.19 | 20.66 | 7.45 | 14.86 |

P peumo forest, Q quillay forest, R radial forest, Au autumn, Wi winter, Sp spring, Su summer

Distribution patterns among forest types

Regarding the entire saproxylic assemblage sampled, peumo and radial forests had the same effective species while quillay had a higher diversity value. Species composition showed significant differences among forest types (pseudo- $F=3.2$, $df=2$, $P=0.001$), with quillay and peumo being the most similar forests (47.5%) and quillay and radial the least similar ones (33.9%).

For predator species, quillay and radial had the same effective species while peumo showed the lowest diversity value. Permutation analysis showed significant differences in composition (pseudo- $F=2.13$, $df=2$, $P=0.004$) with quillay and peumo forests being the most similar forests (40.8%), and quillay and radial the least similar ones (35.2%).

All forests presented differences in saprophagous communities. Radial had the highest diversity and peumo the lowest. We did not detect significant compositional differences among forest types for this guild (pseudo- $F=1.27$, $df=2$, $P=0.19$).

Regarding xylomycetophagous species, peumo had the highest diversity while quillay and radial had the same effective species values. We found significant compositional differences in xylomycetophagous species among forest types (pseudo- $F=3.38$, $df=2$, $P=0.001$). As for predators, peumo and quillay forests proved to be the most similar (57.7%) and quillay and radial the least similar (37.3%).

For xylophagous species, radial had almost three times less diversity than peumo and quillay. Species composition showed significant differences among forest types (pseudo- $F=3.34$, $df=2$, $P=0.001$). For this guild, peumo and radial forests were the most similar in species composition (41.6%) and quillay and radial the least similar (24.3%).

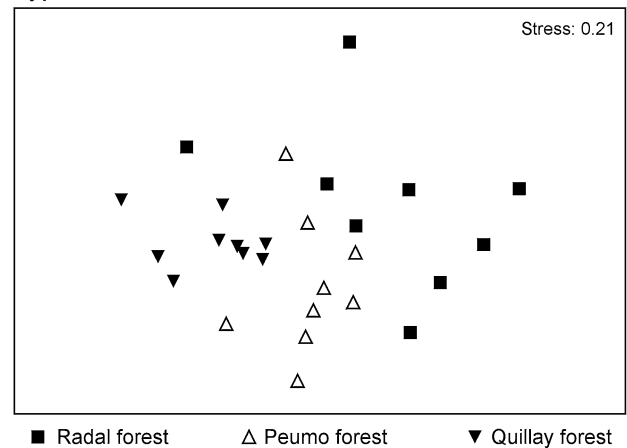
Distribution patterns among seasons

Regarding the entire saproxylic assemblage sampled, spring and autumn showed the highest effective species while winter showed the lowest diversity value. Species composition showed significant differences among seasons (pseudo- $F=8.4$, $df=3$, $P=0.001$), with autumn and winter being the most similar (47.3%) and summer and winter the least similar (9%).

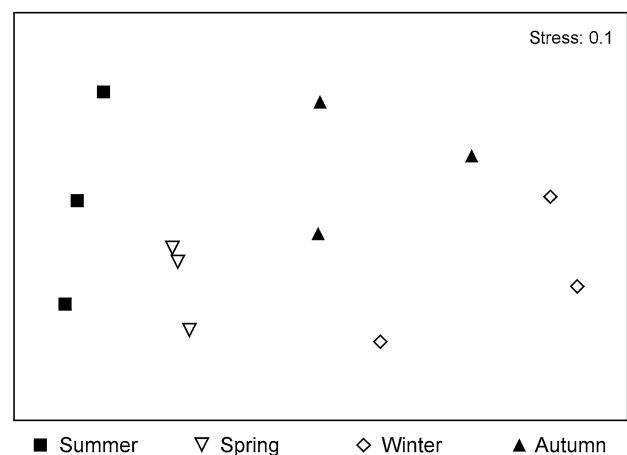
Winter was the season that showed the lowest values of diversity for predator species. Significant differences in composition of predators among seasons were found (pseudo- $F=4.08$, $df=3$, $P=0.001$). Summer and winter and spring and winter showed the lowest similarities in composition (3.9 and 6.3%, respectively). Spring and summer were the most similar seasons compositionally (45.3%).

For saprophagous species, the summer season presented two times less diversity than spring. There were significant differences in composition of saprophagous species

Type of forest



Season



Perturbation degree

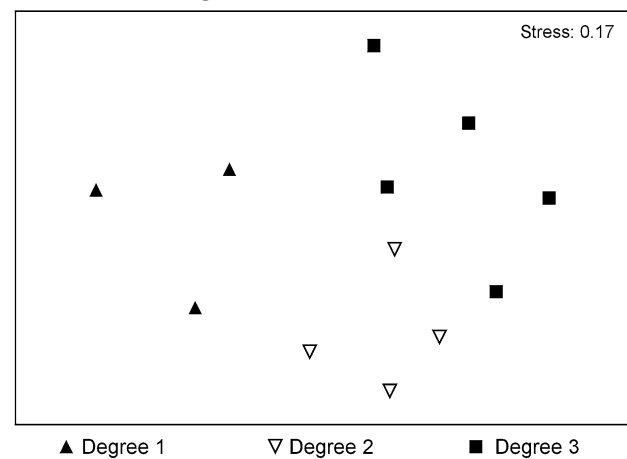


Fig. 2 NMDS ordination of type of forest, season and perturbation degree as defined by Bray-Curtis distances calculated from saproxylic beetles species abundances

among seasons (pseudo- $F=5.10$, $df=3$, $P=0.001$), with the similarities between summer and winter and between summer and autumn being the lowest ones (2.1 and 4.1%,

respectively). With respect to predators, spring and summer were the most similar seasons compositionally (48.9%).

Autumn and spring had the same diversity for xylomycetophagous, showing higher values than summer and winter, which had the same diversity. There were significant differences in the composition of xylomycetophagous species among seasons (pseudo- $F=2.41.08$, $df=3$, $P=0.002$). This guild showed the highest similarities among seasons, reaching a 70% similarity between autumn and spring. The lowest similarity was found between summer and autumn (28.1%).

For xylophagous species, summer appeared as the most diverse season, with nearly three times more diversity than the other seasons, which showed no differences in diversity among them. There were significant differences in the composition of xylophagous species among seasons (pseudo- $F=5.25$, $df=3$, $P=0.001$). Summer and winter showed the lowest similarity (9.3%), while autumn and winter showed the highest one (33%).

Distribution patterns among perturbation degrees

Regarding the entire saproxylic assemblage, the perturbation degree 3 area (highest level of perturbation) showed the highest number of effective species, with two times more diversity than the perturbation degree 1 area (less altered area). Species composition showed significant differences among perturbation degrees (pseudo- $F=2.2$, $df=2$, $P=0.001$), with degrees 2 and 3 being the most similar (39.8%) and degrees 1 and 3 the least similar (26.4%).

With respect to predator species, the area under perturbation degree 3 had two times more diversity than the other groups. There were significant differences in composition of predator species among perturbation degrees (pseudo- $F=2.21$, $df=2$, $P=0.002$).

Saprophagous species showed similar diversity values for all perturbation degrees. There were differences in the composition of saprophagous species (pseudo- $F=1.99$, $df=2$, $P=0.008$).

Xylomycetophagous species in perturbation degrees 1 and 2 had two times more diversity than in degree 3. We did not detect significant compositional differences in xylomycetophagous species (pseudo- $F=1.18$, $df=2$, $P=0.3$).

Regarding xylophagous species, the area under perturbation degree 1 showed the highest diversity, having three times more diversity than degree 2. There were significant differences in the composition of xylophagous species among perturbation degrees (pseudo- $F=1.62$, $df=2$, $P=0.036$).

Compositional similarities among perturbation degrees were quite uniform for all the guilds and comparisons (≈ 40 – 60%), except for predators, for which the highest similarity was only of 21% between degrees 1 and 2.

Environmental variables affecting guild distribution

The most important stand variables explaining abundance distribution patterns were the volume of deadwood in the first stage of decomposition and the mean tree diameter (Tables 3, 4). In the case of the variables associated with the tree where the trap was placed, the most explanatory ones were the presence of damage, the presence of hollows, and the diameter of the tree. Each trophic guild presented different responses to these variables. The richness of predators was influenced by the presence of tree hollows, while the saprophagous, xylomycetophagous, and xylophagous richness were affected by the tree diameter. In the case of the saprophagous and xylophagous guilds, the volume of deadwood in the first stage of decomposition was also related to the number of species. With respect to the abundance, predators and saprophagous species showed a relationship between the presence of damage on the tree and the number of individuals. Xylomycetophagous abundance was explained by the mean diameter of the trees in the stand, and xylophagous abundance did not fit any model (Table 4).

Indicative species of perturbation degree

For the analysis of the indicator value species with fewer than five specimens collected were not considered, leaving 39 species for analysis. Only the perturbation degrees 1 and 2 and the group containing both of them had characteristic beetle species associated with significant indicator values (Table 5). All the species associated with perturbation degrees 1 and 2 were exclusive to each area. On the other hand, the two species associated with the group of perturbation degrees 1 and 2 were exclusive of this group of areas not having been collected in the most perturbed area.

Discussion

Species diversity, abundance and composition of saproxylic beetles assemblages varied significantly spatiotemporally among the studied forests types and among perturbation degrees, showing different patterns depending on the analyzed guild (Table 1).

Spatial variation of saproxylic beetles diversity

All of the analyzed trophic guilds were present in all of the studied forests, with predators and xylomycetophagous species being those with the highest richness and abundance (Table 1). Although quillay forest appears as the most rich and diverse regarding the entire saproxylic assemblage, there was no general pattern that could allow us to define a particular one as the most important for the conservation of the richness

Table 3 Variation of tree and stand environmental variables per forest type inside the Reserve

| Variable | | Type of forest | | |
|-------------------------------------|-----------|------------------|---------------|------------------|
| | | P | Q | R |
| Stand variables | | | | |
| <i>Diam</i> (cm) | Mean ± SE | 14.18 ± 1.43 | 25.36 ± 2.71 | 16.55 ± 1.38 |
| | Range | (7.96–22.92) | (11.45–36.29) | (10.82–22.28) |
| <i>TreeCov</i> (%) | Mean ± SE | 71 ± 9 | 16 ± 5 | 60 ± 11 |
| | Range | (30–90) | (2–40) | (15–90) |
| <i>ShrubCov</i> (%) | Mean ± SE | 24 ± 11 | 32 ± 4 | 34 ± 10 |
| | Range | (5–85) | (20–50) | (10–75) |
| <i>TreeDens</i> (no of trees/ha) | Mean ± SE | 2485.18 ± 444.97 | 955.6 ± 239.9 | 1785.18 ± 320.16 |
| | Range | (800–4400) | (266.67–1967) | (733.33–3533.33) |
| <i>MeanDiam</i> (cm) | Mean ± SE | 12.17 ± 0.52 | 15.6 ± 1.6 | 12.24 ± 0.51 |
| | Range | (9.9–15.32) | (9.65–25) | (9.6–14.72) |
| <i>WoodVol</i> (m ³ /ha) | Mean ± SE | 123.46 ± 57.74 | 68.85 ± 23.24 | 174.55 ± 133.52 |
| | Range | (6.02–411.46) | (0.93–231.56) | (1.5–1206.66) |
| <i>Wood1</i> (m ³ /ha) | Mean ± SE | 115.32 ± 56.12 | 34.19 ± 13.76 | 10.35 ± 4.19 |
| | Range | (2.53–409.88) | (0–129.74) | (0.76–34.67) |
| <i>Wood2</i> (m ³ /ha) | Mean ± SE | 5.08 ± 2.2 | 15.75 ± 11.01 | 105.21 ± 83.8 |
| | Range | (0–21.03) | (0–101.7) | (0.05–754.67) |
| <i>Wood3</i> (m ³ /ha) | Mean ± SE | 3.05 ± 1.36 | 13.57 ± 6.47 | 58.99 ± 46.25 |
| | Range | (0–13.47) | (0–63.06) | (0.02–417.33) |
| Tree variables | | | | |
| <i>Hol</i> | (%) | 22 | 67 | 22 |
| <i>DeadP</i> | (%) | 0 | 11 | 0 |
| <i>Dam</i> | (%) | 44 | 89 | 22 |

Mean number and standard error for each continuous ecological variable is provided. For categorical variables we give the percentage of trees in which they were present

For the stand variables the area where they were measured was 0.1 ha plots around each trap

P peumo forest, *Q* quillay forest, *R* radial forest, *Diam* tree diameter, *TreeCov* tree, *ShrubCov* shrub coverage, *TreeDens* tree density, *MeanDiam* mean tree diameter, *WoodVol* total deadwood, *Wood1*, *Wood2*, *Wood3* each stage of decomposition, *Hol* presence of hollows, *DeadP* presence of dead parts, *Dam* presence of damage

and diversity of all saproxylic trophic guilds (Table 1). This result points to the fact that environmental differences among forest types influence the trophic guilds in different ways. For example, the process of wood decay determines a succession of saproxylic fauna in which xylophagous and saprophagous species appear mainly associated with the first and the last wood decomposition states, respectively (Stokland et al. 2012). In this way, the highest diversity of saprophagous species in radial forest and the lowest in peumo forests could be related to the fact that radial forest is the one with the greatest amount of wood in the most advanced stage of decay, while peumo forest has the least (Table 3). On the other hand, radial forest showed the lowest diversity for the xylophagous guild, which could be related to the fact that this forest is the poorest in volume of wood in the first stage of decay.

With respect to the general pattern of abundance, we found that quillay forest showed the highest number of individuals of all the guilds (Table 1). This is probably related to

the high openness of this type of forest (Table 3) that usually increases the beetles’ abundance (Horak et al. 2014; Koch Widerberg et al. 2012).

Focusing on the species composition and assuming that the dispersal ability of individuals can influence the observed turnover, producing a decrease in the proportion of species shared between two stands when the distance separating them increases (Qian 2009), we could expect that the fauna associated with radial forest show lower similarities with the other two forests, as this ecosystem appears furthest in the Reserve. However, this pattern is only evident for saprophagous species (Table 2). This is consistent with the results on the strong influence of environmental variables on the richness and abundance of saproxylic beetles (Table 4) and agrees with other studies (Micó et al. 2013; Müller and Goßner 2010) that verify that dispersal limitation might not be the most important factor influencing beta diversity among forest sites. In many areas it has been shown

Table 4 Microenvironmental variables correlated with species richness and abundance

| Trophic guilds | <i>F</i> | <i>R</i> ² | <i>P</i> | Model |
|-----------------------------|----------|-----------------------|----------|--------------------------------|
| Entire assemblage richness | 13.44 | 0.52 | <0.001 | $11.09 + 0.65Diam + 0.03WoodI$ |
| Entire assemblage abundance | 9.80 | 0.53 | 0.004 | $50 + 35.57Dam$ |
| Predators richness | 4.84 | 0.16 | 0.03 | $6.70 + 2.19Hol$ |
| Predators abundance | 8.09 | 0.24 | 0.009 | $3.38 + 2.10Dam$ |
| Saprophagous richness | 12.91 | 0.51 | <0.001 | $0.59 + 0.16Diam + 0.007WoodI$ |
| Saprophagous abundance | 5.3 | 0.18 | 0.03 | $2.66 + 1.19Dam$ |
| Xylomycetophagous richness | 6.21 | 0.2 | 0.02 | $2.07 + 0.088Diam$ |
| Xylomycetophagous abundance | 14.85 | 0.37 | <0.001 | $0.45 + 0.17MeanDiam$ |
| Xylophagous richness | 11.54 | 0.49 | <0.001 | $3.46 + 0.27Diam + 0.01WoodI$ |

Xylophagous abundance did not have a relationship with any variable

Ho presence of hollows, *Dam* presence of damages, *Diam* tree diameter, *WoodI* dead wood volume in the first degree of decay, *MeanDiam* mean tree diameter

that diversity turnover among forests can be explained by differences in woodland characteristics and individual tree structure (Goßner et al. 2008; Micó et al. 2013; Müller and Goßner 2010; Müller et al. 2012). Here, we confirm this relationship; however, the influence of the environmental variables varies among the guilds. Our results indicated different ecological preferences among trophic habits (Table 4). In the case of predator species, their relationship with the presence of trees with hollows and instances of damage is probably related to the fact that these structures can act as a congregation place for the saproxylic species they prey on. For their part, xylophagous species were influenced by the volume of wood in the first stage of decomposition, which is expected as this guild usually dominates in the first stages of decay (Saint-Germain et al. 2007). For all the guilds, richness was always associated with tree variables linked to the age and size of the tree (e.g. the presence of hollows and the tree diameter) (Table 4). This outcome emphasizes the importance of the presence of old and large tree individuals for saproxylic biodiversity and highlights the key role they play in preserving this fauna (Lindhe et al. 2005; Micó et al. 2010; Regnery et al. 2013; Stokland et al. 2012).

Temporal variation of saproxylic beetles diversity

We can confirm that in the Neotropical Mediterranean region, as it happens in the Palaeartic Mediterranean areas, species activity is maintained all year long, underscoring the importance of an extended sampling period over different seasons in these areas. Significant differences in diversity and composition between seasons appear to be related to species preferences (Table 1). However, diversity distribution varied greatly among guilds. The only general trends found showed a decline of richness, abundance and diversity during winter and a peak between the end of spring and the beginning of summer, as it has been shown for Iberian Mediterranean forests (Ramírez-Hernández et al. 2014b)

(Table 1). With the exception of the xylomycetophagous group, the composition of which was similar between spring and autumn, we found the highest similarities between spring and summer faunas and between winter and autumn faunas (Table 2; Fig. 2) as found in other Mediterranean forests (Estrada and Solervicens 2004; Ramírez-Hernández et al. 2014b). The difference between the xylomycetophagous and other species may be related to the development of the fungal fruiting bodies used by the former (Table 2), and differences in life-cycles (Gaylord et al. 2006). We found several families that appeared only during one or two seasons, such as spring-summer (e.g. Anthicidae, Cerambycidae, Tenebrionidae), or autumn-winter (e.g. Corylophidae). Other families are present all year, but their abundances vary depending on the season. For example, individuals of Cryptophagidae may avoid the hot and dry summer months, with the resulting decrease in their abundance (autumn: 25 individuals, winter: 26, spring: 44, summer: 4), as also occurs in other Mediterranean forests in Europe (Ramírez-Hernández et al. 2014b). On the other hand, other families seemed to be adapted to the warmest months, showing their highest abundance during summer (e.g. Bostrichidae, Buprestidae, Curculionidae, Scarabaeidae) or spring (e.g. Elateridae).

Effect of degree of perturbation

The obtained results on the effects of perturbation showed that anthropogenic activities in the area affect the species assemblage but do not necessarily reduce its richness and diversity. Data showed high diversity, richness, and abundance values for all the perturbation areas. Moreover, depending on the guild, these values were higher in the most disturbed ones (Table 1). In these perturbed areas, the remaining quillay trees are old and large individuals that had not been cut down in order to maintain them as ornamental features and also for the benefit of their shadow. These trees, therefore, act as refuges for saproxylic species that do not find other

Table 5 Percentage indicator values ($P < 0.05$) of beetle species for each perturbation degree and group

| Perturbation degree | Beetles species (family) | Indval (%) |
|--------------------------|-------------------------------------------------------------------------|------------|
| Degree 1 (0–2.18 km) | <i>Amecocerus giraudi</i> (Solier, 1849) (Melyridae) | 100 |
| | <i>Scaptia</i> sp.1 (Scaptiidae) | 100 |
| | <i>Ischyropalpus maculosus</i> (Fairmaire y Germain, 1860) (Anthicidae) | 87 |
| Degree 2 (5.2–6.5 km) | <i>Mimodromius chilensis</i> (Solier, 1849) (Carabidae) | 87 |
| | <i>Cotyachryson philippii</i> (Porter, 1925) (Cerambycidae) | 87 |
| Degrees 1 + 2 | <i>Hadrobregmus expansicolle</i> (Pic, 1923) (Ptinidae) | 88 |
| | <i>Hadrobregmus spinolae</i> (Solier, 1849) (Ptinidae) | 87 |

suitable microhabitats in the surroundings. Moreover, among the beetles that take advantage of the saproxylic microhabitats offered by these trees, we can find species from the undisturbed areas and those linked to anthropic activities such as the individuals of *Ahasverus advena* (Waltl, 1834) (Silvanidae), *Stegobium paniceum* (Linnaeus, 1758) (Ptinidae), *Micrapate scabrata* (Erichson, 1847) (Bostrichidae), *Scolytus rugulosus* (Müller, 1818) (Curculionidae) and the genus *Carpophilus* Stephens, 1830 (Elateridae), which increases the richness and diversity of these fragmented areas. Perturbation seems to favour predator species and disadvantage the xylomyce-tophaous ones (Fig. 1; Table 3). Xylophagous species showed higher diversity in the less disturbed zone, as they depended on the availability of a large volume of deadwood, which is lower in the areas under anthropic modifications.

All three perturbation degrees had an important number of unique species (degree 1: 22; degree 2: 19; degree 3: 16). This, along with the aforementioned richness and diversity, that are maintained in the fragmented and modified areas, highlights the role of these old scattered trees as ‘keystone-structures’ in the ecosystem (Sirami et al. 2008). However, the number of indicator species and their indicator values decreased when perturbation increased (Table 5). Hence, species such as *Amecocerus giraudii* (Solier 1849) (Melyridae), a predator of saproxylic organisms, and the saprophagous *Scaptia* sp.1 (Scaptiidae), both with an IndVal of 100%, can be especially helpful in identifying areas with a low degree of perturbation.

Conclusions

This first study in Chilean Mediterranean forests highlights their importance for saproxylic beetle diversity and also identified marked spatial and seasonal heterogeneity.

As occurs in Mediterranean European ecosystems (Buse et al. 2010), the presence of different types of natural forest and adjacent fragmented areas, where scattered old native trees are maintained, is directly related to the high biodiversity observed. This highlights the need to maintain both protected areas (which contain a wide range of vegetation types), and also zones where fragmentation has taken place. An action as simple as promoting the conservation of old native trees in disturbed areas can result in the conservation of species of significant value. Given the growing demand for land, there are few opportunities to increase the number of protected areas in central Chile, where species richness and endemism are particularly high and where protected zones are scarce (Pliscoff and Fuentes-Castillo 2011). Initiatives to raise awareness of the value of the perturbed areas around native forests is required, as they can act as critical remnant sites to help sustain the biodiversity not only of the region, but also of other ecosystems around the world (Simonetti et al. 2012).

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