How does the replacement of native forest by exotic forest plantations affect the diversity, abundance and trophic structure of saproxylic beetle assemblages?

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ABSTRACT

Native forest in central Chile has been increasingly replaced by exotic forest plantations. In particular, saproxylic beetles could be highly sensitive to exotic forest plantations due to the clear-cutting management decreases deadwood accumulation while promoting the incompleteness of the decay cycle. We assessed the diversity and density of saproxylic beetle species at two spatial levels (habitat and microhabitat) and compared them among native Maulino forest (Native), Blue-gum eucalyptus plantations (Eucalyptus) and Monterrey pine plantations (Pine). We sampled for adult beetles at 972 logs and stumps. Although exotic plantations and Native had relatively similar amounts of deadwood, beetle species were less diverse and abundant in exotic plantations. Such a decreased density and diversity of saproxylic beetles in plantations depended on the substrate type (logs or stamps), decay stage of wood and trophic level. With the exception of Polyphagous, the richness of all species and trophic guilds decreased in forest plantations, with Eucalyptus supporting the lowest density and richness. The microclimate and the toxic leaf litter in Eucalyptus probably caused the woody biomass to be unsuitable for beetles. Although the guilds of late-successional species were underrepresented in Pine, our results provide the first evidence that saproxylic beetles benefit from exotic woody debris available in Chilean pine plantations. An increased beetle density at expenses of reduced species richness in Pine indicates that ecosystem services provided by saproxylic beetles are not limited in Pine. We suggest the conservation of saproxylic beetles in Pine plantations involves the retention of woody debris along the management cycle.

1. Introduction

Monoculture plantations of commercial species, such as pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.), are increasingly replacing temperate and tropical native forests worldwide, currently covering more than 7% of the global forest area (Payn et al., 2015). Sustainable management of forest plantations, as stated in the Strategic Plan for Biodiversity 2011–2020 of the Convention on Biological Diversity (CBD, 2010), is particularly difficult to achieve because forestry practices disrupt vegetation structure, soil properties and microclimate, thus promoting the loss of biodiversity and environmental services

(Brockerhoff et al., 2008; Niklitschek, 2015). The widespread application of the clear-cutting system in pine and eucalyptus stands causes the simplification of forest and soil structure mainly during the early stages of plantation development (Rosenvald and Lõhmus, 2008; Pawson et al., 2011; Riffell et al., 2011). However, as forest plantation stands get old, they are increasingly perceived as a potential habitat by wildlife fauna (including threatened species), that find supplementary or alternative resources for survival and reproduction (Pawson et al. 2008; Ramirez-Collio et al., 2017). Forest management for wildlife conservation requires understanding how species respond to change of habitat quality through provision, or retention, of particular habitat

features such as canopy-shaded sites, dense understory and coarse woody debris (Gossner et al., 2013a; Simonetti et al., 2013; Cerda et al., 2015).

Forest plantations are thought to act as potential habitats for biodiversity by resembling the structural heterogeneity of native forests (Brockerhoff et al., 2008; Pawson et al., 2010; Paquette and Messier, 2010, 2011). Nonetheless, this assumption is weakly supported for species that are closely related to ecosystem processes inherent to forest habitats, such as saproxylic beetles (deadwood-dependent species) by which tree mortality and wood decay rates are necessary for reproduction, growth and/or survival (Speight, 1989; Grove, 2002; Stokland et al., 2012). Indeed, the abundance and richness of saproxylic beetles are higher when increasing the availability and connectivity of suitable woody debris microhabitats (e.g., larger and decayed logs and stumps; see Schiegg, 2000, Müller and Bütler, 2010; Hjältén et al., 2010). Although the impacts of exotic forest plantations on native saproxylic beetles have not been studied in depth (e.g., see Lachat et al., 2006, 2007; Buse et al., 2010), several reasons do exist to state that pine and eucalyptus plantations could act as unsuitable habitats for saproxylic beetles. Forest plantations tend to accumulate reduced amounts of deadwood due to their short harvesting cycles (usually 10–20 years), as well as by the frequent removal of biomass from thinning, pruning or biofuel extraction (Rudolphi and Gustafsson, 2005; Jonsson and Siitonen, 2012). The wood-decaying process is abruptly interrupted during the clear-cutting operations, when logging wastes are mechanically destructed and burned, consequently preventing woody substrates to be colonized by late-successional saproxylic species (Hjältén et al., 2010; Seibold et al., 2015; Pons and Rost, 2017). Deadwood substrates are smaller and less diverse, coming from tree species that are taxonomically distant from native species, and hence, physically and chemically different (Jonsson and Siitonen, 2012). The subsequent application of insecticide, herbicide and fertilizers reduces the habitat quality for saproxylic biota (e.g., Miller and Miller, 2004; Przewloka et al., 2007).

Forest management intended to benefit saproxylic biota usually focuses on the retention and enrichment of deadwood in managed forest stands (Müller et al., 2015 Gossner et al., 2013b, 2016). However, the partial knowledge about how saproxylic species use and colonize deadwood in forest plantations may make these management prescriptions useless for conservation purposes. Saproxylic beetles conform a rich assemblage of interacting species, with some trophic guilds being more diverse under advanced stages of wood decay, such as Zoophagous (predators), Mycophagous, Xylomycophagous and Saproxylophagous (Vanderwel et al., 2006; Micó et al., 2015). The underrepresentation of saproxylic beetle species in forest plantations, however, could be compensated by the increased abundance of some beetle species using exotic deadwood, including exotic (i.e. non-native) beetle species that would facilitate the subsequent use of woody substrates by native species (Lachat et al., 2007; Bertheau et al., 2009; Buse et al., 2010; McCarthy et al., 2013). The conservation of saproxylic beetles diversity in forest plantations is justified by the environmental services rendered by them (Paquette and Messier, 2011). Saproxylic beetles act as a major driver of deadwood decay rates, contributing to the productivity of forest plantations by releasing nutrients, but also through decreasing the risk of fire (Edmonds and Eglitis, 1989; Fayt, 2004; Ulyshen, 2013, 2016).

Central Chile is considered a hotspot of biodiversity (Myers et al., 2000), with a high endemism of saproxylic beetles (see Paulsen, 2010). The accelerated loss and replace of the Maulino forest by fast-growth plantations of Blue gum eucalyptus (*Eucalyptus globulus*) and Monterrey pine (*Pinus radiata*), faces the challenge of achieving sustainable forest management focused on saproxylic beetle species with conservation concerns and the maintenance of environmental services provided by them. Here, we evaluate the diversity, composition and abundance of saproxylic beetles living in Maulino forest and exotic forest plantations (Blue gum eucalyptus and Monterrey pine) at two spatial levels: habitat (forest stands) and microhabitat (individual logs and different stages of decay). Specifically, we hypothesize that Maulino forest offers better habitat conditions for saproxylic beetles than eucalyptus and pine plantations. This hypothesis poses that forest plantations provide saproxylic beetles with low quality and quantity of deadwood, which reduces the persistence of beetle populations sensitive to anthropogenic forest disturbances, while altering the diversity and trophic structure of beetle communities. The following three predictions derived from this hypothesis were tested:

(i) At the habitat level, Maulino forest should support a more diverse assemblage of saproxylic beetles than forest plantations (eucalyptus and pine stands).

(ii) At the microhabitat level, individual logs and stumps in Maulino forest should have a higher abundance and richness of saproxylic beetles than those in forest plantations, with those differences being more pronounced as logs or stumps become more decayed.

(iii) Trophic guilds associated with logs and stumps in an advanced state of decay should be poorly represented in forest plantations.

2. Materials and methods

2.1. Study area

The study was conducted at the Coastal Range of the Maule Region, South-Central Chile (35°36′10″S, 72°20′60″W and 36°00′36″S, 72°20′60″W), an area originally covered by Maulino forest, and more recently, dominated by extensive plantations of Blue gum eucalyptus (*Eucalyptus globulus*) and Monterrey pine (*Pinus radiata*) (Fig. 1). Saproxylic beetles were sampled in 24 different stands, with eight stands per habitat type, including fragments of native Maulino forest, stands of "mature" (20–30 years-olds) Monterrey pines and stands of mature (10–13-year-olds) Blue gum eucalyptus; hereinafter referred to as Native, Pine and Eucalyptus, respectively. Pine and Eucalyptus were selected to represent the dominant type of forest management applied in the study area, which considers the retention of deadwood. Thus, the few stands (n = 2) where we did not detect deadwood pieces were not included for analysis because in these stands logging wastes are intensively extracted by local communities for firewood and coal production. The minimum distance between stands was ca. 2 km. The area of Native ranged between 25 and 50 ha and were composed by secondary forests dominated by *Nothofagus glauca*, and accompanied by *Cryptocaria alba*, *Laurelia sempervirens*, *Persea lingue* and *Nothofagus obliqua*. Trees in Native were 15–20 m in height and 20–40 cm in diameter at the breast height (DBH). The understory vegetation at Native covered 50 to 75%, and was composed mainly by native young trees, shrubs and creepers. The size of Pine ranged between 100 and 400 ha. Pine trees were 25–35 m in height and 20–35 cm in DBH. The understory at Pine covered 20–50% and was composed mainly by the native and exotic shrubs. The size of Eucalyptus ranged between 50 and 100 ha. Eucalyptus trees were 15–20 m in height and 15–25 cm in DBH. The understory of Eucalyptus covered 15–35% and was composed by native and exotic shrubs (e.g. *Teline monspessulana* and *Rubus constrictus*). The identity of deadwood varied among habitats. In Native, deadwood included *Nothofagus* logging residues from charcoal harvesting and from naturally fallen branches and trunks. In Pine and Eucalyptus, deadwood was composed by logging wastes from clear cutting, thinning and pruning of pine plantations. Eucalyptus were first rotation stands, therefore, lacked coarse woody debris (> 6 cm diameter) from eucalyptus trees, but *Pinus* logging wastes remained from the previous plantations (see below for Section 2.3).

2.2. Saproxylic habitat

We characterized each habitat type (Native, Pine and Eucalyptus) at the stand-level by estimating variables recognized to influence
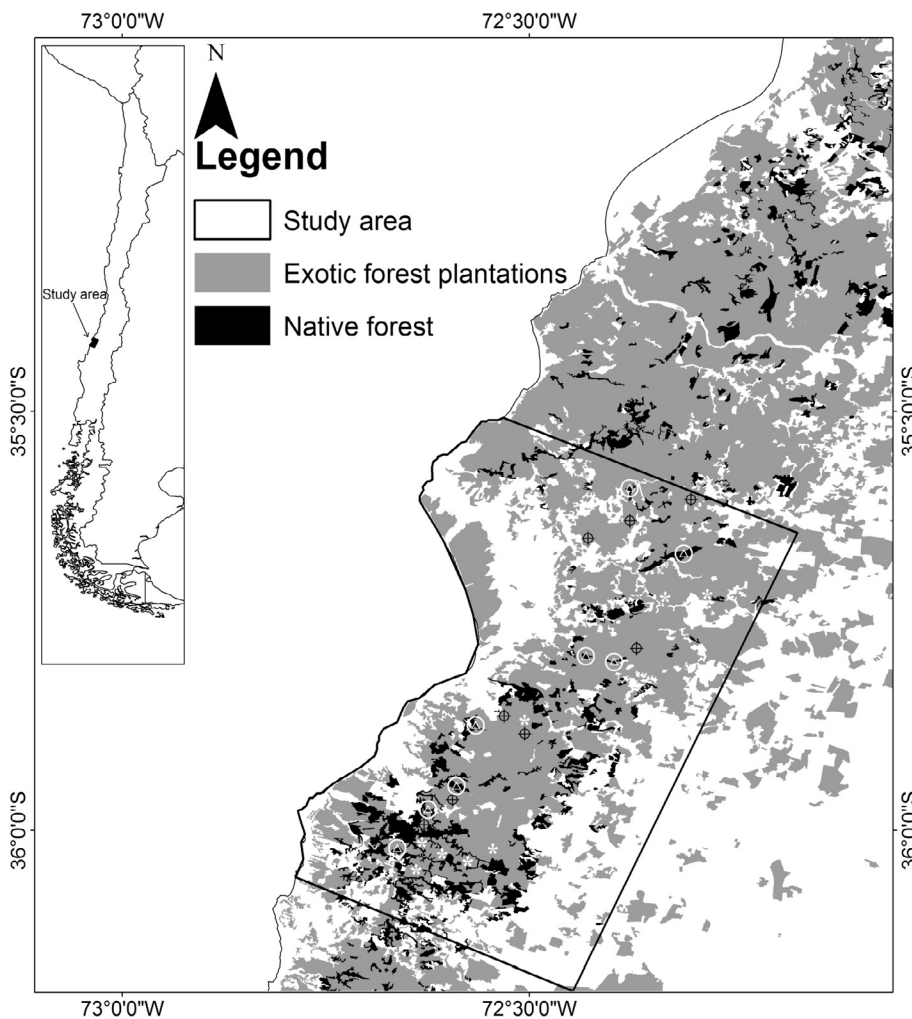
Fig. 1. Map of the study landscape comprising the sampling stands of Blue gum eucalyptus (*Eucalyptus globulus*) (white asterisks), Monterrey pine (*Pinus radiata*) (black circles with black crosses inside) and Maulino deciduous forest (white circles with white triangles inside).

saproxylic beetle diversity (Grove, 2002). In each sampled stand, variables were measured in six square plots of 0.04 ha, thus giving a total of 144 plots. We included five variables, three of them describing deadwood amounts (Müller and Bütler, 2010) and two variables associated with vegetation structure:

(i) *Density of deadwood:* the number of pieces of deadwood per ha, including the total number of logs and stumps > 6 cm and > 10 cm in diameter, respectively, recorded at each plot.
(ii) *Volume of deadwood:* it involved the measurement of each deadwood piece (log or stump) found by using the Newton's truncated cone formula:

$$V = \frac{L \times (A_b + 4 \times A_m + A_t)}{6}$$

where V is the volume (m^3/ha) of a log or stump, L its length and A_b, A_m, A_t the areas at the base, middle and top, respectively (Harmon and Sexton, 1996).

(iii) *Diversity of deadwood:* we used the index of Siitonen et al. (2000), which is based on the number of possible combinations (n = 48) of deadwood attributes, as follow: (1) the identity (exotic or native trees); (2) substrate type (log or stump); (3) diameter (four classes: 6–10 cm, 10–20 cm, 20–30 cm, > 40 cm); and (4) decay stages (three classes: early, intermediate and late; see Franc et al. (2007) for details).
(iv) *Canopy cover:* the percentage of canopy covering the ground based on 30 digital photographs (5 per plot) taken to the sky. Using the

Gap Light Analyzer program (GLA v2), color pixels were converted into black and white pixels, and then counted for estimation of the proportion of visible sky.
(v) *Understory cover:* the cover (%) of herbs, shrubs, and tree saplings estimated visually at 0.5 and 1 m height in each plot.

2.3. Beetle sampling

Adult beetles were sampled at a total of 972 pieces of deadwood (n = 648 logs and n = 324 stumps), with a total of 216 logs and 108 low stumps per habitat type. We selected logs and stumps with sizes within the range commonly found in forest stands: logs were 50–150 cm in length and 6–20 cm in diameter, whereas stumps were 10–40 cm in height and 10–40 cm in diameter. In each stand (Native, Pine and Eucalyptus), stumps and logs were searched intensively by four trained observers who walked through zigzagging transects. The selected stumps and logs were located more than 15 m apart in order to reduce spatial dependence. Once found, each log or stump was measured (length and diameters for volume estimation, as described above) and classified into one of three possible decay stages based on pressure exerted by a knife on the wood piece, as described by Franc et al. (2007). Three decaying classes were considered: early, intermediate and late. In some stands we did not find all substrate types and decay classes. To avoid incomplete sampling and obtain a balanced design, we replicated six times each possible combination of substrate type (log or stump) and decay class (see above) in each habitat type, with a replicate consisting of 12 logs and 6 stumps. The identity of deadwood changed with habitat type: only deadwood from *Nothofagus glauca* trees

was sampled at Native, whereas in Eucalyptus and Pine only deadwood from pine was sampled. Pieces whose tree species identity was difficult to classify were discarded.

We used the "wood dissection" method (*sensu* Saint-Germain et al., 2007) to search beetles by progressively breaking deadwood into smaller woody pieces on a 4 m² white sheet for a period between 10 and 20 min (total sampling effort was 251 h distributed along 50 days). This sampling methodology ensured to capture insects exclusively occupying deadwood, and hence it provided more clarity regarding deadwood preferences by saproxylic beetle species (Saint-Germain et al., 2007). Once captured, all beetles were identified to species level and posteriorly released *in situ*, or preserved in 70% ethyl alcohol, when unknown. These unknown beetles were identified in laboratory by using taxonomic keys, and compared with specimens deposited in the Entomological Collection of the National Museum of Natural History (MNHN).

Based on the trophic ecology of the larvae (Elgueta and Arriagada, 1989; Beutel and Leschen, 2005; Leschen et al., 2010), the captured species were assigned to a particular trophic guild, as proposed Bouget et al. (2005) and Micó et al. (2015). Seven trophic guilds were considered: (1) Mycophagous (generalist fungivorous); (2) Xylomycophagous (fungivorous specialized in saproxylic fungi); (3) Xylophagous (detritivores specialized in early stages of decay); (4) Saprophagous (generalist detritivores); (5) Saproxylophagous (detritivores specialized in intermediate or late stages of decay); (6) Polyphagous (broad dietary preferences); and (7) Zoophagous (predators of invertebrates).

2.4. Analysis of habitat variables

Standardized habitat variables were compared among Native, Pine and Eucalyptus using univariate Gaussian Generalized Lineal Mixed Models (GLMMs), including the forest stand as a random effect factor. Due to insufficient data and collinearity problems, habitat variables were not used in microhabitat-level analysis (see below). Model performance was evaluated using Likelihood Ratio Test (LRT), while Tukey's test was used to compare between factor levels. Analyses were carried out in R v.3.3.2 (R Development Core Team, 2017).

2.5. Habitat-level analysis

We compared the diversity of saproxylic beetles between habitats using sampled-size and coverage methods (sample completeness) based on rarefaction (interpolation) and extrapolation (prediction) of Hill numbers (effective number of species) of order q (q = 0, 1 and 2; Hill, 1973; Jost, 2006; Chao et al., 2014). When q = 0, the species diversity (^0D) is the species richness, with rare and abundant species being equally weighted. When q = 1, ^1D is the Shannon diversity, weighting species according to their relative abundances. When q = 2, ^2D is the Simpson diversity, with the most abundant (dominant) species contributing disproportionately to diversity. For each habitat, we also compared diversity between substrate types (logs vs. stumps), as explained above. Since we sampled a larger number of logs than stumps (n = 648 vs. n = 324), diversity comparisons between substrates were based on species incidence. Species diversity was estimated using the

iNEXT R package (Hsieh et al., 2016). Species diversity was also evaluated through assessing patterns of species abundance distributions (Magurran, 2004). Rank-abundance curves, ranking species from the most abundant to the least abundant, were analyzed by fitting different rank-abundance models with the sad R package. We compared two models, MacArthur broken-stick distribution and Geometric series, because these models are commonly used and represent different community structures (Fattorini et al., 2016). The geometric series represents communities with a less equitable distribution and characterized by the high dominance of a few species (Magurran, 1988, 2004), while the MacArthur broken-stick distribution represents communities with a more equitable distributions (Wilson, 1993). Finally, we compared the composition of saproxylic beetles between habitats using the Bray-Curtis dissimilarity index (Magurran, 1988) with square root transformed data to avoid biases towards the more abundant species (Clarke, 1993). Bray-Curtis matrix was ordered with a non-metrical multidimensional scaling (NMDS) to visualize similarities (Clarke and Ainsworth, 1993). Habitat effects on species composition was estimated through PEMANOVA with 5000 Monte Carlo permutations run in PRIMER 6 + PERMANOVA (Anderson, 2001; Anderson et al., 2008; Clarke and Gorley, 2006).

2.6. Microhabitat-level analysis

The density of species (hereinafter referred to as "richness") and individuals per volume of dead wood (s/cm³ and n/cm³, respectively) of saproxylic beetles measured at individual logs and stumps were assessed using GLMMs. We specified the density and richness of beetles at individual logs or stumps as the response variables. We estimated the richness of all species and for each guild, while density data was pooled for all species and each trophic guild. Due to their overdispersed distributions, abundance and richness data were assumed to be negative binomially distributed (e.g., Gough et al., 2014), and thus, modelled with a log-link function using the glm.nb function from MASS R package. Overdispersion parameter of the negative Binomial model was above 1.0 for all density and richness variables. Evidence of overdispersion was tested though the "dispersiontest" function from the AEER R package and the odTest function from the pscl R package. The volume of each individual log and stump, log (cm³), was specified as an offset covariate (i.e., a variable whose coefficient is fixed to equal one) in order to provide a density measurement. We used an information-theoretic approach based on the Akaike Information Criterion (AIC; Burnham and Anderson, 1998) to select the most parsimonious models from a set of candidate models. We used the dredge function from the MuMIn R package, which carries out an automated model selection procedure using all possible combinations of predictor variables from a global model. The model.avg function from the MuMIn R package was used to estimate model-averaged coefficients for the explanatory variables contained in the set of best-supported models.

Table 1
Differences in habitat variables (Mean ± SE) among stands of native forest (Native), eucalyptus plantation (Eucalyptus) and pine plantation (Pine). Significant differences (p < 0.05) among habitat types are indicated by different letters, as based on Tukey's test for multiple comparisons.

Habitat variables	Native Mean ± SE	Pine Mean ± SE	Eucalyptus Mean ± SE	p
Canopy cover	80.68 ± 8.97 a	76.66 ± 1.26 a	49.68 ± 4.96 b	0.0017
Understory cover	62.26 ± 5.92 a	34.42 ± 7.05 b	23.02 ± 3.61 b	< 0.001
Deadwood volume	12.70 ± 2.74	8.33 ± 1.62	9.30 ± 1.67	0.1089
Deadwood density	272.5 ± 33.24 b	339.50 ± 75.52 ab	531.0 ± 102.76 a	0.0264
Deadwood diversity	18.24 ± 2.29	19.50 ± 2.13	23.13 ± 3.01	0.2464

Table 2

Values of extrapolation and interpolation of saproxylic beetle diversity estimates on different habitats (Native, Pine and Eucalyptus) and substrate types (logs and stumps). N: number of individuals (when habitats are compared) or number deadwood pieces (when substrate types are compared). S obs.: richness observed, S exp.: richness expected, C hat: sample coverage, ^0D: effective species richness, ^1D: Shannon diversity or the effective number of common species, ^2D: Simpson diversity or the effective number of dominant species.

| Diversity estimator	Habitats			Logs				Stumps			
	Native	Pine	Eucalyptus	Total	Native	Pine	Eucalyptus	Total	Native	Pine	Eucalyptus
N	9312	8733	4765	648	216	216	216	324	108	108	108
S obs.											
^0D	251	247	178	246	246	238	155	165	165	136	136
^1D	141.63	106.77	86.83	144.58	164.39	139.50	98.76	106.86	121.70	98.48	94.72
^2D	95.95	63.41	58.31	109.52	131.14	103.59	77.26	87.56	101.24	83.30	77.15
S exp.											
^0D	253.75	254.49	190.84	249.77	251.42	246.21	166.54	178.16	174.89	150.36	146.67
^1D	142.89	107.83	88.03	145.68	167.24	142.39	101.87	108.37	126.50	102.2	98.25
^2D	96.45	63.63	58.66	110.10	132.77	104.76	78.78	88.38	104.43	85.65	79.168
C hat	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.98	0.99	0.98
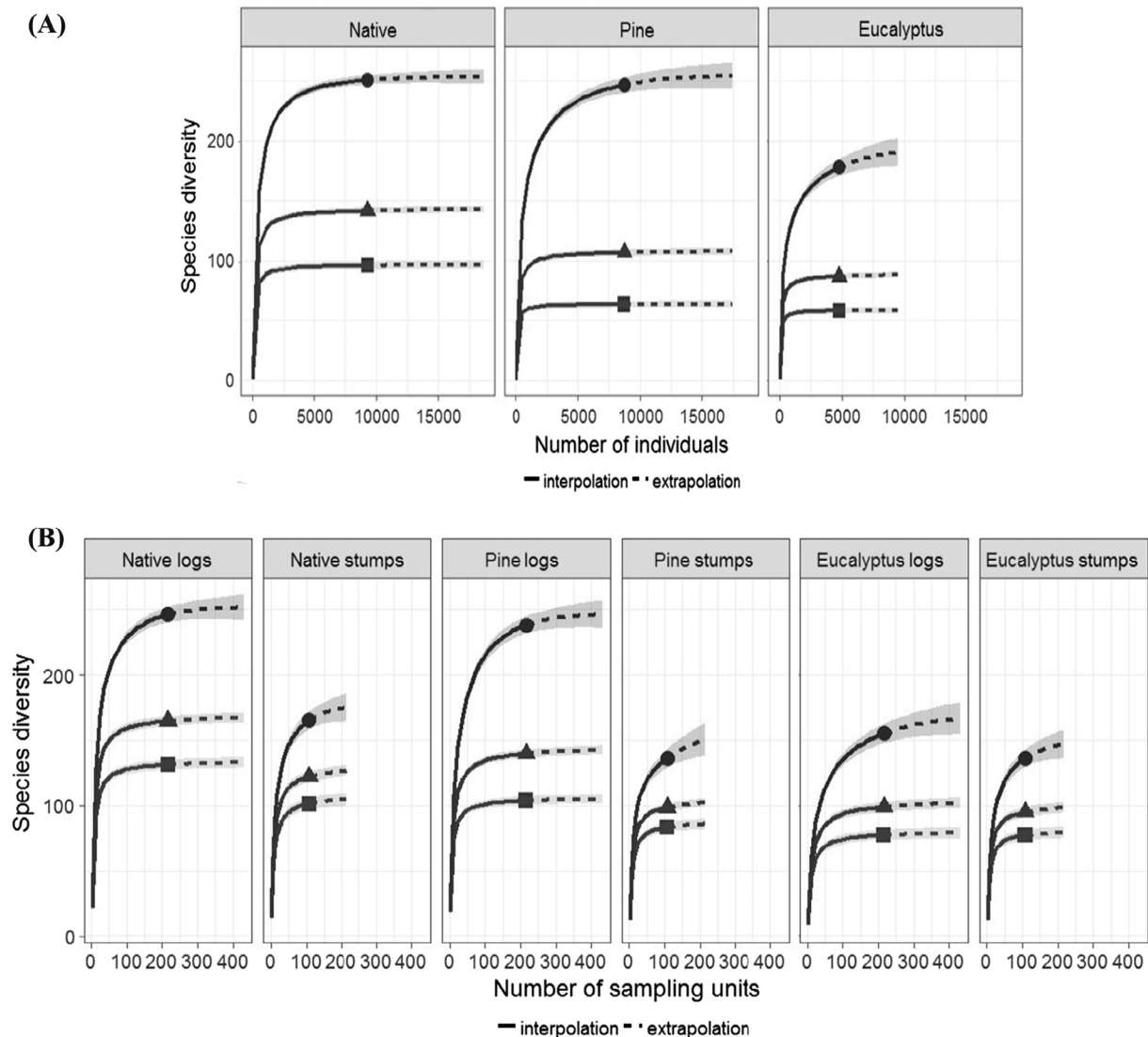
Fig. 2. Curves (dotted lines) of rarefaction and extrapolation of Hill's numbers diversity for saproxylic beetle species for: (A) three habitat types: Native (Maulino deciduous forest), Eucalyptus (stands of Blue gum eucalyptus) and Pine (stands Monterrey pine) and (B) two deadwood substrate types (logs and stumps), independently shown for each habitat type (Native, Eucalyptus and Pine). Species diversity, based on Hill's numbers of order q represents the effective species numbers, with species richness given (q = 0), Shannon diversity (q = 1) and Simpson diversity (q = 2). Shaded areas correspond to 95% confidence intervals.
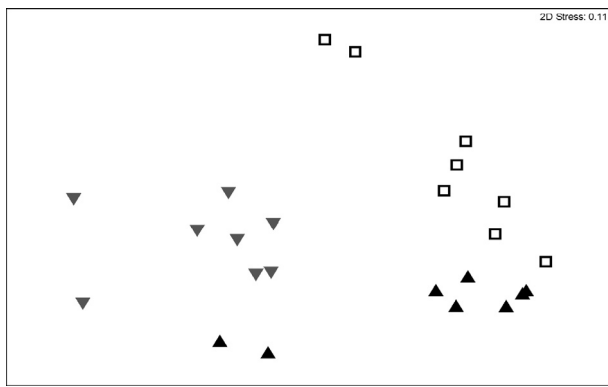
Fig. 3. NMDS ordination of the study forest stands (n = 24) based on Bray-Curtis distances between saproxylic beetle assemblages of eucalyptus plantations (inverted grey triangles), Monterrey pine plantations (white square) and Maulino deciduous forest (black triangles).

3. Results

3.1. Saproxylic habitat

GLMMs showed the density of deadwood was higher in Eucalyptus than Native, but Eucalyptus and Pine did not differ (Table 1). The volume and diversity of deadwood did not vary among habitats (Table 1). Conversely, canopy and understory cover responded to habitat, with canopy cover being larger in both Native and Pine than Eucalyptus, while understory cover in Native was larger than in both Pine and Eucalyptus (Table 1).

3.2. Assemblage characterization

We recorded 22,810 beetles belonging to 259 species and 41 families, with a total of 9312, 8733 and 4765 in Native, Pine and Eucalyptus, respectively (Appendix 1, Table 1). The three most abundant species were *Nothocoxelus angustatus* (Solier, 1851) (Zopheridae), *Heliofugus impressus cribicephalus* (Freude, 1960) (Tenebrionidae) and *Archephthora penai* Kaszab, 1978 (Tenebrionidae), which comprised 4.4%, 3.6% and 3.1% of individuals, respectively. In Native, Pine and Eucalyptus 36, 24 and 22 species accounted for half of all individual, respectively. Only four exotic species (i.e. non-native) were found, *Hylastes ater* Paykull, 1800 (Curculionidae), *Atomaria lewisi* Reitter, 1877 (Cryptophagidae), *Litargus balteanus* LeConte, 1856 (Mycetophagidae) and *Ernobius mollis* (Linnaeus, 1758) (Ptinidae), which together comprised ca. 0.4% of individuals. The trophic guilds with more individuals and species were Zoophagous (28.4% of individuals, with 92 species), Xylomycophagous (26.1% of individuals, with 39 species), Mycophagous (21.3% of individuals, with 55 species) and Saproxylophagous (19.9% of individuals, with 47 species).

3.3. Habitat-level diversity and composition

Overall, species diversity decreased from Native to Eucalyptus. However, depending on the order (q) of the Hill number, diversity differences between Pine and Native were not completely consistent. ^0D at Native and Pine was higher than Eucalyptus, while ^1D and ^2D were higher in Native than both Pine and Eucalyptus (Table 2, Fig. 2A). When compared by substrate type, ^0D, ^1D and ^2D were higher in logs than in stumps. When compared the different combinations of substrate and habitats, also diversity differences were observed among habitats. For logs, ^0D, ^1D and ^2D decreased in Eucalyptus relative to Native and Pine (Table 2, Fig. 2B). For stumps, ^0D, ^1D and ^2D were higher in Native, and similar between Pine and Eucalyptus (Table 2, Fig. 2B).

Native supported an assemblage of saproxylic beetles with a more equitable distribution of abundance among species than that of forest plantations characterized by the dominance of rare species and the presence of a few dominant species (Appendix 2). The Broken-stick distribution was best fitted to the species abundance distribution of Native than the geometric series, while the geometric series was best fitted for species abundance distribution of Pine and Eucalyptus (Appendix 2). Beetle assemblage composition differed significantly among habitats (PERMANOVA: $F_{2,21} = 5.38$, $p < 0.001$; Fig. 3), with Native and Pine being more similar between themselves (Bray-Curtis = 58.42%; PERMANOVA: $t_{14} = 1.78$, $p = 0.021$) than Native and Eucalyptus (Bray-Curtis = 55.20%; $t_{14} = 2.55$, $p = 0.002$) and Eucalyptus and Pine (Bray-Curtis = 54.27%; PERMANOVA: $t_{14} = 2.59$, $p < 0.001$).

3.4. Microhabitat-level density

The most parsimonious GLMMs (ΔAICc < 2) indicated that density of saproxylic beetles was affected by habitat type, substrate type and decay stage, but also by the interactions "Habitat × Substrate" and "Habitat × Decaying" (Table 3). The coefficients of the best supported GLMMs showed that the density of all species, and trophic guilds, decreased at Eucalyptus, when compared with Native (Table 4). However, when compared with Pine, only the density of Zoophagous, Mycophagous and Polyphagous decreased, relative to Native, while Saprophagous increased in Pine relative to Native (Table 4). Logs supported a higher density of saproxylic beetles than stumps for all species and trophic guilds (Table 4). The density increased with decay stage, except for Polyphagous, Saprophagous and Xylophagous, with the latter decreasing as the decay stage became more advanced (Table 4). The interaction Eucalyptus × Stump was positive for all species and trophic guilds, indicating that the negative stump effect on density, relative to logs, decreased at Eucalyptus (Table 4). Zoophagous exhibited a negative significant effect of Pine × Stump interaction, which indicates the negative effect of stumps on the density of Zoophagous becomes weaker at Pine (Table 4). The decay stage effect on the density saproxylic beetles was dependent on habitat, as shown by Habitat × Decaying interactions. The density of saproxylic beetles tended to

Table 3
The best-supported (ΔAIC < 2) Generalized Linear Mixed-effects Models (GLMMs) testing for the effects of habitat, substrate type and decay stage (and their interactions) of logs and stumps on the density of individuals (n/cm^3) of all species and different trophic guilds of saproxylic beetles.

Response	Models	df	Log-Lik	AIC	ΔAIC	Weight
All species	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate	9	−573.67	1167.18	0.00	0.66
	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−569.32	1168.50	1.32	0.34
Zoophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−431.19	892.26	0.00	1.00
Mycophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−412.53	854.94	0.00	1.00
Polyphagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−193.58	417.02	0.00	0.70
	log(n) ~ Habitat + Substrate + Decaying + Habitat × Decaying	11	−196.98	418.72	1.69	0.30
Saprophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate	9	−240.42	500.66	0	0.70
Xylophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Decaying	11	−172.09	368.93	0	0.83
Saproxylophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−422.91	875.70	0	0.96
Xylomycophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate	9	−470.07	959.96	0	0.93

Table 4
Model-averaged coefficients from the best-supported (ΔAICc < 2) Generalized Linear Mixed-effects Models (GLMMs; Table 3) testing for the effects of habitat, substrate type and decay stage (and their interactions) of logs and stumps on the density of individuals (n/cm³) of all species and trophic guilds of saproxylic beetles. Different letters indicate statistically significant difference (p < 0.05) among groups based on Tukey's test for multiple comparisons.

Variables	Levels	All species	Zoophagous	Mycophagous	Polyphagous	Saprophagous	Xylophagous	Saproxylophagous	Xylomycophagous
Habitat	Eucalyptus	−1.08 (0.17)b ***	−2.42 (0.21)c ***	−2.28 (0.22)c ***	−3.65 (1.03)c ***	−0.91 (0.31)b ***	−0.35 (0.16)b *	−1.51 (0.22)b ***	−0.85 (0.15)b ***
	Pine	−0.11 (0.12)a	−1.18 (0.18)b ***	−0.93 (0.18)b ***	−1.88 (0.50)b ***	0.45 (0.22)b *	−0.12 (0.15)a	0.12 (0.18)a	0.08 (0.16)a
Position	S	−2.96 (0.10)b ***	−2.88 (0.11) ***	−2.92 (0.11) ***	−2.83 (0.20) ***	−2.79 (0.23) ***	−2.08 (0.14) ***	−3.13 (0.13) ***	−3.09 (0.15) ***
Decaying	CII	0.98 (0.13)b ***	1.04 (0.14)b ***	1.13 (0.15)b ***	0.48 (0.25)	0.29 (0.19)	−3.17 (0.37)b ***	0.80 (0.16)b ***	0.89 (0.12)b ***
	CIII	0.98 (0.12)b ***	1.15 (0.14)b ***	1.25 (0.15)b ***	0.34 (0.25)	−0.29 (0.25)	−3.55 (0.67)b ***	0.79 (0.16)b ***	0.57 (0.13)b ***
Habitat × Position	Eucalyptus × Stump	0.77 (0.15) ***	0.66 (0.17) ***	1.29 (0.17) ***	0.65 (0.32) *	0.75 (0.37) *		0.85 (0.19) ***	0.87 (0.21) ***
	Pine × Stump	−0.02 (0.14)	−0.44 (0.17) **	0.26 (0.17)	−0.16 (0.31)	−0.43 (0.33)		0.14 (0.18)	0.12 (0.21)
Habitat × Decaying	Eucalyptus × CII	0.47 (0.17) **	1.68 (0.24) ***	0.97 (0.24) ***	3.35 (1.05) ***		−0.09 (0.59)	0.76 (0.25) **	
	Eucalyptus × CIII	0.40 (0.17) *	1.78 (0.24) ***	0.98 (0.24) ***	3.54 (1.05) ***		27.67 (29.27)	0.68 (0.25) **	
	Pine × CII	0.12 (0.17)	1.04 (0.22) ***	0.66 (0.21) **	2.22 (0.54) ***		1.30 (1.44)	−0.02 (0.23)	
	Pine × CIII	0.08 (0.17)	1.27 (0.22) ***	0.74 (0.21) ***	2.50 (0.54) ***		1.91 (1.61)	−0.23 (0.23)	

increase with the decay stage, but such an increase was not proportional among habitats, as exhibited by all species, Zoophagous, Mycophagous, Polyphagous and Saproxylophagous (Table 4, Fig. 4A). Overall, for those guilds, the density differences between Native and Eucalyptus increased as the decay stage increased (Fig. 4A). Furthermore, for Native and Pine, the densities of Zoophagous and Mycophagous tended to be similar as the decay stage increased (Fig. 4A).

3.5. Microhabitat-level richness

We found 251, 247 and 178 species of saproxylic beetles in Native, Pine and Eucalyptus, respectively (Appendix 1, Table 1). The most parsimonious GLMMs (ΔAICc < 2) indicated the richness of saproxylic beetles was affected by habitat, substrate type, decay stage and the Habitat × Substrate and Habitat × Decaying interactions (Table 5). Overall, coefficients of the best supported GLMMs showed that all species and trophic guilds exhibited a higher richness in Native than forest plantations (Table 6). Logs supported a higher richness than stumps for saproxylic beetles of all species and trophic guilds (Table 6). The richness of all species and trophic guilds was higher in deadwood with intermediate and late decay stages than early decay stage, with the exception of Saprophagous and Xylophagous, with the latter decreasing as the decay stage becomes more advanced (Table 6). The interactions Eucalyptus × Stump and Pine × Stump were positive for all species, Zoophagous, Saproxylophagous and Xylomycophagous, which indicates that, for these species, the negative effect of stumps, relative to logs, was weakened in forest plantations (Table 6). The differences in species richness between Native and Eucalyptus changed as the decay stage of wood increased. These differences increased for all species, Mycophagous and Xylomycophagous, while richness differences between Native and Eucalyptus decreased for Zoophagous and Saproxylophagous (Table 6). Richness differences between Native and Pine increased for all species and Saproxylophagous from DI to DII (i.e., early to intermediate decay stage), but decreased from DII to DIII (i.e., intermediate to later decay stage; Table 6, Fig. 4B). Mycophagous and Xylomycophagous in Pine exhibited richness differences with Native for DI only, while Zoophagous in Pine differed with Native for DI and DII (Table 6, Fig. 4B).

4. Discussion

Forest plantations are believed to act as an alternative, but impoverished habitat for several forest-specialist species, such as carnivores, birds, small mammals and insects (e.g., Vergara and Simonetti, 2004; Pawson et al., 2008; Simonetti et al., 2013; Cerda et al., 2015). Our results, however, showed that exotic forest plantations (Pine and Eucalyptus) have similar, or higher volume, density and diversity of deadwood than Native. Despite of providing a similar availability of deadwood, saproxylic beetle assemblages of Pine and Eucalyptus were less diverse and abundant than that of Native.

Previous studies suggest that not only the amount of deadwood is important for the survival, reproduction and population persistence of saproxylic beetle species, but factors associated with the quality of deadwood (e.g., diversity, diameter and host tree) and their interactions with microclimate conditions are also important (Müller and Bütler, 2010; Seibold et al., 2015, 2016). We did not find such an association between deadwood amounts and both, diversity and density, of saproxylic beetle species because plantations (especially Eucalyptus) seemed to support low deadwood quality for native species. Low rates of decomposition of exotic deadwood resulting from an impoverished assemblage of saproxylic organisms (e.g., fungi and bacteria) would contribute to reduce deadwood quality in forest plantations. First, forest plantations may fail in ensuring environmental conditions suitable for the decay of deadwood (e.g. humid microhabitats), as deduced from the low cover of canopy and understory (e.g., Table 1), as well as from the increased water consumption and soil compaction observed in forest
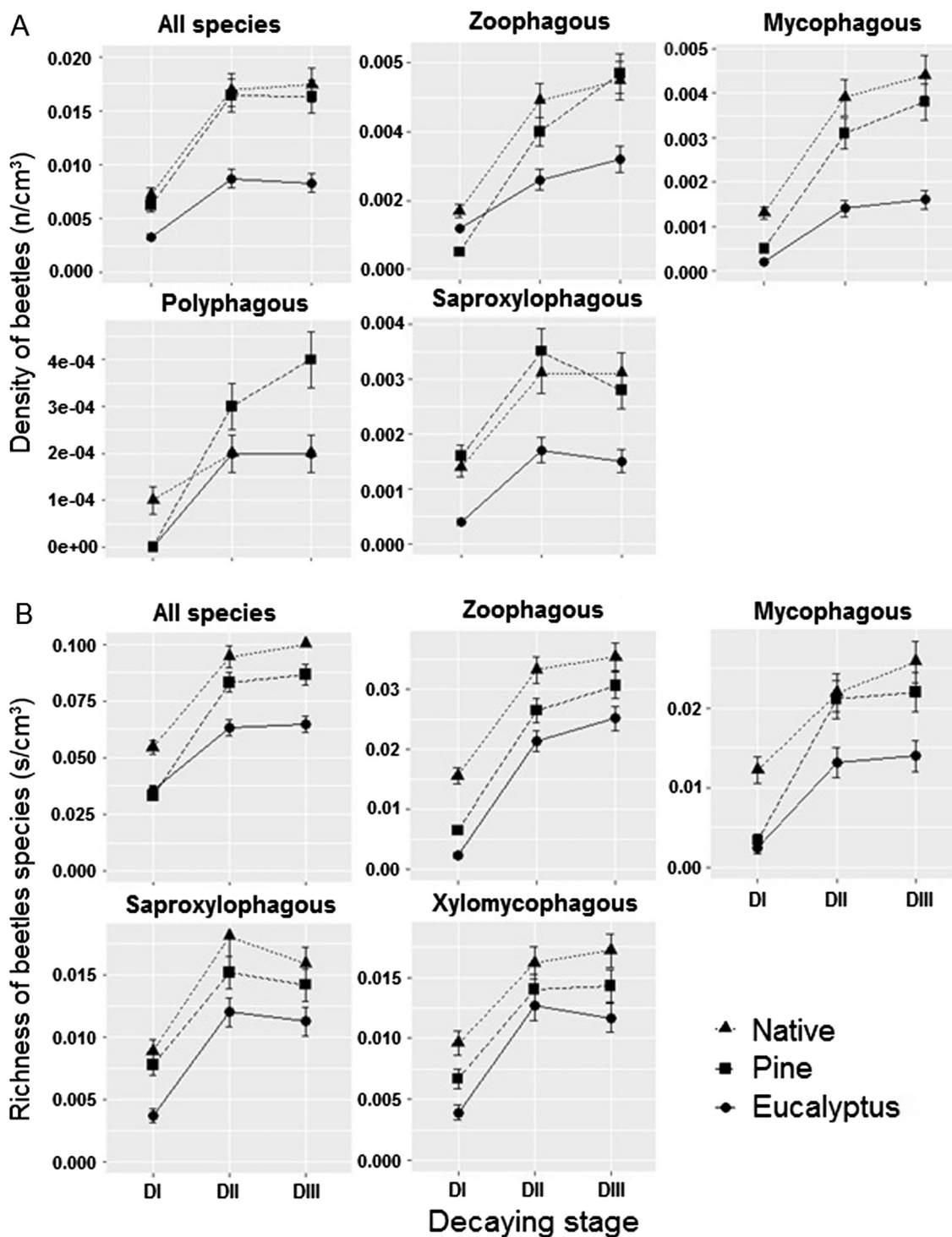
Fig. 4. (A) Density (n/cm³), and, (B) species richness (s /cm³) of saproxylic beetle species in logs and stumps found in Native, Eucalyptus and Pine with a different decay stage: DI = early decay stage of wood; DII = intermediate decay stage of wood, DI = late decay stage of wood. Density and richness values are predicted from GLMMs fitted to data of 648 logs and 324 stumps (see Tables 3 and 5).

plantations (Farley et al., 2005; Little et al., 2009). Second, forest plantations had deadwood derived from logging waste of pine planta- tions, rather than from native *Nothofagus* species. Woody debris from Monterrey pine has physical and chemical properties (e.g., fibrous and resinous woods) inherent to coniferous tree species (Stokland, 2012), which in deciduous Maulino forest are infrequent and only represented by *Podocarpus saligna* (Podocarpaceae; Arroyo et al., 2005). Third, and as a consequence of the above, plantations could have an insufficient diversity or abundance of insect and fungi species for ensuring the rapid

wood decomposition (e.g., Jonsson and Siitonen, 2012). These differ- ences in microclimate, wood properties and biological agents of dead- wood decay, could slow the wood-decay rate, thus promoting the ac- cumulation of above-ground woody debris biomass in forest plantations (Ulyshen, 2016).

Native forest and pine plantations were relatively similar in terms of ^0D and assemblage composition (Fig. 2). However, Pine supported an impoverished assemblage in terms of ^1D and ^2D, indicating more equitability in Native than Pine, where a few species have a large

Table 5

The best-supported (ΔAIC < 2) Generalized Linear Mixed-effects Models (GLMMs) testing for the effects of habitat, substrate type and decay stage (and their interactions) of logs and stumps on the species richness (s/cm^3) of all species and different trophic guilds of saproxylic beetles.

Response	Models	df	Log-Lik	AIC	ΔAIC	Weight
All species	log(n) ~ Habitat + Substrate + Decaying + Habitat * Substrate + Habitat × Decaying	13	−406.38	842.64	0	1
Zoophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−324.71	679.29	0	1
Mycophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−282.6	595.08	0	1
Polyphagous	log(n) ~ Substrate + Decaying	5	−126.34	263.27	0	0.79
Saprophagous	log(n) ~ Habitat + Substrate + Decaying	7	−148.8	312.73	0	0.59
	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate	9	−147.19	314.21	1.48	0.28
Xylophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Decaying	11	−120	264.75	0	0.89
Saproxylophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate	9	−279.03	577.89	0	0.54
	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−274.19	578.24	0.35	0.46
Xylomycophagous	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate + Habitat × Decaying	13	−262.81	555.5	0	0.57
	log(n) ~ Habitat + Substrate + Decaying + Habitat × Substrate	9	−268.11	556.05	0.55	0.43

dominance. Estimates of species diversity were consistent with the theoretical models fitted to species abundance distributions. Beetle assemblages in Native followed a Broken-stick distribution, characterized by relatively high degree of equitability, while assemblages in Pine and Eucalyptus exhibited distributions consistent with the geometric series. These results contrast with those reported for assemblages of tropical tree species (Steege et al., 2013; Ulrich et al., 2016) and arthropod species (Fattorini et al., 2016), whose species–abundance distributions typically follow log-series or geometric series. When comparing diversity between plantations, Eucalyptus was a more hostile habitat than Pine, with these differences being mostly explained by ^0D and ^1D. However, Pine and Eucalyptus had a low ^2D, indicating both forest plantations may be less suitable habitat for dominant species of saproxylic beetles (Jonsson and Siitonen, 2012). Although the type of deadwood substrate (logs or stump) was an important factor explaining the diversity of saproxylic beetle species, our results further suggest that the likelihood of saproxylic beetles to occupy stumps or logs depends on the habitat type and trophic guild. In particular, logs had a relatively high density and richness of saproxylic beetles in Native and Pine (see Fig. 4A and B; Tables 4 and 6), which, for management purposes, is consequent with the log enrichment strategy in forest plantations (Müller et al., 2015; Gossner et al., 2016). Conversely, saproxylic beetles in Eucalyptus did not exhibit such a positive response to logs. Possibly, logs in Eucalyptus are exposed to environmental conditions that are particularly unfavorable to wood decomposition and colonization by saproxylic beetles (e.g., dry conditions, toxic leaf litter; Gayoso and Iroumé, 1995; Oyarzún et al., 1999).

The decay stage of wood was an important factor for not only determining the diversity and density of saproxylic beetles, but also shaping the response of trophic guilds to forest plantations. All species and most guilds (Zoophagous, Mycophagous, Saproxylophagous, Xylomycophagous and Saprophagous) benefited when wood became more decayed, while Xylophagous were richer at early decay stages, as found in managed native forest (Table 6; Vanderwel et al., 2006). When compared with Pine and Eucalyptus, the positive response to decay stage was particularly strong in Native for all species and the guilds of late-successional species (e.g. Zoophagous, Mycophagous, and Saproxylophagous). Such an increased response of these late-successional species to native deadwood in an advanced state of decay suggests higher colonization rates resulting from better habitat conditions and increased abundance of reproductive adult individuals (Stokland et al., 2012; Ulyshen, 2016). Although the habitat-dependent responses to decay stage (habitat × decaying interactions) may be complex to interpret for some guilds (e.g., see Polyphagous, Fig. 4A), our results provide clear evidence that saproxylic beetles benefit from the decayed wood available in Pine. Indeed, deadwood in an advanced state of decay in Native and Pine has similar beetle density for all species (Table 4). This result involves two ecological phenomena that should be considered for the development of sustainable forestry. First, an increased beetle density at expenses of reduced species richness (as shown

by all species and Zoophagous in Fig. 4A and B), suggests that ecosystem services provided by saproxylic beetles (i.e., wood decomposition) are not limited in Pine, where the density of saproxylic beetles is relatively similar than Native. Foresters may take advantage from saproxylic beetles through reducing costs of fertilization while decreasing the risk of fire (Edmonds and Eglitis, 1989; Ulyshen, 2013, 2016). Second, forestry guidelines should promote the retention of woody debris along management cycles (e.g., residual logs and stumps from previous rotations) in order to ensure the provision of deadwood in advanced decay stages that potentially host a diverse saproxylic assemblage.

The findings of this study provide the first evidence on the assemblages of saproxylic beetles in exotic forest plantations of southern South America, but also indicate their response to plantations depends on the substrate type (logs or stamps), decay stage of wood and trophic level. We also highlight the needs to be cautious about considering the amount of deadwood present in forest plantations as a proxy of the diversity and abundance of saproxylic beetles. The microclimate and the toxic leaf litter could affect the decomposition rate of the woody substrates in Eucalyptus forest plantations, thus promoting the accumulation of woody biomass. Management goals of forestry companies in the Maulino forest region are increasingly being directed towards replacing pine plantations by eucalyptus plantations and these changes in forestry strategies could have important impacts on saproxylic beetles, thus preventing the adoption of sustainable forest practices. Although to date, there are relatively few stands of eucalyptus in this region (with most stands being first-rotation plantations), these changes in forestry strategies could have important impacts on saproxylic beetles. Landscape-scale factors (e.g., connectivity and forest cover) also may be responsible for diversity and abundance of saproxylic beetles (e.g., Franc et al., 2007; Müller and Bütler, 2010; Lassauce et al., 2011), hence sustainable management should be focused on improving habitat quality for saproxylic beetles while promoting landscape-scale conditions favorable for metapopulation and metacommunity processes.

Table 6

Model-averaged coefficients from the best-supported (ΔAICc < 2) Generalized Linear Mixed-effects models (GLMMs; Table 5) testing for the effects of habitat, substrate type and decay stage (and their interactions) of logs and stumps on the species richness (s/cm³) of all species and different trophic guilds of saproxylic beetles. Different letters indicate statistically significant difference (p < 0.05) among groups based on Tukey's test for multiple comparisons.

Variable	Level	All species	Zoophagous	Mycophagous	Polyphagous	Saprophagous	Xylophagous	Saproxylophagous	Xylomycophagous
Habitat	Eucalyptus	−1.20 (0.09)c ***	−2.04 (0.21)c ***	−2.01 (0.21)c ***		−0.78 (0.25)b **	−0.12 (0.18)a	−0.90 (0.22)c ***	−0.98 (0.28)b ***
	Pine	−0.56 (0.08)b ***	−0.80 (0.15)b ***	−1.43 (0.18)b ***		0.10 (0.18)a	−0.16 (0.18)a	−0.29 (0.18)b *	−0.52 (0.15)b ***
Substrate	S	−2.42 (0.05) ***	−2.34 (0.08) ***	−2.45 (0.08) ***	−2.05 (0.17) ***	−2.43 (0.19) ***	−1.73 (0.14) ***	−0.52 (0.10) ***	−2.52 (0.10) ***
Decaying	CII	0.55 (0.07)b ***	0.75 (0.10)b ***	0.59 (0.10)b ***	1.37 (0.41)b ***	0.42 (0.19)b *	−2.90 (0.52)b ***	0.71 (0.12)b ***	0.63 (0.12)b ***
	CIII	0.61 (0.07)b ***	0.82 (0.10)b ***	0.75 (0.10)b ***	1.42 (0.37)b ***	−0.05 (0.25)a	−1.13 (0.68)b ***	0.65 (0.12)b ***	0.65 (0.13)b ***
Habitat × Substrate	Eucalyptus × Stump	0.63 (0.08) ***	0.36 (0.12) **	0.94 (0.17) ***		0.52 (0.41)		0.50 (0.15) ***	0.76 (0.15) ***
	Pine × Stump	0.17 (0.08) **	−0.25 (0.12) *	0.19 (0.17)		−0.23 (0.35)		0.70 (0.14) ***	0.62 (0.14) ***
Habitat × Decaying	Eucalyptus × CII	0.56 (0.11) ***	1.47 (0.23) ***	1.11 (0.24) ***			0.13 (0.73)	0.55 (0.21) **	0.65 (0.20) ***
	Eucalyptus × CIII	0.53 (0.11) ***	1.56 (0.22) ***	1.01 (0.24) ***			0.44 (1.47)	0.55 (0.21) *	0.51 (0.21) *
	Pine × CII	0.37 (0.10) ***	0.65 (0.17) ***	1.23 (0.21) ***			1.34 (1.60)	0.03 (0.17)	0.21 (0.18)
	Pine × CIII	0.36 (0.10) ***	0.73 (0.16) *	1.11 (0.21) *			1.55 (3.47)	0.01 (0.18)	0.18 (0.18)

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.026.

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