



## Original Articles

# A native long horned beetle promotes the saproxylic diversity in exotic plantations of Monterrey pine

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## ABSTRACT

Native saproxylic (deadwood dependent) beetle species living in exotic forest plantations may provide environmental services for forestry companies, but their sensitivity to forest management makes them difficult to conserve. Here, we used Structural Equation Models (SEM) to assess the role of the endemic beetle *Acanthinodera cumingii* in native forest and exotic pine plantations as an ecosystem engineer that improves the quality of deadwood for saproxylic beetles. Deadwood quality in native forest and pine plantations was accounted for by *A. cumingii* density and deadwood decay stage. In native forest, diversity of predators and fungivores responded positively to deadwood quality, while in the pine plantations the diversity of all functional groups, with exception of detritivores, was positively affected by deadwood quality. In addition, all saproxylic functional groups were less diverse in stumps than in logs. These findings suggest that *A. cumingii* larvae contribute to make more diverse the assemblages of saproxylic beetles in deadwood. We suggest that sustainable management of pine plantations based on the role of *A. cumingii* as an ecosystem engineer and biodiversity indicator must necessarily consider forest practices intended to mimic the native forest conditions that regulate the deadwood decay dynamics.

## 1. Introduction

Monterrey pine plantations (*Pinus radiata*) mainly destined to wood pulp and lumber production cover approximately 4 million hectares worldwide (Estades, 2012; Payn et al., 2015). Unfortunately, the option of sustainable management of Monterrey pine plantations, as stated in the Strategic Plan for Biodiversity 2011–2020 of the Convention on Biological Diversity (CBD, 2010), poses a complex challenge for environmental policy. Monterrey pine plantations are managed under a clearcutting system, which involves mechanical and chemical site preparation after clearcutting, thus disrupting vegetation structure, microclimate and soil properties (Miller and Miller, 2004; Rosenvald and Lõhmus, 2008; Pawson et al., 2011; Niklitschek, 2015). The harvest of pine stands also results in reduced carbon storage and exportation of nutrients with ecosystem outflows increasing as logging residues are removed for biofuel (Hjältén et al., 2010; Riffell et al., 2011). However, Monterrey pine plantations not necessarily are green desert (Hartley, 2002), because as they get older, their habitat structure resembles that of native forest, thus offering complementary and supplementary resources to wildlife (Lindenmayer and Hobbs, 2004; Brockerhoff et al., 2008; Pawson et al., 2010; Estades, 2012; Simonetti et al., 2013).

Adult Monterrey pine plantations may provide suitable habitat conditions for some wildlife species that use the leaf litter, understory and canopy of plantations, such as some small-mammals, insectivore

birds and insects (Greze et al., 2003; Vergara and Simonetti, 2004; Pawson et al., 2008; Russek et al., 2017; Fierro et al., 2017; Ramirez-Collio et al., 2017). However, for saproxylic (i.e., deadwood-dependent species), pine plantations could act as an alternative habitat only if deadwood microhabitats are available, such as stumps, snags, logs and thinning debris (Speight, 1989; Grove, 2002a; Stokland et al., 2012). Indeed, occupancy of pine plantations stands by saproxylic species requires maintaining critical levels of volume, diversity and connectivity of deadwood (e.g., large and decayed logs and stumps; Schiegg, 2000; Müller and Bütler, 2010; Stokland et al., 2012). Moreover, saproxylic species are also benefited from the presence of other saproxylic species responsible for the creation of particular deadwood microhabitats, such as insects that excavate large galleries, as well as wood-decaying fungi serving as food or habitat (Ranius, 2002; Buse et al., 2008; Micó et al., 2015).

Saproxylic beetles are one of the more diverse assemblages of forest ecosystems (Grove, 2002a,b; Langor et al., 2008). The conservation of saproxylic beetles in forest plantations may offer economic advantages for forest landowners and managers through the environmental services they provide (Paquette and Messier, 2011; Jonsson et al., 2012). Saproxylic beetles may increase productivity of forest plantations by increasing the rates of deadwood decay and nutrient release, while decreasing the risk of fire and insect pest outbreaks (Edmonds and Eglitis, 1989; Ulyshen, 2013, 2016). In addition, saproxylic beetles may be

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important prey for, or provide reproductive microhabitats to forest species, such as understory birds (e.g., Vergara and Simonetti, 2004, 2006), small mammals (e.g., Loeb, 1999; Lassaue et al., 2011) and carnivores (Zúñiga et al., 2008, 2009; Fauteux et al., 2012). However, the diversity of saproxylic beetles depends mainly on the diversity and quality of the deadwood microhabitats (rather than on the amount of deadwood), with these two variables being difficult to measure and highly correlated with the amount of dead wood (Müller and Bütler, 2010; Seibold et al., 2016). Consequently, the monitoring of saproxylic beetles may become expensive and time consuming due to it requires to assess different types of deadwood substrates, such as logs and stumps in their different decay stages (Lindenmayer et al., 2000; Brin et al., 2009; Gao et al., 2015).

Biodiversity indicator species and structure-based indicators are frequently used to assess the effects of specific management practices on biodiversity and ecosystem processes (Lindenmayer et al., 2000; Spellerberg, 2005). Sustainable forestry management usually requires establishing structure-based biodiversity indicators, such as deadwood volume (Lassaue et al., 2011), deadwood diversity (Brin et al., 2009) and basal area (Grove, 2002b). Moreover, some saproxylic beetle species can serve as biodiversity indicators when their larvae generate deadwood microhabitats or improve deadwood quality for saproxylic biota (e.g., *Osmoderma eremita* (Scopoli, 1763) and *Cerambyx cerdo* Linnaeus, 1758; Ranius, 2002; Buse et al., 2008; Micó et al., 2015). Beetles species with large-sized larvae and considered as biodiversity indicators usually act as ecosystem engineer through increasing the availability of suitable deadwood microhabitats (Ranius, 2002; Buse et al., 2008). In particular, some saproxylic beetles build large and complex gallery networks and contribute to the development of the “wood mould” (i.e., a bed of woody debris mixed with digestive residues of larvae) in tree cavities, thus providing suitable conditions for wood-decaying, fungi as well as for fungivorous and predator beetles (Ranius, 2002; Buse et al., 2008; Ranius et al., 2009; Quinto et al., 2012; Micó et al., 2015).

Fast-growth plantations of Monterrey pine (*Pinus radiata*) have extensively replaced the temperate Maulino forest of Central Chile (Echeverría et al., 2006), which supports high levels of endemism, particularly of saproxylic beetles (Myers et al., 2000, Paulsen, 2010). As pine plantations grow, they increasingly accumulate a high volume, diversity and density of deadwood, thus increasing the availability of dead wood for saproxylic beetles over time (Fierro et al., 2017). However, the dead wood accumulated on the ground of pine plantations not necessarily represents a suitable microhabitat for saproxylic beetles (Fierro et al., 2017). Previous studies suggest that the quality of deadwood for saproxylic beetles depends on habitat structure (e.g., understory or canopy cover; Buse et al., 2010) and deadwood attributes (substrate type or decaying stage; Brin et al., 2009; Fierro et al., 2017), but also on some species influencing deadwood decay processes (Ranius, 2002; Buse et al., 2008; Micó et al., 2015).

The saproxylic longhorn beetle *Acanthinodera cumingii* Hope, 1833 (locally known as “Madre de la culebra”) is a species that potentially could improve the microhabitat conditions for saproxylic beetles in Monterrey pine plantations (Fig. 1; Fierro et al., 2017). The endemic *A. cumingii* is the largest beetle species of temperate forest of South America, whose larva develops in deadwood of native and exotic trees, including Monterrey pine (Cerdeña, 1974; Artigas, 1994; Solervicens, 2014). Larvae of *A. cumingii* bore wide, long and complex galleries, along which it is possible to find moist sawdust and cavities (Artigas, 1994). These changes in the physical–chemical deadwood properties resulting from the activity of *A. cumingii* larvae is expected to promote the diversity of saproxylic beetles (Buse et al., 2008). Besides being relatively abundant, its large size makes *A. cumingii* easy to identify, detect, collect and, therefore, inventory (Fig. 1). Since *A. cumingii* is easy to inventory, and eventually, could be strongly correlated with presence of other saproxylic species, *A. cumingii* could be considered as an indicator of a species-rich fauna (Ranius, 2002). Here, we assessed

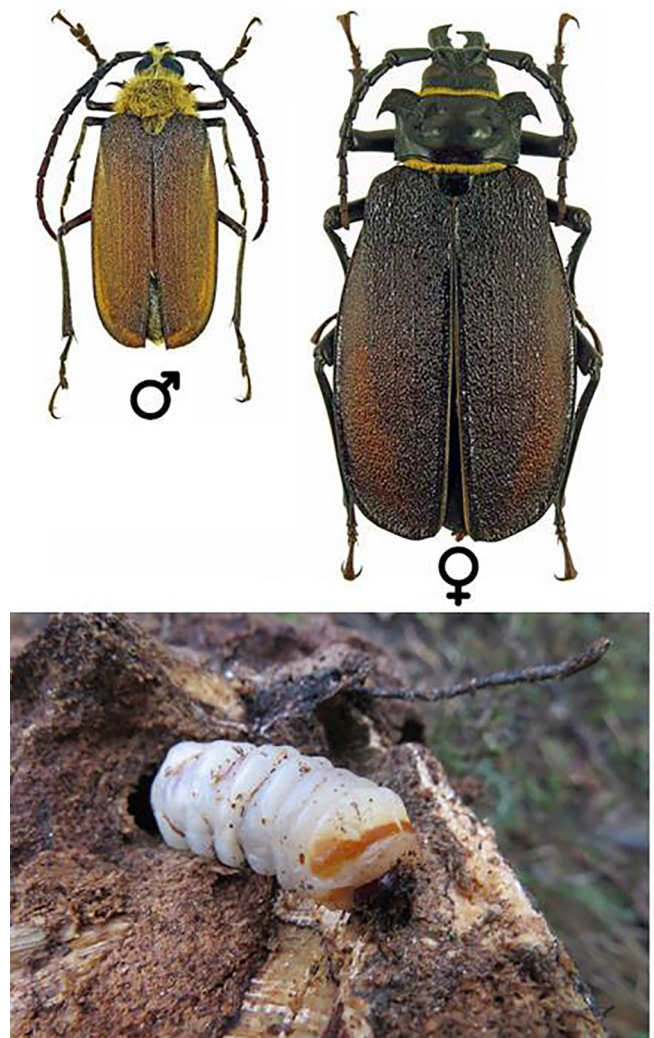


Fig. 1. Above: Adult male (left) and female (right) of *Acanthinodera cumingii*. Below: *A. cumingii* larval (photo: Pablo Fuentes).

the potential of *A. cumingii* as a promoter and indicator of diversity of saproxylic beetle species in logs and stumps of native forest and Monterrey pine plantations. Specifically, we hypothesize that *A. cumingii* larvae improve microhabitat quality for saproxylic beetle species. In addition, we hypothesized the role of *A. cumingii* as a promoter and indicator of biodiversity does not change with the habitat type (pine plantations vs. native forest). Testing such a hypothesis, however, requires controlling for the effects of other ecological factors (e.g., habitat structure and deadwood attributes), but also considering saproxylic beetles as a heterogeneous and complex species group. Accordingly, here we used Structural Equation Modelling (SEM) to disentangle causal relationships between multiple ecological variables, while assessing the contribution of *A. cumingii* to the microhabitat quality for saproxylic beetle species.

## 2. Methods

### 2.1. Study species

*Acanthinodera cumingii* is a sclerophyll and temperate forest-dwelling beetle species, endemic to central southern Chile (29°–38°) and common in exotic forest plantations of this region (Artigas, 1994). Larvae of *A. cumingii* reach 150 mm length and 25 mm wide, and their development (ca. 5–6 years) takes place in deadwood of at least 28 tree

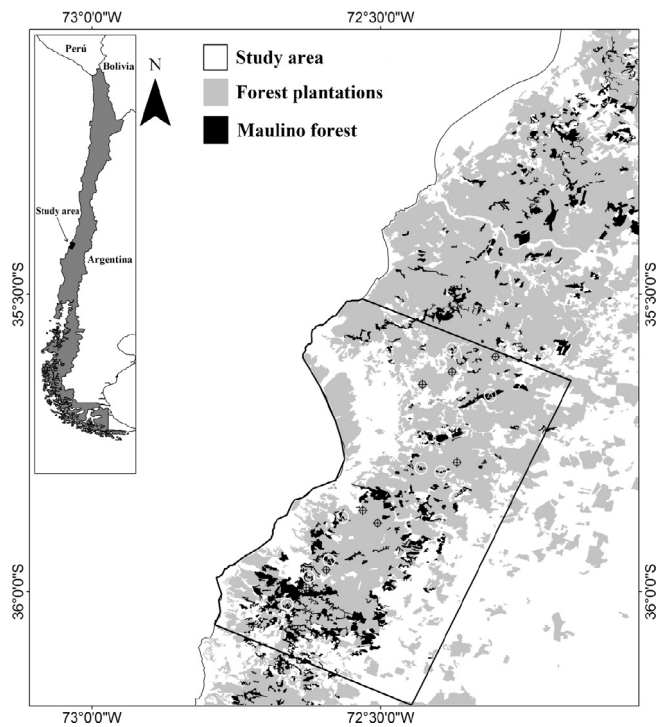


Fig. 2. Map of the study landscape comprising stands of exotic forest plantations and remnants of Maulino native forest.

species, including the native *Nothofagus glauca* (Phil.) Krasser, 1896, *N. obliqua* (Mirb.) Oerst., 1872, *N. dombeyi* (Mirb.) Oerst., 1872, *Peumus boldus* Molina, 1782, *Cryptocarya alba* (Mol.) Looser, 1810, *Beilschmiedia miersii* (Gay) Kosterm., 1938, *Persea lingue* Ness, 1833, *Drimyis winterti* J.R. Forst. and G. Forst., 1776 and *Crinodendron patagua* Molina, 1782, as well as the exotic *Pinus radiata* D. Don., 1837, *P. pinaster* Ait., 1789, *Populus deltoides* Bartr. ex Marsh., 1785, *Eucalyptus globulus* Labill., 1800 and *Quercus robur* Linnaeus, 1753 (Angulo and Weigert, 1974; Artigas, 1994; Fuentes and Araneda, 2016). Adults of *A. cumingii* emerge during the austral spring (October–December), are 50–80 mm length and 25–40 mm wide, not feed and exhibit marked sexual dimorphisms. Females are wingless, diurnal and larger than the winged and nocturnal males (Fig. 1; Cerda, 1974; Artigas, 1994).

## 2.2. Study area

The study landscape is located at the Coastal Range of the Maule Region, South-Central Chile (35°36'S, 72°20'W and 36°00'S, 72°20'W) and comprises remnants of native Maulino forest surrounded by a matrix of Monterey pine plantations (*Pinus radiata*) (Fig. 2; Donoso, 1994). We used a two-levels (habitat and microhabitat; Fig. 3) sampling design according which larvae of *A. cumingii* and adult of saproxylic beetles were counted in deadwood microhabitats (logs and stumps) available in eight remnants of native forest (25–50 ha) and eight stands of “mature” Monterey pines (100–400 ha and 20–30 years-old). Forest stands and native forest remnants were more than 2 km apart. Native forest is dominated by *N. glauca*, whose deadwood is used by *A. cumingii*. Canopy of native forest occasionally included *C. alba*, *P. lingue* and *N. obliqua*. Understory vegetation of native forest and pine plantations covered, on average, 60% and 35%, respectively. Native trees were 15–20 m in height and 20–40 cm in diameter at the breast height (DBH), while pine trees were 25–35 m in height and 20–35 cm in DBH. Deadwood available in native forest came mainly from *N. glauca* while in pine stands it was logging wastes. In particular, *N. glauca* deadwood is easily recognizable by its characteristic bark (e.g., gray-reddish and rough) which remains for years before decomposing. Pine wood was

identified on basis of its resinous bark and its properties inherent to conifers (i.e., no other conifer species are present in Maulino forest). Consequently, in native forest we sampled deadwood from *N. glauca* trees while in pine plantations it was sampled from *P. radiata* trees.

## 2.3. Habitat variables

We characterized the habitat structure of native forest and pine plantations through variables recognized to influence saproxylic beetle diversity, such as the volume of deadwood, canopy cover and understory cover (Schiegg, 2000; Grove, 2002a; Müller and Bütler, 2010). In each native forest remnant and pine plantation, structural habitat variables were quantified in six 0.04 ha plots regularly distributed (distanced 80 m from each other), as described in details in Fierro et al., (2017).

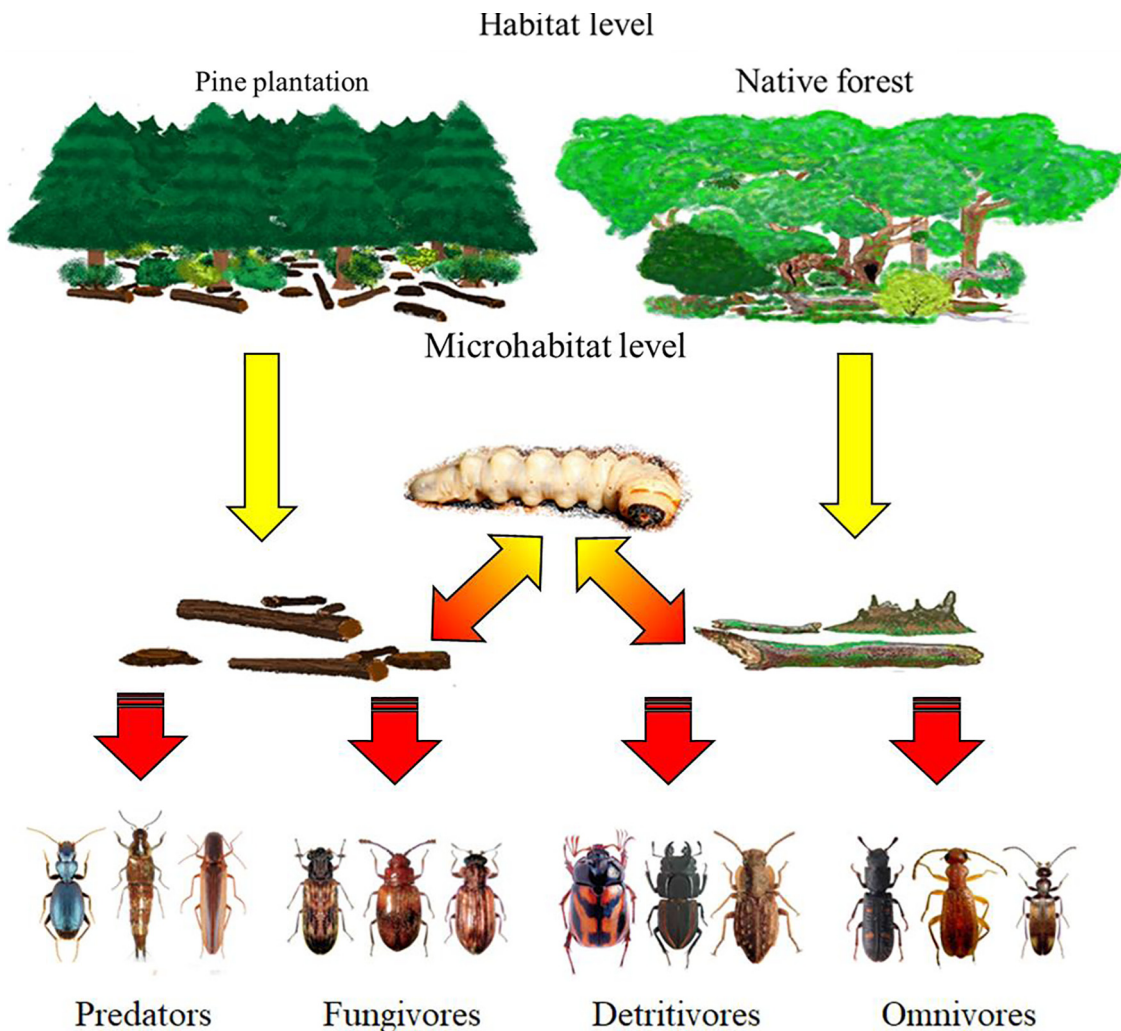
## 2.4. Beetle sampling

Larvae of *A. cumingii* and adults of other beetle species were sampled in 648 pieces of deadwood ( $n = 432$  logs and  $n = 216$  stumps), with logs and stumps being equally represented in pine stands and native forest remnants. Four trained observers walked along zigzagging transects in pine stands and native forest remnants, searching for stumps and logs located more than 15 m apart in order to reduce spatial dependence. Logs were 50–150 cm in length and 6–20 cm in diameter while stumps were 10–40 cm in height and 10–40 cm in diameter. Once found, the length and diameter of each log or stump was measured for volume estimation. The criterion proposed by Franc et al., (2007) was used to classify log and stumps into three possible decay stages (i.e., early, intermediate and late). For each pine stand or native forest remnant a sample consisted of 36 logs and 18 stumps (i.e., 12 logs and 6 stumps of each decay class), with logs being oversampled (in relation to stumps) due to their larger abundance.

Larvae of *A. cumingii* and adult of the other beetle species were collected by using the “wood dissection” method (*sensu* Saint-Germain et al., 2007), according which deadwood is progressively partitioned into smaller woody pieces in order to capture insects exclusively occupying deadwood. Dissection of each log or stump was carried out for a period between 10 and 20 min (total sampling effort was 251 h. distributed along 50 days) on a 4 m<sup>2</sup> white sheet. When known, beetles were identified to species level and posteriorly released *in situ*. Unknown beetle species were preserved in 70% ethyl alcohol to be compared with specimens deposited in the Entomological Collection of the National Museum of Natural History (MNHN). All captured species were assigned to a particular trophic guild (Bouget et al., 2005; Micó et al., 2015) based on knowledge about the trophic ecology of larvae and adults (Elgueta and Arriagada, 1989; Beutel and Leschen, 2005; Leschen et al., 2010). We considered only larvae of *A. cumingii* longer than 40 mm (corresponding approx. to their third instar, or older stages; Artigas, 1994), in order to avoid confusion with other Prioninae species present in forest plantations. For facilitating the interpretation of the community-level effect of *A. cumingii*, beetles were classified into four functional groups, as based on their trophic ecology: predators (zoophages), detritivores (xylophages, saprophages and saproxylophages), fungivores (mycophages and xylomycophages) and omnivores (polyphages).

## 2.5. Data analysis

We conducted Structural Equation Modelling (SEM; e.g., Rosseel, 2012) to assess the relative contribution of *A. cumingii* to the diversity of beetle species belonging to different functional groups (Fig. 3). SEM provides a flexible framework for testing causal models that include observed variables (endogenous and exogenous) and latent (unobserved) variables (Pugesek et al., 2003; Fan et al., 2016). SEM were constructed based on knowledge about saproxylic food webs described



**Fig. 3.** Conceptual representation of the ecological processes involving the generation of deadwood and its transformation into suitable microhabitat for saproxylic beetles caused by positive feedback between *A. cumingii* and decaying process. At the habitat level, influx of deadwood causes it to be available in pine plantations and native forest (yellow arrows). At the micro-habitat level, deadwood substrates (logs and stump) are occupied by *A. cumingii* whose adults colonize deadwood based on its decay stage (double arrows, yellow heads) while their larvae contribute to improve quality through changes in the physical–chemical properties of deadwood (double arrows, red heads). Saproxylic beetles belonging to different functional groups benefit from the improvement of micro-habitat quality (red arrows). Below: from left to right some representative species of each functional groups of saproxylic beetle species are shown. Predators are: *Cyanotarus andinus* (Germain, 1855) (Carabidae), *Lynxyella suturalis* (Candènze, 1865) (Elateridae) and *Loncovillius discoideus* (Fairmaire & Germain, 1862) (Staphylinidae); Fungivores are: *Protosphindus chilensis* Burakowski & Slipinski, 1987 (Sphindidae), *Chiliotis formosa* Reitter, 1875 (Cryptophagidae) and *Enicmus transversithorax* Dajoz, 1967 (Lathridiidae); Detritivores are: *Oryctopmorphus bimaculatus* Guérin-Méneville, 1855 (Scarabaeidae), *Erichius vittatus vittatus* (Eschscholtz, 1822) (Lucanidae), *Hexagonochilus tuberculatus* Germain, 1855 (Tenebrionidae); Omnivores are: *Acalanthus quadrisignatus* Erichson, 1842 (Trogossitidae), *Protoanthicus marziae* Moore & Vidal, 2006 (Anthicidae) and *Ischyropalpus* sp.1 (Anthicidae). With the exception of the image of *A. cumingii* larvae (Photo: Cesar Aceituno), *P. marziae* (A. Fierro) and *A. quadrisignatus* (<http://www.bookofinsect.com>), the remaining beetle images are from Solervicens (2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for forest ecosystems (Stokland et al., 2012), and more recently, applied to pine plantations (e.g., Fierro et al., 2017). This causal model proposes that diversity of saproxylic beetle species in deadwood depends on the quality of deadwood microhabitat, an ecological propriety of deadwood that was specified as a latent variable. Deadwood substrates (stumps or logs) are expected to be more suitable for saproxylic beetles when the former offers beetles with more feeding recourses (e.g., fungal mycelium or prey), as well as environmental conditions necessary to survive (e.g., microclimate conditions). Therefore, the quality of logs and stumps resulting from the activity of *A. cumingii* larvae and decay process has a positive effect on the diversity of predator, fungivorous, detritivorous and omnivorous species of saproxylic beetles (Fig. 3). Fungivorous and detritivorous beetles should benefit from the galleries (e.g., used as refuges or breeding sites) and the sawdust produced by *A. cumingii* larvae, which promote the proliferation of fungi and other

organisms (e.g., cellulose-decomposing bacteria). Predator beetles should respond numerically to increased prey availability in logs and stumps occupied by *A. cumingii* larvae, while omnivores should be more diverse as deadwood occupied by *A. cumingii* larvae becomes increasingly inhabited by saproxylic organisms. In addition, SEM also considered the correlation between density of *A. cumingii* larvae and deadwood decaying stage. Thus, we controlled for the positive feedback between activity of *A. cumingii* larvae and deadwood decay, according which *A. cumingii* larvae accelerate the decay of wood, while *A. cumingii* adults are more probable to colonize deadwood pieces as wood becomes increasingly decomposed. Functional groups of saproxylic beetle species also interact among them. Since we lack an appropriate experimental design to analyze causal links between species (e.g., predator exclusion), we specified correlations (i.e. undirected paths) between functional groups. In addition, we also included the effect of

substrate type (logs vs. stumps) on the density of *A. cumingii* larvae and diversity of saproxylic beetles. SEM considered the effects of habitat variables at the stand-level on the diversity of saproxylic beetles and density of *A. cumingii*, including understory cover, canopy cover and deadwood volume. We did not include a causal relationship between habitat variables and decaying stage because decaying stage was a fixed variable rather than a random variable (see above).

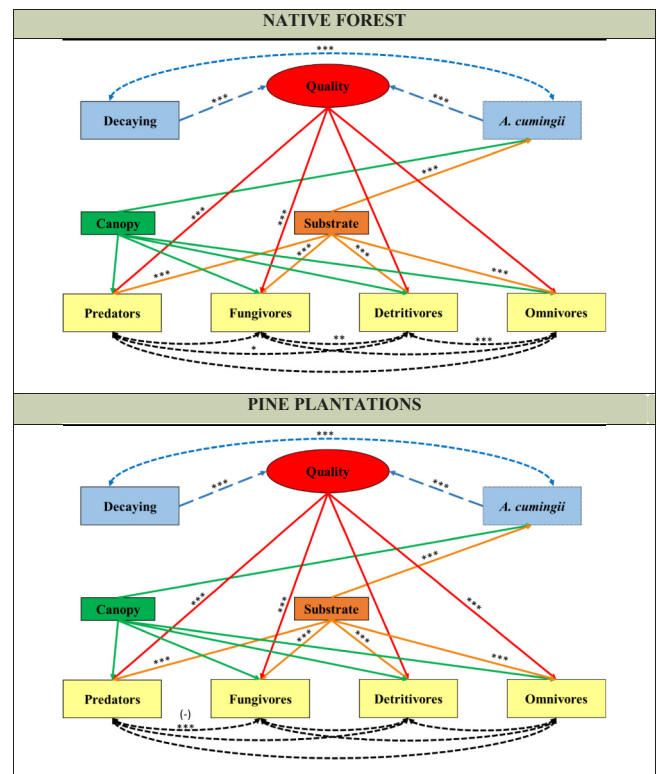
Multimodel inference based on the Akaike Information Criterion (AIC) was used to rank the support of candidate SEM (Akaike, 1974; Burnham and Anderson, 2004). We built a set of candidate SEM including different combinations of exogenous variables (i.e., habitat variables and substrate type). Models with  $\Delta AIC < 2$  (AIC difference with the best model) were considered strongly supported by the data. The goodness of fit of candidate SEM was assessed through the Chi-square ( $\chi^2$ ) statistic (non-significant test is indicative of good fit), the root mean square error of approximation (RMSEA, with RMSEA  $\sim 0$  indicating perfect fit), the standardized root mean square residual (SRMR, with SRMR  $< 0.09$  indicating good model fit), the comparative fit index (CFI, ranging from 0.0 to 1.0, with higher CFI indicating a better model fit) and Tucker-Lewis index (TLI, where TLI  $> 0.90$  are considered acceptable) (Hu and Bentler, 1999; Fan et al., 1999, 2016).

The density of *A. cumingii* and beetle diversity were expressed, respectively, in individuals and species per volume of dead wood ( $n/cm^3$ ) using as reference the volume of each sampled deadwood piece (log or stump). Response variables were standardized prior to analysis in order to facilitate model interpretation by providing comparable coefficients while ensuring model convergence. SEM were run by specifying habitat type as a “grouping” factor. Thus, models were fitted separately for native forest and pine plantations because the effect of *A. cumingii* on the quality of deadwood could change with habitat type. Habitat differences in SEM coefficients were interpreted as *A. cumingii* having a more important role as a biodiversity promoter or ecosystem engineer in a certain habitat type. SEM were fitted with the *sem* function available in the R package ‘lavaan’ (Rosseel, 2012).

### 3. Results

A total of 340 larvae (149 and 191 in native forest and pine plantations, respectively) of *A. cumingii* were recorded occupying logs ( $N = 288$ ; 67%) and stumps ( $N = 52$ ; 24%) (Table S1). We recorded 92 predator species (88 and 86 species in native forest and pine plantations, respectively); 94 fungivorous species (92 species in both habitat types); 68 detritivorous species (65 and 64 species in native forest and pine plantations, respectively); and 4 omnivorous species in both habitat types (Table S1). We found support for only one SEM ( $\Delta AIC = 0$ ; AIC = 1436.7), which included canopy cover and type deadwood substrate as exogenous variables affecting *A. cumingii* density and diversity of saproxylic beetles (Table S2). This best supported model had acceptable goodness of fit statistics:  $p$ -value ( $\chi^2$ ) = 0.66, CFI = 1.0, RMSEA = 0.00, SRMR = 0.01 and TLI = 1.02 (Table S2).

The best-supported SEM included the positive effect of *A. cumingii* density and deadwood decay stage (Decaying) on the latent deadwood quality (Quality) variable (Fig. 4), with these effects being significant in native forest and pine plantations (Fig. 4; Table 1). We found a positive and significant correlation between *A. cumingii* and Decaying in native forest and pine plantations (Table 1). Overall, the effect of Quality was positive on the diversity of saproxylic beetles, but this effect also depended on functional group and habitat type (Fig. 4; Table 1). In native forest, the diversity of predators and fungivores responded positively to Quality, while in pine plantations diversity of all functional groups, with the exception of detritivores, were positively affected by Quality (Fig. 4; Table 1). In native forest and pine plantations, all functional groups of saproxylic beetle species were less diverse in stumps than in logs (Table 1; Fig. 4). Canopy cover affected neither diversity of saproxylic beetles nor density of *A. cumingii* (Table 1; Fig. 4). Predators correlated positively with detritivores and negatively with fungivores in



**Fig. 4.** Diagram of the best-supported SEM (Table S2) for native forest (above) and Monterrey pine plantations (below) showing the causal relationships among: 1) the latent microhabitat-quality variable (Quality); 2) Quality indicators, including *A. cumingii* density (*A. cumingii*) and deadwood decay stage (Decaying); 3) Exogenous observed variables, including canopy cover (Canopy) and Substrate type (Substrate; i.e., logs and stumps); and 4) Endogenous observed variables that include the diversity of four functional groups of saproxylic beetles (predators, fungivores, detritivores and omnivores). Solid arrows with single head represent the effects of the latent variable and exogenous variables on diversity of saproxylic beetles as well as exogenous variables on *A. cumingii*. Dashed arrows with single head represent the contribution to Quality by its indicators. Pointing arrows with double-headed represent correlations between variables. Significance of standardized coefficients are shown (\*\*\*:  $p \leq 0.001$ , \*\*:  $p \leq 0.01$ , \*:  $p \leq 0.05$ ). All path coefficients were positive, except for the path labelled with (-).

native forest and pine plantations, respectively. In native forest, fungivores were positively correlated with detritivores, while the latter were positively correlated with omnivores (Table 1; Fig. 4).

### 4. Discussion

Results supported our hypothesis that *A. cumingii* promotes diversity of saproxylic beetles in exotic pine plantations through improving the quality of deadwood microhabitats. Thus, if the best supported SEM (Fig. 4) is an unbiased representation of reality, then, based on model results, *A. cumingii* could be considered as a biodiversity indicator and ecosystem engineer (Brin et al., 2009; Müller and Büttler, 2010; Bouget et al., 2013). In addition, these findings provide important insights on the sustainable management of forest plantations in central Chile. Sustainable management planning based on the ecological role of *A. cumingii*, however, requires unraveling the mechanisms by which *A. cumingii* improves habitat quality for saproxylic beetles. However, our results are preliminary, hence further research is needed to establish minimum abundance levels of *A. cumingii* above which this beetle species offers environmental services to forestry companies, such as biodiversity maintaining and nutrient cycling (e.g., Edmonds and Eglitis, 1989; Ulyshen, 2013, 2016).

**Table 1**

Coefficients of best-supported SEM (Fig. 4; Table S2). Paths between the latent and their indicator variables (large rightwards arrows); paths between indicators, exogenous and endogenous variables (double rightwards arrows); and correlations between indicators and between functional groups (left right double arrow). \*\*\*:  $p \leq 0.001$ , \*\*:  $p \leq 0.01$ , \*:  $p \leq 0.05$ .

| Habitat   | Path               |              | Estimate           | SE    | p value |       |     |
|-----------|--------------------|--------------|--------------------|-------|---------|-------|-----|
| Native    | Decaying           | →            | Quality            | 0.79  | 0.07    | 0.000 | *** |
|           | <i>A. cumingii</i> | →            | Quality            | 0.65  | 0.07    | 0.000 | *** |
|           | Substrate          | ⇒            | <i>A. cumingii</i> | 0.60  | 0.07    | 0.000 | *** |
|           | Canopy cover       | ⇒            | <i>A. cumingii</i> | 0.14  | 0.10    | 0.167 |     |
|           | Quality            | ⇒            | Predators          | 0.33  | 0.05    | 0.000 | *** |
|           | Substrate          | ⇒            | Predators          | 0.92  | 0.02    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Predators          | 0.14  | 0.13    | 0.267 |     |
|           | Quality            | ⇒            | Fungivores         | 0.27  | 0.05    | 0.000 | *** |
|           | Substrate          | ⇒            | Fungivores         | 0.96  | 0.01    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Fungivores         | 0.04  | 0.16    | 0.826 |     |
|           | Quality            | ⇒            | Detritivores       | 0.04  | 0.06    | 0.549 |     |
|           | Substrate          | ⇒            | Detritivores       | 0.97  | 0.01    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Detritivores       | 0.07  | 0.15    | 0.649 |     |
|           | Quality            | ⇒            | Omnivores          | 0.11  | 0.14    | 0.437 |     |
|           | Substrate          | ⇒            | Omnivores          | 0.88  | 0.04    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Omnivores          | 0.14  | 0.15    | 0.359 |     |
|           | <i>A. cumingii</i> | ⇔            | Decaying           | 0.64  | 0.07    | 0.000 | *** |
|           | Fungivores         | ⇔            | Predators          | 0.33  | 0.59    | 0.573 |     |
|           | Omnivores          | ⇔            | Predators          | 0.32  | 0.39    | 0.412 |     |
|           | Detritivores       | ⇔            | Predators          | 0.71  | 0.28    | 0.012 | *   |
|           | Detritivores       | ⇔            | Fungivores         | 0.72  | 0.27    | 0.008 | **  |
|           | Omnivores          | ⇔            | Fungivores         | 0.21  | 0.47    | 0.653 |     |
| Omnivores | ⇔                  | Detritivores | 0.62               | 0.17  | 0.000   | ***   |     |
| Pine      | Decaying           | →            | Quality            | 0.64  | 0.07    | 0.000 | *** |
|           | <i>A. cumingii</i> | →            | Quality            | 0.57  | 0.10    | 0.000 | *** |
|           | Substrate          | ⇒            | <i>A. cumingii</i> | 0.64  | 0.08    | 0.000 | *** |
|           | Canopy cover       | ⇒            | <i>A. cumingii</i> | 0.01  | 0.16    | 0.946 |     |
|           | Quality            | ⇒            | Predators          | 0.61  | 0.06    | 0.000 | *** |
|           | Substrate          | ⇒            | Predators          | 0.83  | 0.07    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Predators          | -0.02 | 0.17    | 0.927 |     |
|           | Quality            | ⇒            | Fungivores         | 0.59  | 0.07    | 0.000 | *** |
|           | Substrate          | ⇒            | Fungivores         | 0.80  | 0.06    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Fungivores         | 0.11  | 0.16    | 0.463 |     |
|           | Quality            | ⇒            | Detritivores       | 0.05  | 0.06    | 0.387 |     |
|           | Substrate          | ⇒            | Detritivores       | 0.95  | 0.05    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Detritivores       | 0.05  | 0.18    | 0.793 |     |
|           | Quality            | ⇒            | Omnivores          | 0.67  | 0.09    | 0.000 | *** |
|           | Substrate          | ⇒            | Omnivores          | 0.70  | 0.09    | 0.000 | *** |
|           | Canopy cover       | ⇒            | Omnivores          | 0.11  | 0.17    | 0.511 |     |
|           | <i>A. cumingii</i> | ⇔            | Decaying           | 0.47  | 0.10    | 0.000 | *** |
|           | Fungivores         | ⇔            | Predators          | -1.55 | 0.45    | 0.001 | *** |
|           | Omnivores          | ⇔            | Predators          | -2.53 | 5.33    | 0.635 |     |
|           | Detritivores       | ⇔            | Predators          | -0.10 | 0.22    | 0.663 |     |
|           | Detritivores       | ⇔            | Fungivores         | -0.18 | 0.39    | 0.651 |     |
|           | Omnivores          | ⇔            | Fungivores         | -3.29 | 6.46    | 0.611 |     |
| Omnivores | ⇔                  | Detritivores | -1.48              | 3.05  | 0.627   |       |     |

Our results suggest that the larval activity of *A. cumingii* contributes to make more diverse the assemblages of saproxylic beetles in deadwood. Most species groups responded positively to the improvement of microhabitat quality by *A. cumingii* in both habitat types (native forest and pine plantations), with the exception of detritivores who did not respond to microhabitat quality and omnivores whose response to quality was observed only in pine plantations. These effects of *A. cumingii* should be understood on basis of their ecological attributes. Larvae of *A. cumingii* has been reported occupying at least 28 host tree species in Chile, including deadwood from the extensively planted exotic Monterey pine and southern blue-gum (*Eucalyptus globulus*) (Fuentes and Araneda, 2016). Thus, the broad preferences of *A. cumingii* larvae for deadwood from different host species (*P. radiata* and *N. glauca*) could benefit to fungivores and predators in native forest and pine plantations (Fig. 4). Such an improvement of deadwood quality by *A. cumingii* larvae in both habitats may have been resulted from the accumulation of sawdust in galleries bored by *A. cumingii* larvae in pine and *Nothofagus* deadwood. Diversity of fungivores and predators may

increase as the moist becomes retained by the sawdust, which would favor the settlement and proliferation of wood-decaying fungi (Vanderwel et al., 2006; Schigel, 2012; Micó et al. 2015). In addition, both wood-decaying fungi and fungivores could be benefited from their high dispersal ability that promotes the colonization of deadwood (Komonen and Müller, 2018). However, lack of an effect of microhabitat quality on detritivores may result from the high trophic amplitude of this group, which includes species with different feeding ecology such as xylophages (dry or early decay deadwood consumers), saproxylophages (consumers of deadwood with advanced decay) and saprophages (detritus consumers).

Contrasting with its broad preferences for tree hosts, our results provide further knowledge about *A. cumingii* in terms of the micro-habitat features required for their larvae. Stumps and deadwood in early decay stages were not suitable microhabitats, while logs and deadwood in more advanced decay stages were the preferred microhabitats for *A. cumingii* larvae, as deduced from the path and correlation coefficients (Table 1). These micro-habitat preferences were relatively similar to those of other saproxylic beetle species. Therefore, these results may lead to confounding interpretation of the role of *A. cumingii* as diversity promoter if its contribution on deadwood quality is not considered in the analysis. Indeed, SEM's results are robust enough to support the contribution of *A. cumingii* larvae on saproxylic beetle species through its positive effect on deadwood quality.

We suggest that sustainable management of forest plantations based on the role of *A. cumingii* as an ecosystem engineer must necessarily consider the retention of deadwood, as well as forest practices intended to mimic the natural habitat conditions found in native forest and that regulate deadwood decay dynamics (e.g., see Jonsson and Siitonen, 2012). The economic benefits that can be obtained by improving the quality of *A. cumingii*'s habitat in forest plantations could be greater than the costs incurred in applying those forestry prescriptions. First, forest stands occupied by *A. cumingii* may increase their levels of soil fertility from nutrient released directly by the activity of their larvae, and indirectly, by the diversification of saproxylic biota associated with *A. cumingii*. Such an environmental service may become important if considering the increasingly shorter rotation period of pine plantation stands (< 18 years), which causes the accumulation of incompletely decomposed woody debris. Adults and larvae of *A. cumingii* also could contribute to the conservation of wildlife through their prey status for some vertebrate species sensitive to the native forest replacement by forest plantations, such as foxes, skunks, grisons and some diurnal or nocturnal raptors (Zúñiga et al., 2008, 2009; Moreira-Arce et al., 2015a,b, 2016). Second, implementing monitoring programs based on density of adults of *A. cumingii* may be a less expensive alternative to conventional approaches used to quantify forest biodiversity. Density of adult *A. cumingii* could be used to represent the deadwood quality in forest plantations. Indeed, our ongoing research indicates that nocturnal and diurnal abundance of adult *A. cumingii* is positively associated to the presence of signs of larvae and emergence holes in deadwood (Fierro, 2016; see also Artigas, 1994). Thus, and in light of these results we conclude that *A. cumingii* promotes and represents the diversity of saproxylic beetles in pine plantations in central Chile. Future environmental policies regulating forestry practices in this Mediterranean region should be focused in sustainable management providing environmental conditions (e.g., advanced deadwood decay stages) for ensuring viable metapopulations of *A. cumingii* across the fragmented landscape.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2018.09.018>.

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