

## Nestedness of bee assemblages in an endemic South American forest: the role of pine matrix and small fragments

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**Abstract** We assessed species richness and distribution of the apoidean fauna of the coastal Maulino forest, an endemic and threatened forest in central Chile. Remnant forest fragments are immersed in commercial pine plantations, who act as the habitat matrix. The bee assemblages depict a non-nested structure at the landscape level at times when pine plantations are standing. However, assemblages are nested in the fauna of forest fragments at times when plantations are harvested, suggesting that plantations might be acting as habitat providing connectivity between remnants of Maulino forest. Therefore, the conservation of apoideans might require a landscape level approach to be successful, including partial reliance on plantations.

**Keywords** Fragmentation · Apoidea · Chile · Conservation · Forestry

### Introduction

Habitat loss and fragmentation modify species richness and composition, and the interactions and processes in which these species take part (Fahrig 2003). The remaining habitat fragments and the surrounding matrix might either lose species or exhibit species enrichment in relation to the original continuous habitat (Fahrig 2003). In the case of species depletion, the remaining biota in forest fragments

and the matrix could be a nested subset of that of the original continuous habitat if the local extinctions are deterministic. In a nested distribution, species assemblages in relatively species-poor sites comprise successive subsets of the species present at richer sites (Patterson 1987; Wright et al. 1998). Alternatively, continuous habitat biota may be nested in the biota of forest fragments and the surrounding matrix if more species inhabit these habitats due to differential invasions (Lomolino 1996).

The Maulino forest is a temperate forest restricted to 100 km of the coastal range of central Chile (*sensu* San Martín and Donoso 1996), being part of the central Chile hotspot of biodiversity (Arroyo et al. 1999). This forest has been severely deforested and fragmented. During the last 25 years the annual forest loss rate reached 4.5% per year, reducing its area by 67% (Echeverría et al. 2006). Remaining forest fragments are immersed in large Monterey pine (*Pinus radiata*) plantations, who act as the matrix surrounding native vegetation (Grez et al. 2003). In this forest, species richness of several taxa such as birds, coleopterans, and dipterans is higher in forest fragments and pine plantations than in the continuous forest, rendering small fragments a high value as conservation reservoirs (Bustamante et al. 2006; Grez 2005), suggesting also that plantations might be acting as habitat providing connectivity between remnants of Maulino forest (Simonetti 2006), shaping a “continuum” of habitats for wildlife (Fisher and Lindenmayer 2006).

Here, we first analysed if apoideans follow the same general pattern that birds, coleopterans and dipterans on increased species richness in fragments of Maulino forest and the surrounding pine plantations. Second, we explore the effect of plantation harvesting upon this fauna. When plantations are harvested, fragments are then surrounded by an open landscape, without any significant shrub or tree

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cover until the next plantation grows, potentially isolating the fauna. Particularly, we tested whether bee's assemblages at small forest fragments are a nested subset of species compared to the fauna of the continuous forest when plantations are absent.

## Methods

We worked in a continuous forest and four forest fragments located in coastal central Chile. The continuous forest is itself a 600 ha remnant of a larger forest available, and contains the Los Queules National Reserve (147 ha) where insect sampling has been performed over the last 8 years as well as in four neighbouring fragments (from 2.3 to 3.4 ha) (Grež 2005). We sampled the Apoidea fauna at the National Reserve, the same four forest fragments as well as two plantation stands of 64 and 11 ha from November 2003 until November 2006. The pine plantation surrounding fragments was harvested in June 2005.

Insects were sampled through interception traps placed on *Aristotelia chilensis*, a common tree in the forest and fragments. In each habitat we set 40 traps, at randomly selected trees located around the geometric centre of each site and sampled monthly. Traps were at least 50 m apart. Overall, similarity insect diversity and abundance was unrelated to the distance among trees, being regarded as independent samples (De la Vega and Grež 2008). This sampling design reduces the probability to register false absences (see Fleishman et al. 2007). Species were determined by keys (Chiappa et al. 1990) and comparison with reference collections. We considered the species composition as the total species registered per habitat during the 3 years before (November 2003–May 2005) and after (June 2005–November 2006) plantation harvesting. Therefore, sampling efforts pre (19 months) and post (18 months) harvesting are similar.

We constructed presence–absence matrices (PAM) with species as rows and sites as columns. PAM elements are either ones or zeroes, denoting presences and absences of species in sites, respectively. For each PAM we first measured their degree of nestedness through the “modified temperature index” (MT, Ulrich and Gotelli 2007). This index is a modification of the “matrix temperature index” (Atmar and Patterson 1993) which measures ‘the biogeographic heat’ of the PAM using the distribution of unexpected species’ presences and absences within the matrix. This index is defined in the range between 0 (perfect order) and 100 (perfect disorder) and to calculate it, the PAM first must be sorted according to row and column totals in order to minimize the matrix temperature. The resulting PAM after this rearrangement is the packed PAM (Atmar and Patterson 1993) which exhibits a

triangular shape when the system is nested. Significance of nestedness was determined comparing the observed MT value with that of 200 random matrices obtained by the null model RANDOM1 (R1, Patterson and Atmar 1986). R1 is more conservative and ecologically realistic than other null models because it fixes the richness of each site and sorts the species proportional to their total incidence (Wright et al. 1998). We used the software Nestedness to carry out this analysis (Ulrich and Gotelli 2007).

## Results

Overall we collected 417 individuals from 12 species belonging to three different families. The fauna before matrix harvesting includes seven species. Forest fragments hold six species, forestry plantations five, and the continuous forest only three species (Table 1). After plantations were harvested, we collected individuals from 10 different species. Fragments support 10 species while plantations and the continuous forest hold only three (Table 2). Fragments differed in species richness and composition. Before matrix harvesting, species richness at three fragments (F1, F2 and F4) and one plantation (P2) was 0.7 times the richness at continuous forest, but richness at single fragment (F3) and one plantation (P1) were 1.7 times that hold by the continuous forest. After plantations were harvested, fragments F3 and F2 were 3.3 and 1.7 times richer than the continuous forest and plantation P1, respectively, while fragments F4 and P2 were hold 0.7 times species than the

**Table 1** Packed presence–absence matrix of apoidean species at the coastal Maulino forest, central Chile: before pine matrix is harvested

	F3	P1	CF	F1	F4	F2	P2	Incidence
<i>Bombus dahlbomii</i> (A)	1	1	1	0	1	1	1	6
<i>Manuelia postica</i> (A)	1	1	1	0	1	1	1	6
<i>Corynura</i> sp1 (H)	1	1	0	1	0	0	0	3
<i>Corynura corynogastra</i>	0	1	1	0	0	0	0	2
<i>Cadeguala occidentalis</i> (C)	1	1	0	0	0	0	0	2
<i>Cadeguala albopilosa</i> (C)	0	0	0	1	0	0	0	1
<i>Ruizantheda</i> sp1 (H)	1	0	0	0	0	0	0	1
<i>Manuelia gayatina</i> (A)	0	0	0	0	0	0	0	0
<i>Apis mellifera</i> (A)	0	0	0	0	0	0	0	0
<i>Ruizantheda proxima</i> (H)	0	0	0	0	0	0	0	0
<i>Corynura lepida</i> (H)	0	0	0	0	0	0	0	0
<i>Agapostemon</i> sp1 (H)	0	0	0	0	0	0	0	0
Site richness	5	5	3	2	2	2	2	

A refers to Apidae family, H to Halictidae and C to Colletidae families. CF represents the continuous forest, F1, F2, F3, F4 are the four forest fragments and P1 and P2 the two forestry pine patches studied

**Table 2** Packed presence–absence matrix of apoidean species at the coastal Maulino forest, central Chile: after pine matrix is harvested

	F3	F2	CF	P1	F4	P2	F1	Incidence
<i>Bombus dahlbomii</i> (A)	1	1	1	1	1	1	1	7
<i>Manuelia postica</i> (A)	1	1	1	1	1	1	0	6
<i>Cadeguala occidentalis</i> (C)	1	0	0	1	0	0	0	2
<i>Cadeguala albopilosa</i> (C)	1	1	0	0	0	0	0	2
<i>Manuelia gayatina</i> (A)	1	0	1	0	0	0	0	2
<i>Apis mellifera</i> (A)	1	1	0	0	0	0	0	2
<i>Agapostemon</i> sp1 (H)	1	1	0	0	0	0	0	2
<i>Ruizantheda proxima</i> (H)	1	0	0	0	0	0	0	1
<i>Corynura lepida</i> (H)	1	0	0	0	0	0	0	1
<i>Corynura corynogastra</i> (H)	1	0	0	0	0	0	0	1
<i>Corynura</i> sp1 (H)	0	0	0	0	0	0	0	0
<i>Ruizantheda</i> sp1 (H)	0	0	0	0	0	0	0	0
Sites richness	10	5	3	3	2	2	1	

A refers to Apidae family, H to Halictidae and C to Colletidae families. CF represents the continuous forest, F1, F2, F3, F4 are the four forest fragments and P1 and P2 the two forestry pine patches studied

continuous forest, respectively. Fragment F1 hold one species (Table 2).

*Bombus dahlbomii* and *Manuelia postica* were present at the three habitats regardless of matrix harvesting (Tables 1, 2). Before harvesting, *Cadeguala occidentalis* and *Corynura* sp1 were present at forest fragments and plantations, while after harvesting only *C. occidentalis* remained as the common species for both habitats. Plantations and the continuous forest shared *Corynura corynogastra* before but not after matrix harvesting. *Cadeguala albopilosa* and *Ruizantheda* sp1 were restricted to forest fragments before harvesting as *C. albopilosa*, *Apis mellifera*, *Agapostemon* sp1, *Ruizantheda proxima*, *Corynura lepida* were restricted to fragments after the harvesting.

Species composition at the landscape level was random (Table 3). However, there was a significant nestedness of the apoidean fauna after the plantations were harvested (Table 3). Not only there is an increase in species richness

**Table 3** Nestedness analysis for apoidean fauna before (BHM) and after matrix harvesting (AHM)

	BHM	AHM
PAM fill	0.25	0.31
PAM MT	8.46	0.49
Z-score MT for R1	-1.38	-2.13*

PAM fill indicates the proportion of the matrix filled with species presences. PAM MT (modified temperature index, Ulrich and Gotelli 2007) and Z-score (modified temperature of null model RANDOM1 (R1), Patterson and Atmar 1986). \*refers to statistically significance value of MT,  $P < 0.05$

in forest fragments after harvesting, but also fragments hold all species present in other habitats, rendering the fauna of the continuous forests and the matrix a subset of the fauna of fragments, particularly one fragment (F3, Table 3).

### Discussion

The apoidean fauna of the coastal Maulino forest depicts a pattern similar to bird, coleopteran and dipteran assemblages, with bees present in all three habitat types, albeit heterogeneously. Some forest fragments and plantations might hold more species than the continuous forest, strengthening the value of these remnants for biodiversity conservation and plantations as connecting habitat (Grez 2005; Simonetti 2006). This is particularly important, as the coastal Maulino forest, despite its high richness and endemism, is protected in a less than 200 ha in just two reserves. Therefore, currently unprotected forest remnants and productive environments such as plantations will be critical to enhance the conservation of the biodiversity of the coastal Maulino forest (Simonetti 2006).

Bee’ assemblages are non-nested before logging, suggesting that the pine matrix acts at least, as dispersal habitat for apoideans, possibly because most apoideans recorded are poliletic species. That is, they visit a great variety of plants, including those found as understory in pine plantations. As documented in birds (e.g., Fischer and Lindenmayer 2002; Wethered and Lawes 2005), some bee species are able to move through the pine matrix, suggesting that it might act as a habitat continuum rather than a discrete patchwork of habitats and non-habitat for bees and other species. However, pine plantations might be a barrier for *Manuelia gayatina*, as they appear in the continuous forest and fragment F3 only after the plantation was harvested (Tables 1, 2). As well as the potential positive pine effect over species richness, whether plantations are demographic sinks ought to be explored as abundance of pollinators, bees included, tend to be lower in fragments compared to the continuous forest (Valdivia et al. 2006). These dispersal effects combined with the regular isolation of natural forest fragments when plantations are clear-felled, may select the habitat-tolerant and less area sensitive forest species (Fischer and Lindenmayer 2002), triggering differential invasions to forest fragments, hence nestedness in bee’ assemblages. In fact, *Apis mellifera* invades fragments only after harvesting, with consequences yet to be determined. Regardless of this invasion, the conservation of the apoidean assemblage in the endangered Maulino forest will require a landscape level approach, including not only the continuous forest but also forest remnants and the surrounding pine matrix.

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