



The canopy beetle faunas of Gondwanan element trees in Chilean temperate rain forests

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ABSTRACT

Aim To describe the coleopteran fauna occurring in canopies of temperate Gondwanan tree species in terms of their diversity and guild and taxonomic structures, and to test the proposition that this structuring reflects the Gondwanan origins of this fauna.

Location The Andes and the coastal cordillera of temperate Chile.

Methods Canopy fogging was used to sample beetles from 29 trees. The samples were statistically described using S_{chao} and the Simpson diversity index D . Cluster analyses and multi-dimensional scaling (MDS) were performed. The taxonomic and guild structures of the Chilean coleopteran fauna were compared quantitatively with those found in other parts of the world using homogeneity chi-square and t -tests.

Results A collection of 25,497 beetle specimens was obtained primarily from *Nothofagus dombeyi*, *Nothofagus obliqua* and *Araucaria araucana*. The specimens collected were distributed between 485 morphospecies and included 107 putative, new generic-level taxa and 223 apparently undescribed species. Estimates of the size of the canopy beetle fauna showed that 600+ species were likely to be present. The communities found on a tree species differed markedly between years. MDS plots showed less community divergence between tree species for predators than for phytophages and xylophages. The guild structure was similar to that found on Australian 'Gondwanan' trees but differed significantly from the community structures found on 'Laurasian' tropical and temperate trees in supporting fewer phytophages and saprophages, but more xylophages. The predator guild showed a different pattern, with tropical faunas differing from those of more temperate regions, irrespective of hemisphere, as did the distribution of superfamilies.

Main conclusions The beetle fauna found in the canopies of *N. dombeyi*, *N. obliqua* and *A. araucana* was large (600+ species), with about half of the species undescribed. S_{chao} was found to vary with sample size and to give lower estimates of S than species attenuation curves, raising the possibility that the two methods are estimating the sizes of different statistical communities. It is possible that the attenuation curve is estimating the number of species to be found on a particular tree species, while S_{chao} is estimating the 'carrying capacity' for beetle species of individual trees, and this varies from tree to tree. Care also needs to be taken in experimental design when monitoring temporal changes in forest insect communities given the difference in communities found between years in this study. The proportions of phytophages, saprophages and xylophages resemble those of a 'Gondwanan' rain forest from Australia and differ significantly from those of tropical and temperate 'Laurasian' forests.

Keywords

Araucaria, biodiversity, canopy fogging, Chile, Coleoptera, guilds, *Nothofagus*, S_{chao} , temperate rain forests.

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INTRODUCTION

While canopy biodiversity studies have concentrated on tropical biotas (e.g. Erwin, 1982, 1983; Stork, 1987a,b,c, 1991; Hammond, 1990; Guilbert *et al.*, 1994, 1995; Davies *et al.*, 1997; Stork & Hammond, 1997), several authors have raised the possibility of regional differences in coleopteran guild structure in canopies (Watt, 1982; Gaston *et al.*, 1992; Hammond *et al.*, 1996). If such differences are real, they raise the possibility of differences in forest ecosystem function (Stork *et al.*, 1997b) following regional divergence in community structure. The austral temperate forests, which are largely of Gondwanan origin, offer further biodiverse, uniquely derived assemblages of species (Platnick, 1992) to test ideas on structure, diversity and history. The beetles in these assemblages are, as elsewhere, a large and ecologically diverse group suitable for such studies.

In Chile, the order Coleoptera includes 1289 described genera and 4241 species (e.g. Elgueta & Arriagada, 1989; Arias, 2000, 2001a,b, 2004, 2006, 2007; Elgueta, 2000, 2006). The Chilean beetle fauna shows a high level of endemism at the species level, while many genera are shared with Australia and New Zealand rather than with the tropical regions of South America (Arias, 2000; Elgueta, 2000). As a consequence, a common Gondwanan origin for these faunas could be hypothesized. Little work, however, has been conducted on the beetles that inhabit the canopies of Chilean forests that are the subject of this study.

The guild concept of community structure (Root, 1973) has been successfully applied to the description of the arthropod communities of canopies (e.g. Stork *et al.*, 1997a). Warren & Gaston (1992) demonstrated the generality of an observation made by Moran & Southwood (1982) that guilds (e.g. predators and phytophages) show consistency in the proportions of the species assigned to them in communities from a wide variety of environments. Because of their long, independent history, however, it is possible that Gondwanan communities may have followed a different evolutionary path from those with Laurasian origins. The number of canopy fauna data sets collected in a fashion allowing statistical comparison of the results, however, is small (one northern temperate, one southern temperate and four tropical) and it has not been possible yet to make meaningful comparisons. The collection of a second southern temperate data set, however, changes the situation. It is now possible to establish whether the relative sizes of the canopy guilds of Gondwanan-derived forests are consistent with or divergent from those found in other regions.

This study is intended to describe the coleopteran diversity of the canopies of two important Gondwanan tree genera, *Nothofagus* Blume and *Araucaria* Koch. Information on species richness and dominance, the proportion of undescribed species and the guild and taxonomic structures of this temperate rain forest fauna is provided and compared with that found in other biogeographical regions. It is hypothesized that, because of their common Gondwanan origin, the Chilean fauna will be more similar in feeding guild and taxonomic

structures to those found in Australian temperate forests than to those with Laurasian origins, even if from South America.

MATERIALS AND METHODS

Host trees

The tree species selected for this study have clear Gondwanan links, especially *Nothofagus* and *Araucaria*. The genus *Nothofagus*, the southern beeches, comprises about 35 species restricted to the temperate regions of southern South America, New Zealand, Australia, New Caledonia and New Guinea (Romero, 1988; McQuillan, 1993). In Chile the genus includes nine species (Donoso, 1995). The two most common tree species in the area were used in this study, *Nothofagus dombeyi* (Mirb.) Blume and *Nothofagus obliqua* (Birb.) Blume. Beetles associated with species of *Nothofagus* are listed in Gentili & Gentili (1988), Barriga *et al.* (1993) and Arias (2000).

Like *Nothofagus*, the genus *Araucaria* occurs in both South America and Australasia. *Araucaria araucana* (Molina), the monkey-puzzle tree, is trans-Andean. This species once had a more extensive distribution, as indicated by patches of *A. araucana* in very isolated sites, and by fossilized trunks of *A. araucana* in the now treeless pampas of Argentina (Herrmann, 2006). Several studies (Morrone, 1998; Kuschel, 2000) have been conducted on beetles known to feed on *A. araucana*, but not on beetles from the canopy.

Examples of several other Gondwanan element species found in the same areas were also fogged to see if there was consistency in the faunas. The species were *Laurelia semper-virens* (R. et Pavon) intermingled with either *Aextoxicum punctatum* R. et Pavon or *Podocarpus nubigena* Lindl, and *N. dombeyi* intermingled with *Drimys winteri* J.R. et G. Forster.

Trees between 15 and 45 m in height were chosen, as the canopies of trees over 40 m are difficult to fog completely. The trees selected had thick canopies, minimal understorey and were located in relatively wind-protected areas.

Study area

The areas of richest forest biodiversity in Chile are located between latitudes 35.6° and 41.3°S (Armesto *et al.*, 1998), where this study was conducted. The specific study sites (Fig. 1), with their latitudes, longitudes, mean temperatures, mean rainfall and collecting dates, are listed in Tables 1–4.

Collection and storage methods

A 'Golden Eagle' branch fogger was used to disperse a mix of diesel and the pyrethroid Cyperkill 25 EC (cypermethrin, 250 g L⁻¹) at a dose of 100–133 mL L⁻¹ of diesel fuel. Fogging was carried out between 10:00 and 14:00 h, and after 17:00 h when the wind speed was ≤ 2 km h⁻¹, for an 8–12-min period. Forty rounded collecting trays were placed under each selected tree and left in place for an hour after fogging unless wind speed increased. Each tray had an area of 1 m². The contents of



Figure 1 Map of Chile showing the location of collecting sites.

all the trays under a tree were pooled and stored in 95% ethanol. The alcohol was replaced once after 3 weeks and again in the laboratory in spring 2001 and summer 2003.

Sorting, mounting and identification

Samples were processed in the Essig Museum of Entomology (EMEC) by Elizabeth Arias and at the California Department of Food and Agriculture (CDFA) by Fred Andrews. The species identifications were carried out at the Museo Nacional de Historia Natural, Santiago, where vouchers of specimens were deposited. Guild placement of each species was assigned by John Lawrence (CSIRO), Rich Leschen (Landcare Research New Zealand), Rolf Oberprieler (CSIRO) and Adam Slipinski (CSIRO) working in concert on the basis of their knowledge of the biology of the species or the taxon to which it belongs.

Data analysis

Standard statistical descriptors of richness (n , number of individuals; S_{obs} , observed number of species; S_{chao} , estimated number of species) and diversity (Simpson D) were estimated for each sample using ESTIMATES software (Colwell, 2005). Jaccard similarities between all pairs of samples were calculated and the distances used in a cluster analysis using CLUSTERING CALCULATOR software (Brzustowski, 2002) and 100 bootstrapped replicates. Multi-dimensional scaling (MDS) plots were developed using PRIMER 5.2.7 software (Primer-E, Plymouth, UK) with Bray–Curtis distances and square-root transformed data. The analysis of similarities among the communities was also carried out using ANOSIM in PRIMER. The significance of differences between Gondwanan and Laurasian guild and superfamily structures was tested using homogeneity chi-square and t -tests.

RESULTS

In total, 25,497 beetles were collected from the canopies of 29 trees and sorted to 485 morphospecies (see Appendix S1 in

Table 1 Summary of descriptive statistics for beetle communities collected from *N. dombeyi* and sample IDs used in Figs 3 & 4 and Appendix S1. Temperature and precipitation values sourced from Anon. (2007a,b).

Tree species	<i>N. dombeyi</i>									
Locality	Total	Chillán Cordillera		Nahuelbuta	Flor del Lago			Puyehue		
Geographical area		Inland		Coast	Lowland			Inland		
Precipitation (mm)		3000		1000–1500	2000			4200		
Mean temp. (°C)		13		13	12			9.2		
Date		30 Nov. 2001	1 Dec. 2001	8 Dec. 2001	9 Dec. 2001	12 Jan. 2003	12 Jan. 2003	11 Jan. 2003	14 Jan. 2003	23 Jan. 2003
Latitude (°S)		36.92	36.92	37.81	37.81	39.17	39.17	39.20	40.66	40.65
Longitude (°W)		71.46	71.44	73.03	73.07	72.01	71.98	72.12	72.26	72.18
Altitude (m)		1274	1327	1219	961	633	440	365	226	340
Sample ID		nd1	nd2	nd3	nd4	nd5	nd6	nd7	nd8	nd9
n	12,348	383	2222	1056	1534	1384	1946	412	1130	2281
S_{obs}	294	29	77	48	63	73	63	51	71	86
S_{chao}	406.9	59.3	141.3	73	87.5	122.5	92.4	73.0	108.5	147.5
95% CI	362.0	35.3	100.8	56.4	71.5	93.2	73.5	58.9	86.0	113.0
95% CI	481.2	174.1	250.3	122.6	133.9	194.2	145.4	112.6	164.6	226.2
Simpson D	0.905	0.788	0.934	0.457	0.778	0.836	0.843	0.854	0.819	0.751

Table 2 Summary of descriptive statistics for beetle communities collected from *A. araucana* and sample IDs used in Figs 3 & 4 and Appendix S1. Temperature and precipitation values sourced from Anon. (2007a,b).

Tree species		<i>A. araucana</i>									
Locality	Total	Nahuelbuta Coastal range									Malalcahuello High land
Geographical area		1000–1500									2000
Precipitation (mm)		13									12
Mean temp. (°C)											
Date		7 Dec.	7 Dec.	6 Dec.	6 Jan.	7 Jan.	8 Jan.	8 Jan.	25 Jan.	19 Dec.	20 Dec.
		2001	2001	2001	2003	2003	2003	2003	2003	2001	2001
Latitude (°S)		37.81	37.81	37.80	37.80	37.80	37.80	37.80	37.81	38.44	38.44
Longitude (°W)		73.03	73.04	73.04	73.03	73.03	73.03	73.03	73.04	71.51	71.52
Altitude (m)		1182	1181	1182	1191	1191	1223	1219	1218	1204	1208
Sample ID		aa1	aa2	aa3	aa4	aa5	aa6	aa7	aa8	aa9	aa10
<i>n</i>	6114	604	1155	644	1030	147	58	1432	429	310	305
<i>S</i> _{obs}	168	26	44	54	74	29	17	82	38	13	16
<i>S</i> _{chao}	210.9	30.5	72.2	81.6	119.0	53.0	33.0	108.0	52.1	13	20.5
95% CI	189.1	36.8	50.9	63.4	91.7	34.7	20.0	92.2	41.9	13	16.5
95% CI	255.3	50.9	159.2	134.8	188.6	129.7	101.8	148.6	89.3	13	56.9
Simpson <i>D</i>	0.949	0.474	0.892	0.902	0.871	0.936	0.902	0.869	0.679	0.834	0.806

Table 3 Summary of descriptive statistics for beetle communities collected from *N. obliqua* and sample IDs used in Figs 3 & 4 and Appendix S1. Temperature and precipitation values sourced from Anon. (2007a,b).

Host		<i>N. obliqua</i>				
Locality	Total	Flor del Lago				
Geographical area		Lowland				
Precipitation (mm)		2000				
Mean temp. (°C)		12				
Date		13 Dec. 2001	8 Dec. 2001	13 Jan. 2003	24 Jan. 2003	13 Jan. 2003
Latitude (°S)		39.21	39.21	39.21	39.20	39.20
Longitude (°W)		72.14	72.14	72.01	72.14	72.14
Altitude (m)		282	282	315	306	281
Sample ID		no1	no2	no3	no4	no5
<i>n</i>	5142	1041	1041	1777	624	659
<i>S</i> _{obs}	179	51	65	86	72	65
<i>S</i> _{chao}	259.2	69.8	99.6	126.8	108.5	121.9
95% CI	221.8	56.5	76.8	103.5	85.9	87.4
95% CI	329.1	115.4	166.6	181.3	167.9	209.5
Simpson <i>D</i>	0.939	0.880	0.908	0.885	0.901	0.827

Supplementary Material). The average population density of beetles across all sites was 22 beetles m⁻² of sampled area (i.e. of ground area). This is similar to the densities reported by Davies *et al.* (1997), of 20.2 beetles m⁻² (Brunei) and 35.4 beetles m⁻² (Venezuela). With 8–86 (mean 54) species per tree, diversity was also of the same order of magnitude as the number of species per tree found by Mawdsley & Stork (1997), of 45–270 species per tree in Brunei. The morphospecies were then identified where possible. They included members of 13 superfamilies, 54 families and 252 previously described species. A total of 107 putative new taxa at generic level and approximately 233, possibly new, species, were found. When described, these would increase the size of the Chilean beetle

fauna to 1396 genera and 4748 species. Species represented by one or two individuals were present as 0.5% and 0.3%, respectively, of the total beetles collected. The predicted number of species (*S*_{chao}) for the combined samples was 601, of which 485 were collected.

The material collected from *N. dombeyi* trees (Table 1) consisted of 12,348 specimens (1372 beetles per tree) and 294 putative species, of which 121 species and 53 genera are probably new. Only 15 species were found of the 33 species previously reported from this tree species (Gentili & Gentili, 1988; Barriga *et al.*, 1993; Arias, 2000).

From *A. araucana* host trees (Table 2), 6114 specimens (611 beetles per tree) and 168 putative species were collected, of

Table 4 Summary of descriptive statistics for beetle communities collected from various tree species and sample IDs used in Figs 3 & 4 and Appendix S1. Temperature and precipitation values sourced from Anon. (2007a,b).

Tree species	Combined data					
	for all 29 trees (Tables 1–4)	<i>A. punctatum</i> + <i>L. sempervirens</i>	<i>A. punctatum</i> + <i>L. sempervirens</i>	<i>P. nubigena</i> + <i>L. sempervirens</i>	<i>P. nubigena</i> + <i>L. sempervirens</i>	<i>N. dombeyi</i> + <i>D. winteri</i>
Locality		Flor del Lago ranch	Flor del Lago ranch	Palmar lake	Palmar lake	Chinquén Island
Geographical area			Lowland		Highland	
Precipitation (mm)			2000			2200–3000
Mean temp. (°C)			12			10.7
Date		11 Jan. 2003	24 Jan. 2003	23 Jan. 2003	23 Jan. 2003	20 Jan. 2003
Latitude (°S)		39.21	39.21	40.79	40.82	42.70
Longitude (°W)		72.13	72.14	72.33	72.38	73.93
Altitude (m)		319	279	693	678	63
Sample ID		ot1	ot2	ot3	ot4	ot5
<i>n</i>	25497	135	20	285	1299	154
<i>S</i> _{obs}	488	45	8	56	84	27
<i>S</i> _{chao}	601	177.3	10.7	76.0	102.7	32.8
95% CI	560	77.2	8.4	63.0	91.5	28.3
95% CI	665	588.3	26.9	113.2	130.6	52.3
Simpson <i>D</i>	0.953	0.967	0.747	0.918	0.718	0.744

which 71 species and 35 genera are probably new. Eighteen species of weevils were found of the 23 already reported for this tree species (Barriga *et al.*, 1993; Morrone, 1998; Arias, 2000).

From *N. obliqua* host trees (Table 3), 5142 specimens (1028 beetles per tree) and 179 putative species were collected, of which 71 species and 34 genera are probably new. Only 7 species were found of the 20 already recorded from this tree species (Gentili & Gentili, 1988; Welch, 1988; Barriga *et al.*, 1993; Arias, 2000).

From the *A. punctatum* plus *L. sempervirens* trees (Table 4), 155 specimens (78 beetles per tree) and 53 putative species were collected. There are no previous records of beetle species for this tree association. On *P. nubigena* plus *L. sempervirens*, 1584 specimens (792 beetles per tree) and 140 putative species were found. There are no previous records of beetle species for this tree association. From *N. dombeyi* plus *D. winteri* trees (Table 4), 154 specimens (154 beetles per tree) and 27 putative species were collected. There are no previous records of beetle species for this tree association.

Fogging during the early or even late evening was found to be more effective, as the wind was weaker during these periods, although more beetles are available during warmer day temperatures. Fogging effectiveness also seemed to be unaffected by periods of light rain, although Guilbert *et al.* (1995) reported that sampling using canopy fogging was affected by rain in their study.

Diversity statistics

An estimated two-thirds of the species likely to be found on a given tree were collected by fogging (i.e. *S*_{obs} as a proportion of *S*_{chao}; Tables 1–4). A total of 294 different species were found on *N. dombeyi*, 168 on *A. araucana* and 179 on *N. obliqua*. Estimates of 406, 211 and 259 species were predicted (*S*_{chao}

calculated on the total sample for that tree species) for these tree species, indicating that 70–80% of the species likely to be found on each host tree were collected at least once during the survey, but only 15–25% of the available species were collected from any given tree. Similarly, a total of 488 species were collected from all tree species, whereas the estimated number of beetle species (*S*_{chao}) likely to be present was 601 (Table 4).

The structure of the beetle faunas of some tree communities (nd3, aa1, aa8, ot2, ot4, ot5) showed evidence of stress (i.e. their Simpson *D* values were well below 0.8) and these trees tended to support smaller numbers of species with one or a few species present in large numbers, as expected in stressful situations (Richardson & Oberprieler, 2007). The position and condition of the trees, however, gave no clue as to the nature of the stressor(s).

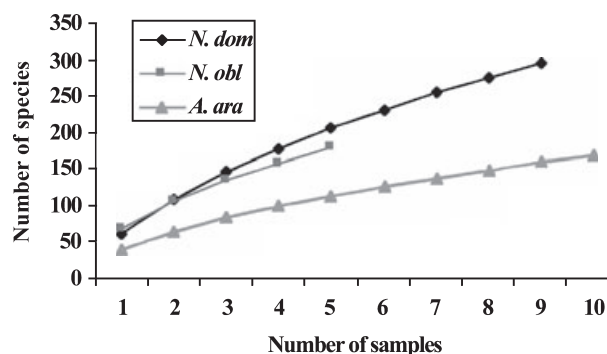


Figure 2 Species accumulation curves calculated using randomised sampling order (50 runs) (Colwell, 2005). (The predicted numbers of species likely to be present on each tree species are 406, 259 and 211, respectively.) *N. dom*, *Nothofagus dombeyi*; *N. obl*, *Nothofagus obliqua*; *A. ara*, *Araucaria araucana*.

The species accumulation curves (Fig. 2) clearly show that the number of species collected remained well below the predicted true number for the three best studied hosts (as shown above). These curves also show that detection of species on *Araucaria* is accumulating at a slower rate than on *Nothofagus*. This could be due to the limited geographical range of localities used, or, more likely, it means that there are genuinely fewer species on this tree species. The *Nothofagus* curves are quite similar, though the *N. obliqua* curve is rising more slowly than that of *N. dombeyi*, which may be due to the limited geographical range of trees sampled of the latter species. Rarefaction estimates (as MMEans; Colwell, 2005) of likely species gave values of 535, 250, 293 and 682 on *N. dombeyi*, *A. araucana*, *N. obliqua* and total fauna, respectively, compared with 407, 211, 259 and 601 calculated as S_{chao} on the combined samples for each tree species.

Relationships between communities

The cluster analysis using Jaccard distances showed that communities on the two *Nothofagus* species are more similar to each other than to those on *A. araucana* (Fig. 3). Within *N. obliqua*, the mean value of *J* over all combinations was 0.18 and within *N. dombeyi* it was 0.15, while between *N. obliqua* and *N. dombeyi* *J* = 0.14. Within *A. araucana*, *J* was 0.21 and

the similarities to *N. obliqua* and *N. dombeyi* were *J* = 0.08 and *J* = 0.06, respectively. For each tree species, samples from 2001 (nd1–nd4; no1–no2; aa1–aa3) clustered together, as did those from 2003 (nd5–nd9; no3–no5; aa4–aa7). The 2003 *N. dombeyi* samples apparently cluster with *N. obliqua*; however, the dichotomy is not significant (Fig. 3). For *A. araucana*, the Nahuelbuta trees (aa1–aa8) were also clearly distinguishable from those from Malalcahuello (aa9 and aa10, Figs 3 and 4). The two latter trees are also quite different from each other (*J* = 0.04). There was no evidence of consistent geographical differences within the samples from either *Nothofagus* species; however, the effect of latitude was partly confounded with year.

Inclusion of the intermingled *Laurelia* plus *Aextoxicum* (ot1) and *Podocarpus* plus *Laurelia* (ot3) trees in the analysis (Fig. 4) shows that these communities cluster within the *N. dombeyi* communities, though the terminal branch lengths are very long and the internodes short.

The MDS analysis (Fig. 5a) also separates the communities by tree species (stress 0.14, typical for ecological communities), with the two *Nothofagus* communities being closer to each other than to the *Araucaria* community. Aa9 and aa10, again, are shown to differ from the remainder and from each other, as was found in the cluster analysis. Nd1 was also well separated from the other samples from *N. dombeyi* (Fig. 5a); however,

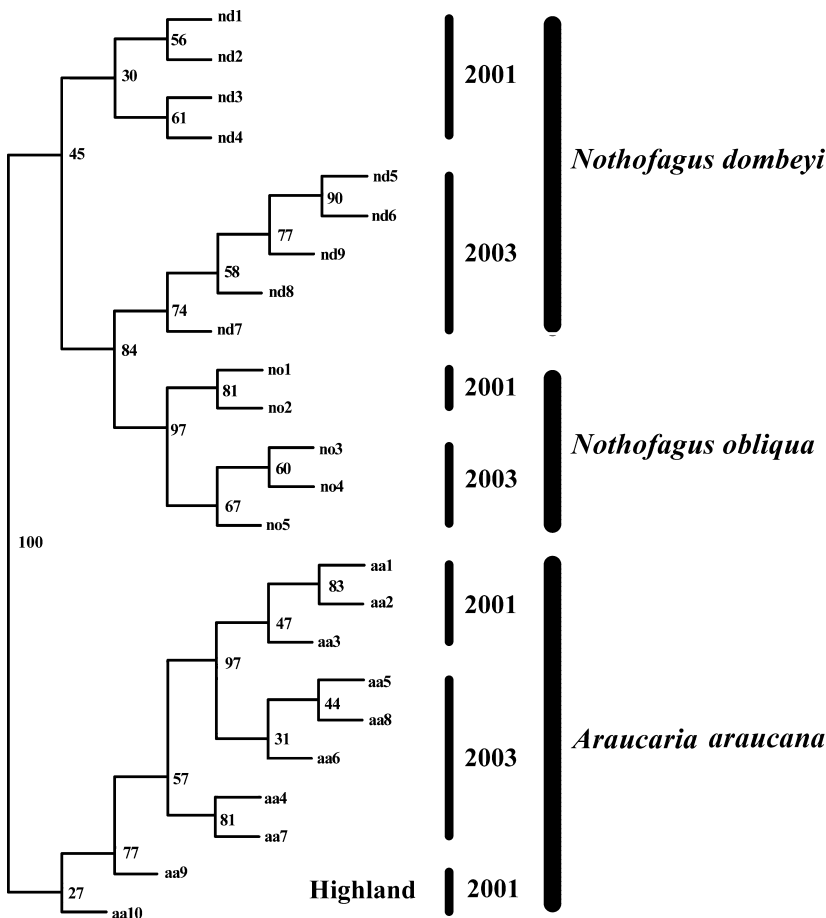


Figure 3 Clustering using unweighted arithmetic averaging based on Jaccard similarities. Stability analysis was carried out using bootstrapping (100 runs) (Brzustowski, 2002). The data are for *N. dombeyi*, *N. obliqua* and *A. araucana* only. Information on each sample set is given in Tables 1–4.

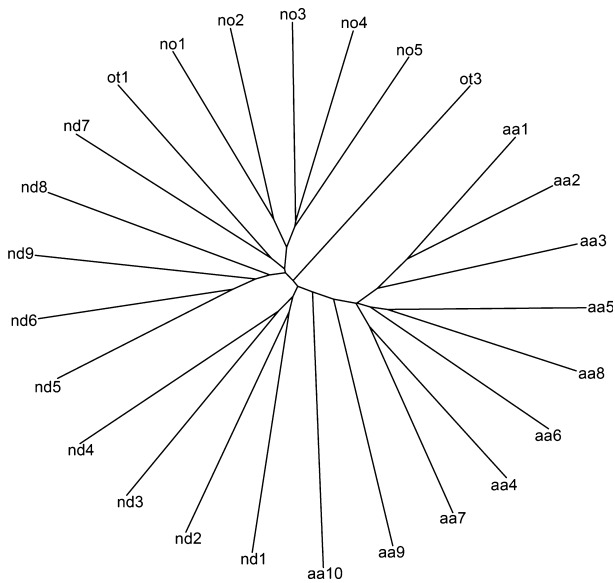


Figure 4 Clustering using unweighted arithmetic averaging based on Jaccard similarities, bootstrapped 100 times (% probabilities are shown). Data are for all collections that included sufficient specimens used to show placements of *Aextoxicum punctatum* + *Laurelia sempervirens* (ot1) and *Podocarpus nubigena* + *Laurelia sempervirens* (ot3) relative to *Nothofagus* and *Araucaria* samples. See Tables 1–4 for details on each sample.

this sample (Table 1) contained fewer species and specimens and showed some symptoms of stress (Simpson $D < 0.8$; Richardson & Oberprieler, 2007) compared with the other samples. ANOSIM shows that the communities on each tree species are significantly different (at the $P < 0.0001$ level).

Unfortunately, insufficient mycetophagous and saprophagous species were collected to allow MDS analysis of community structures of these guilds. MDS plots of predators (Fig. 5b, hypothesis: more mobile and less tree specific) and xylophages plus phytophages (Fig. 5c, hypothesis: less mobile and more host specific) show support for such within-community differences in structure, with less differentiation detected in the predator-based plot (stress 0.21) and more in the xylophages plus phytophages guild communities (stress 0.12).

Guild structure

A comparison of the guild structure in Chile on the three tree species (Table 5) showed they were not significantly different ($\chi^2 = 14.8$, d.f. = 8, $P = 0.07$). However, when the beetle guild structure of the current combined sample was compared using a homogeneity test with those of beetle faunas from other ‘Gondwanan’ and ‘Laurasian’ rain forest canopies collected using fogging in a similar fashion to that used here and for which comparable data sets have been published (Table 5), the data set is not homogeneous ($\chi^2 = 263$, d.f. = 20, $P < 0.0001$). As a consequence, the hypothesis that there are regional differences in guild structures (Watt, 1982; Gaston *et al.*, 1992; Hammond *et al.*, 1996) is supported. Cluster analysis of these

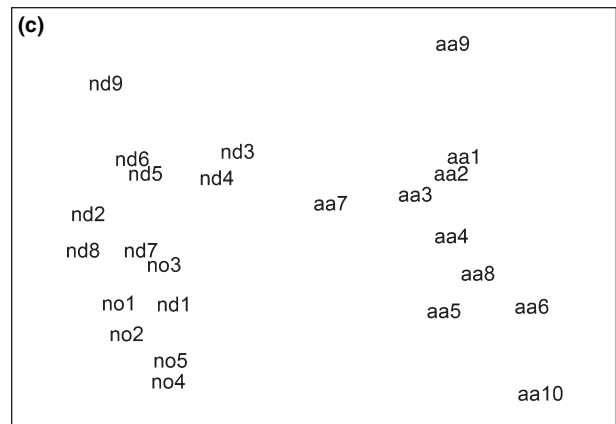
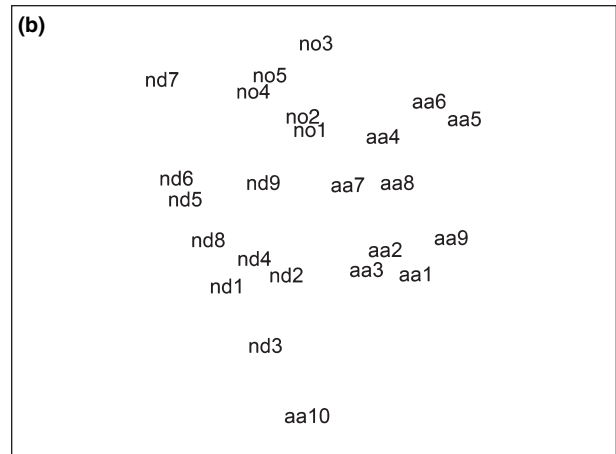
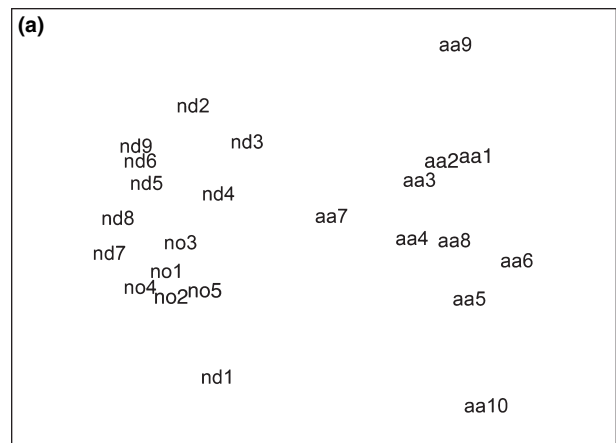


Figure 5 MDS output using data sets collected on *N. obliqua* (no), *N. dombeyi* (nd) and *A. araucana* (aa): (a) using data for all species (stress 0.14), (b) using data only for predator species (stress 0.21) and (c) using only data for phytophages and xylophages (stress 0.12). See Tables 1–4 and Appendix S1 in Supplementary Material for details on each sample. Axis 1 is the horizontal axis.

data (Fig. 6a) shows that the two ‘Gondwanan’ samples (Australia and Chile) diverge from the four ‘Laurasian’ samples. The terminal branch lengths, however, are relatively long and, as a consequence, the bootstrap values not significant. Examination of the guilds separately show that the

Locality: tree	Mycetophages	Phytophages	Saprophages	Predators	Xylophages	S _{obs}
Chile						
All tree species	16.9	13.8	7.2	36.1	24.3	485
<i>N. dombeyi</i>	20	15	6	23	19	289
<i>N. obliqua</i>	20	16	5	39	19	176
<i>A. araucana</i>	15	18	7	42	17	167
Australia	23.1	19.8	8.4	27.3	21.1	454
UK	26.5	23.5	11.0	29.0	10.0	200
Sulawesi	27.5	25.1	13.8	17.4	16.1	1355
Brunei	18.5	34.6	15.5	23.7	7.7	875
Venezuela						
All tree species	22.2	29.7	12.9	21.9	13.3	978
<i>Talisia</i>	22	35	9	22	12	292
<i>Brownea</i>	26	29	8	25	12	168
Polygonaceae	31	16	13	26	14	171
<i>Chrysophyllum</i>	31	26	9	21	13	211
<i>Cassia</i>	8	30	24	18	20	254
<i>Mangifera</i>	15	40	15	20	10	312

Table 5 Comparisons between the trophic guild structures (as % of total species) of beetle faunas collected from the canopies of forest trees by fogging (smaller guilds not included in the analysis). Chilean data: this study. Sulawesi, Brunei, Australia and UK data from Hammond *et al.* (1997) and Venezuela data from Davies *et al.* (1997).

Gondwanan samples have significantly fewer phytophages and saprophages and more xylophages (Table 5; *t*-test analyses not shown, *P* = 0.02–0.05 in each case) and, usually, predators. The alternative hypothesis, that the difference was between temperate and tropical faunas, was not supported, as the UK data were more similar to those from the tropics than to the two southern samples, and the Australian sample was taken from subtropical trees, not temperate ones. The UK fauna did, however, tend to be nearer in structure to the ‘Gondwanan’ samples in maintaining higher numbers of predators than the other Laurasian samples (Table 5). This observation supports the proposal (Gaston *et al.*, 1992) that predator proportions

are higher in temperate zones compared with tropical zones, irrespective of the hemisphere.

Superfamily structure

Comparison of the distribution of species between the nine most common superfamilies from six geographical regions (Table 6) showed that the data were not homogeneous ($\chi^2 = 421.4$, d.f. = 40, *P* < 0.0001). Cluster analysis (Fig. 6b) showed that the Chilean material again clustered with the Australian material and that the tropical samples were also more similar to each other. In this case, however, the UK material clustered with the Australian and Chilean material, unlike the situation with guilds.

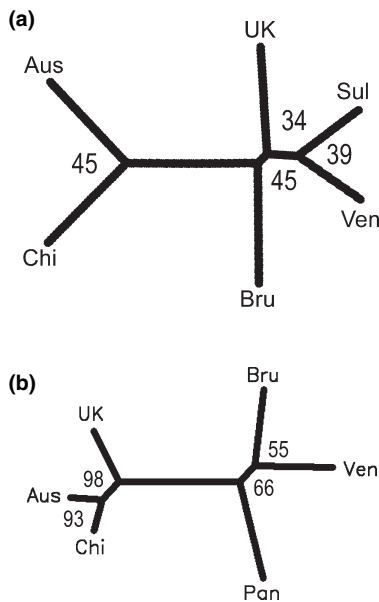


Figure 6 Cluster relationships of (a) guilds and (b) superfamilies based on Euclidean distances and data in Tables 5 and 6. Internode lengths are proportional to distances. Aus, Australia; Chi, Chile; Bru, Brunei; Ven, Venezuela; Sul, Sulawesi; Pan, Panama.

Table 6 Comparisons of the distribution of species between superfamilies (as % of total species) of beetle faunas collected from the canopies of forest trees by fogging (smaller superfamilies not included in the analysis). Panama, Brunei, Australia and UK data from Hammond *et al.* (1997) and Venezuela data from Davies *et al.* (1997).

Superfamily	Chile	Australia	UK	Brunei	Panama	Venezuela
Buprestoidea	3	1	4	4	3	11
Byrrhoidea	0	0	0	2	3	0
Chrysomeloidea	8	9	7	13	23	13
Cleroidea	8	1	1	1	2	2
Cucujoidea	10	17	26	16	14	27
Curculionoidea	19	25	15	21	22	18
Elateroidea	12	6	10	6	5	4
Hydrophiloidea	0	1	3	0	0	0
Scarabaeoidea	2	1	1	0	0	0
Scirtoidea	3	0	2	1	1	0
Staphylinoidea	16	21	19	19	15	12
Tenebrionoidea	18	17	13	16	12	11
S _{obs}	455	444	186	873	1210	969

DISCUSSION

Estimates of the size of the canopy beetle fauna predicted that 601 species are present on *N. dombeyi*, *N. obliqua* and *A. araucana* and, of these, 80% were collected during the study. Nevertheless, a large taxonomic impediment still exists to the detailed study of these communities.

In addition to yielding the greatest number of individual beetles per tree, *N. obliqua* also yielded the greatest diversity of beetle species: 60% of all the species were found on *N. obliqua* (see Appendix S1 in Supplementary Material).

Considerably lower beetle diversity was found among the tree associations *Aextoxicum* + *Laurelia*, *Podocarpus* + *Laurelia* and *N. dombeyi* + *Drimys* (Table 4). The low number of beetles collected from these sample trees could be a result of several factors, such as wind dispersal of the fog or falling specimens, low leaf area, coriaceous leaves (less palatable for phytophagous beetles), a loose or too open canopy or excessive tree height (over 45 m). Because of the low numbers of specimens collected on these trees, they were not included in most of the more detailed analyses; nevertheless they form a coherent cluster with the other Gondwanan communities (Fig. 4).

The S_{chao} estimates of species on each tree is very highly correlated with the number of species collected ($r = 0.93$; Tables 1–4). S_{chao} is considered a good and unbiased estimate of species number (e.g. Walther & Moore, 2005) and this high correlation is therefore of concern as the estimate is directly related to the number of species collected, not to the number of species present in the area on the tree species. In other words, the number of species predicted to be present on a particular tree species at a particular time and place should be the same for each replicate tree and independent of the number of species actually caught on that tree. The single-tree estimates are also only a small fraction of the size of the faunas found on these trees. Perhaps it indicates that the estimates are sensitive to the size of the tree (or some other factor), implying that the carrying capacity varies from tree to tree and this is what S_{chao} is estimating: S_{chao} made from a single fogged sample is certainly not an accurate estimate of the species present in the study area on that tree species. Alternatively it is an estimate of the number of species likely to be found on a specific tree on a specific occasion, or the estimate is an artefact due to the extra species added as singletons as n increases (Walther & Moore, 2005). Azarbayjani & Richardson (1999) used a replicated fogging experiment to measure the power of standard biodiversity statistics used in monitoring programmes to detect changes in diversity and showed that, for example, for the detection of a 30% change in S_{chao} , 80% of the time, 20 replicates would be needed. It is also of concern that the overall estimates of species number made using S_{chao} were 20% lower than those made from the species accumulation curves, again raising the question as to which communities are actually being estimated in each case.

Monitoring of canopy communities using fogging samples can be further confounded by inter-year differences in communities (e.g. Azarbayjani *et al.*, 1999), and such an effect was also found here (e.g. see divergence between nd1–nd4 collected in 2001, and nd5–nd9 collected in 2003; Fig. 3) as 2003 was a much wetter and foggier year than 2001, and this effect is likely to be generally present in the size and composition of samples of insect faunas (Azarbayjani *et al.*, 1999).

The MDS plots showed less community divergence between tree species for predators than for phytophages and xylophages. This is presumably due to differences in mobility and specificity to tree species in the two groups. Monitoring of the insect faunas of specific trees of conservation concern therefore may be more sensitive if host-specific phytophages and xylophages, rather than predators, are used in the analyses.

The possibility of regional differences in guild structure has been raised before (Watt, 1982; Gaston *et al.*, 1992; Hammond *et al.*, 1996). However, the capacity to compare, for the first time, information from Chile with that from Australia using t -tests supports the view that guild structuring in Gondwanan-derived rain forest faunas differs from that in Laurasian-derived rain forest faunas, whether tropical or temperate, in supporting a significantly smaller proportion of phytophages and saprophages but significantly more xylophages (Table 5). The different pattern found for predators, which show the predicted tropical/temperate pattern (see below), clearly confounded the bootstrap analysis over all guilds (Fig. 6a). Beyond the simple historical fact of common origins, explanations for these observations are speculative (Warren & Gaston, 1992; Krüger & McGavin, 2001), as the basis of these differences is unclear, being observation-based rather than hypothesis-driven. It may be that the distribution of guild roles between insect orders differs in the two regions as a historical accident, or that more fundamental differences in the drivers of community structures evolved on the two supercontinents. The greater representation of the xylophages that has been found previously in Australia and New Zealand, for example, has been ascribed to the larger number of curculionids found in austral forests (Watt, 1982; Hammond *et al.*, 1996). There has also been recent discussion on the nature of the links between Australia and Chile, given that molecular clock dates imply faunal exchanges more recently than those related to Gondwana (e.g. Cook & Crisp, 2005). This could provide an alternative explanation for the structural similarities between these faunas.

It has been observed previously (Gaston *et al.*, 1992) that the predator guild shows a different pattern, with tropical faunas differing from those of more temperate regions, irrespective of hemisphere and taxon. The Chilean data fit this pattern (Table 5), with the UK joining Australia and Chile in maintaining high numbers of predator species. Moreover, the pattern becomes more extreme at higher latitudes and it would be of interest to test this hypothesis by examining the faunas of

Nothofagus canopies further south in Chile. A similar tropical/antitropical pattern was found for the distribution of superfamilies.

It is notable (Fig. 6b) that the superfamilial structures of samples of tropical material were similar to each other, irrespective of whether they were from the Old or New World, and that the more temperate regional samples were also similar irrespective of their continent of origin. Thus the hypothesis of Gondwanan and Laurasian divergence in taxonomic structure was not supported, while the alternative hypothesis of temperate versus tropical divergence was.

CONCLUSIONS

The canopy beetle fauna found in the canopies of three Chilean temperate rain forest tree species is estimated to be large (600+ species), with about half of the species presumed to be undescribed. This is a much lower estimate of the proportion of undescribed species than that made previously. S_{chao} was found to vary with sample size and to give lower estimates of S than species attenuation curves, raising the possibility that the two methods are estimating the sizes of different statistical communities. It is possible that the attenuation curve is estimating the number of species to be found on a particular tree species, while S_{chao} is estimating the 'carrying capacity' for beetle species of individual trees, and this varies from tree to tree. Care would also need to be taken when monitoring temporal changes in these forests given the difference in communities found between years. The proportions of phytophages, saprophages and xylophages resemble those of a 'Gondwanan' rain forest from Australia and differ markedly from those of tropical and temperate 'Laurasian' forests. On the other hand, the predator guild and the taxonomic structures of the community showed tropical/antitropical patterns. It is clear that the suggestion of regional differences in guild structures (Watt, 1982; Gaston *et al.*, 1992; Hammond *et al.*, 1996) has been confirmed. The possibility of structural divergence of Laurasian and Gondwanan guild structures was also confirmed, but not for all guilds.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 Species collected and the numbers of specimens of each species in each sample.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01837.x>

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