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

Elizabeth T. Arias¹*, Barry J. Richardson² and Mario Elgueta³

¹University of California, Essig Museum of Entomology, Wellman Hall no. 210, Berkeley, CA 94720, USA, ²CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601, Australia and ³Museo Nacional de Historia Natural, Santiago, Chile

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.
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, Notofagus 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 Laurasan origins, even if from South America.

MATERIALS AND METHODS

Host trees

The tree species selected for this study have clear Gondwanan links, especially Notofagus and Araucaria. The genus Notofagus, 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, Notofagus dombeyi (Mirb.) Blume and Notofagus obliqua (Birb.) Blume. Beetles associated with species of Notofagus are listed in Gentili & Gentili (1988), Barriga et al. (1993) and Arias (2000).

Like Notofagus, 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 sempervirens (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
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 CLUSTER 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).

<table>
<thead>
<tr>
<th>Tree species</th>
<th>N. dombeyi</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Location</td>
</tr>
<tr>
<td></td>
<td>Geographical area</td>
</tr>
<tr>
<td>Precipitation (mm)</td>
<td>3000</td>
</tr>
<tr>
<td>Mean temp. (°C)</td>
<td>13</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (°S)</td>
<td>36.92</td>
<td>36.92</td>
<td>37.81</td>
<td>37.81</td>
<td>39.17</td>
<td>39.17</td>
<td>39.20</td>
<td>40.66</td>
<td>40.65</td>
</tr>
<tr>
<td>Longitude (°W)</td>
<td>71.46</td>
<td>71.44</td>
<td>73.03</td>
<td>73.07</td>
<td>72.01</td>
<td>71.98</td>
<td>72.12</td>
<td>72.26</td>
<td>72.18</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>1274</td>
<td>1327</td>
<td>1219</td>
<td>961</td>
<td>633</td>
<td>440</td>
<td>365</td>
<td>226</td>
<td>340</td>
</tr>
<tr>
<td>Sample ID</td>
<td>nd1</td>
<td>nd2</td>
<td>nd3</td>
<td>nd4</td>
<td>nd5</td>
<td>nd6</td>
<td>nd7</td>
<td>nd8</td>
<td>nd9</td>
</tr>
<tr>
<td>$n$</td>
<td>12,348</td>
<td>383</td>
<td>2222</td>
<td>1056</td>
<td>1534</td>
<td>1384</td>
<td>1946</td>
<td>412</td>
<td>1130</td>
</tr>
<tr>
<td>$S_{obs}$</td>
<td>294</td>
<td>29</td>
<td>77</td>
<td>48</td>
<td>63</td>
<td>73</td>
<td>63</td>
<td>51</td>
<td>71</td>
</tr>
<tr>
<td>$S_{chao}$</td>
<td>406.9</td>
<td>59.3</td>
<td>141.3</td>
<td>73</td>
<td>87.5</td>
<td>122.5</td>
<td>92.4</td>
<td>73.0</td>
<td>108.5</td>
</tr>
<tr>
<td>95% CI</td>
<td>362.0</td>
<td>53.3</td>
<td>100.8</td>
<td>64.8</td>
<td>71.5</td>
<td>122.5</td>
<td>92.4</td>
<td>73.0</td>
<td>108.5</td>
</tr>
<tr>
<td>95% CI</td>
<td>481.2</td>
<td>75.5</td>
<td>150.3</td>
<td>122.6</td>
<td>133.9</td>
<td>194.2</td>
<td>145.4</td>
<td>112.6</td>
<td>164.6</td>
</tr>
<tr>
<td>Simpson D</td>
<td>0.905</td>
<td>0.788</td>
<td>0.934</td>
<td>0.457</td>
<td>0.778</td>
<td>0.836</td>
<td>0.843</td>
<td>0.854</td>
<td>0.819</td>
</tr>
</tbody>
</table>

© 2007 CSIRO
Journal compilation © 2007 Blackwell Publishing Ltd
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 ($S_{\text{chao}}$) for the combined samples was 601, of which 485 were collected.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>A. araucana</th>
<th>N. obliqua</th>
</tr>
</thead>
<tbody>
<tr>
<td>Locality</td>
<td>Total</td>
<td>Flor del Lago</td>
</tr>
<tr>
<td>Geographical area</td>
<td>Coastal range</td>
<td>Lowland</td>
</tr>
<tr>
<td>Precipitation (mm)</td>
<td>1000–1500</td>
<td>2000</td>
</tr>
<tr>
<td>Mean temp. (°C)</td>
<td>13</td>
<td>12</td>
</tr>
</tbody>
</table>

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).

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).

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 ($S_{\text{chao}}$) 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
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 $S_{cha0}$; 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 ($S_{cha0}$ 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 ($S_{cha0}$) 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).
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 MMMeans; 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 \( S_{\text{chao}} \) 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, \( J = 0.21 \) 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,
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 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
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 \( (\chi^2 = 421.4, \text{d.f.} = 40, P < 0.0001) \). 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.

### 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).

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

**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).

<table>
<thead>
<tr>
<th>Superfamily</th>
<th>Chile</th>
<th>Australia</th>
<th>UK</th>
<th>Brunei</th>
<th>Panama</th>
<th>Venezuela</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buprestoidea</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td>Byrrhoidea</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Chrysomeloidea</td>
<td>8</td>
<td>9</td>
<td>7</td>
<td>13</td>
<td>23</td>
<td>13</td>
</tr>
<tr>
<td>Cleroidea</td>
<td>8</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Cucujoidea</td>
<td>10</td>
<td>17</td>
<td>26</td>
<td>16</td>
<td>14</td>
<td>27</td>
</tr>
<tr>
<td>Curculionoidea</td>
<td>19</td>
<td>25</td>
<td>15</td>
<td>21</td>
<td>22</td>
<td>18</td>
</tr>
<tr>
<td>Elateroidea</td>
<td>12</td>
<td>6</td>
<td>10</td>
<td>6</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Hydrophiloidea</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Scarabaeoidea</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Scirtoidea</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Staphylinoidea</td>
<td>16</td>
<td>21</td>
<td>19</td>
<td>19</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td>Tenebrionoidea</td>
<td>18</td>
<td>17</td>
<td>13</td>
<td>16</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>( S_{obs} )</td>
<td>455</td>
<td>444</td>
<td>186</td>
<td>873</td>
<td>1210</td>
<td>969</td>
</tr>
</tbody>
</table>
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, coriaceus 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 $S_{\text{chaos}}$ estimates of species on each tree is very highly correlated with the number of species collected ($r = 0.93$; Tables 1–4). $S_{\text{chaos}}$ 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 $S_{\text{chaos}}$ is estimating: $S_{\text{chaos}}$ 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 $S_{\text{chaos}}$, 80% of the time, 20 replicates would be needed. It is also of concern that the overall estimates of species number made using $S_{\text{chaos}}$ 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. \( S_{\text{est}} \) 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 \( S_{\text{est}} \) 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.

ACKNOWLEDGEMENTS

We are indebted to Norman Platnick, Charles Griswold, Margaret Thayer, Alfred Newton Jr and Fred Andrews for their help and encouragement in this study. We thank Carlos Weber, Ivan Benoit, Claudio Cunaza and Victor Valverde (Corporación Nacional Forestal Santiago Chile) for providing permits for collecting in national parks and reserves and for lodging, to Pablo Wagner and Cornelia Kirsch (Flor del Lago, Villarrica, Chile) for providing a collecting site, Sergio Ocares F. for providing places in the Chillán Cordillera and for his help on field trips. Our thanks also go to Anasac, Alejandro Caroca, Clara Larrea and Patricio Caroca from ChileFog, and Terry Cuneo and Cristian Muñoz for their help in the field. We would like to thank Jaime Solervicens, Gerardo Arriagada and Guillermo Gonzalez for identifying material. Saul Cunningham, Sharon Lawler, Rolfe Oberprieler and Kipling Will provided very helpful editorial advice. Christine Richardson and Nancy V. Arias prepared the figures. We are very grateful to Dr Richard M. Bohart for financial support. This work was also supported, in part, by the Schlinger Foundation and the National Science Foundation (grant no. 0445413 to E.T.A. and K.W.W).

REFERENCES


**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
Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

**BIOSKETCHES**

Elizabeth T. Arias is an Associate Specialist at Essig Museum of Entomology, University of California, Berkeley. Her research interests are in the systematics of the click beetles of Chile, inventories of species-rich but poorly studied areas of Chile and in promoting scientific development and conservation in Chile.

Barry J. Richardson is an honorary research fellow in CSIRO Entomology, having recently retired. His research interests are in general zoology and in the evolutionary process. He has carried out genetic, biochemical, behavioural, ecological and systematic studies on a wide range of organisms, most recently on salticids.

Mario Elgueta is a Curator at the Museo Nacional de Historia Natural, Santiago. His research interests include the systematics of Chilean Coleoptera and the description of the faunas of specific ecosystems.

Editor: Jon Sadler.