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# Host specificity of ambrosia and bark beetles (Col., Curculionidae: Scolytinae and Platypodinae) in a New Guinea rainforest

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**Abstract.** 1. Bark and ambrosia beetles are crucial for woody biomass decomposition in tropical forests worldwide. Despite that, quantitative data on their host specificity are scarce.

2. Bark and ambrosia beetles (Scolytinae and Platypodinae) were reared from 13 species of tropical trees representing 11 families from all major lineages of dicotyledonous plants. Standardised samples of beetle-infested twigs, branches, trunks, and roots were taken from three individuals of each tree species growing in a lowland tropical rainforest in Papua New Guinea.

3. A total of 81 742 beetles from 74 species were reared, 67 of them identified. Local species richness of bark and ambrosia beetles was estimated at 80–92 species.

4. Ambrosia beetles were broad generalists as 95% of species did not show any preference for a particular host species or clade. Similarity of ambrosia beetle communities from different tree species was not correlated with phylogenetic distances between tree species. Similarity of ambrosia beetle communities from individual conspecific trees was not higher than that from heterospecific trees and different parts of the trees hosted similar ambrosia beetle communities, as only a few species preferred particular tree parts.

5. In contrast, phloeophagous bark beetles showed strict specificity to host plant genus or family. However, this guild was poor in species (12 species) and restricted to only three plant families (Moraceae, Myristicaceae, Sapindaceae).

6. Local diversity of both bark and ambrosia beetles is not driven by the local diversity of trees in tropical forests, since ambrosia beetles display no host specificity and bark beetles are species poor and restricted to a few plant families.

**Key words.** Host specificity, Mycetophagy, Mycophagy, net relatedness index, phloeophagy, xylomycetophagy.

## Introduction

While the majority of insects feeding on living plant tissues are host specific, those feeding on dead plant tissues are considered much less so (Novotny & Basset, 2005). Bark and ambrosia beetles (Col., Curculionidae: Scolytinae and Platypodinae) are often cited as an example of generalists feeding on dead plants. This ignores the fact that the group includes species with two fundamentally different feeding strategies: true bark beetles and ambrosia beetles. The true bark beetles are phloeophagous, i.e. they feed directly on the dead host tissues, in most cases on nutrient-rich phloem, and both adults and larvae build their own tunnels as they feed and travel under the bark. In contrast, ambrosia beetles create their galleries almost always inside sapwood of dead or moribund host, where they cultivate and feed on symbiotic fungi. Ambrosia beetles include mycetophages and xylomycetophages. Mycetophages' larvae feed on the symbiotic fungi as their exclusive diet and develop within

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spaces excavated by their parents. In xylomycetophages, larvae and adults ingest pieces of xylem along with the fungal tissue, and both participate in excavating a communal cavity in the tree (Roeper, 1995). Phloeophagy is ancestral in scolytines (Sequeira & Farrell, 2001), while the ambrosial habit is derived and has evolved multiple times (Farrell *et al.*, 2001; Kuschel, 2006). To avoid confusion between the ecological and taxonomic terminology, the term bark beetle is used here strictly for phloeophagous species, while the term ambrosia beetles applies to both xylomycetophages and mycetophages (see Table 2, later).

Herbivore–host associations are determined by the chemical defences of the host tissues (Basset, 1992; Becerra, 1997), host abundance, predictability and nutritive value (Coley *et al.*, 1985), enemy pressure (Basset, 1992), and intensity of competition (Kelley & Farrell, 1998). Spatial and temporal predictability of dead trees is an important issue for both bark and ambrosia beetles. Most phloeophages studied so far are also heavily affected by mutual competition for phloem (Anderbrant *et al.*, 1985), by parasitism and predation (Beaver, 1977), and by the chemistry of host defence mechanisms (Byers, 1995).

In contrast, host chemical defence, competition from other herbivores, and enemy pressure are probably less important for ambrosia beetles (Francke-Grosmann, 1967; Beaver, 1977, 1989). A large majority of ambrosia beetles attack their hosts when these are dying or dead, i.e. at a stage when the host defences have ceased to function. Furthermore, ambrosia beetles are less directly affected by the host defence chemistry as they either do not ingest the host tissues, or ingest only dead xylem predigested by their symbiont. The fungal symbiont might be affected by the host chemicals, but this has not been studied. Water content of the infested wood was shown to influence substrate choice by ambrosia beetles (Leach *et al.*, 1940) but its role in host species choice has not been investigated. The influence of wood density has not been studied. The lack of competition and predator and parasitoid pressure in ambrosia beetles, as opposed to the situation in phloeophages, has been observed commonly in the field, but never tested rigorously (L. R. Kirkendall, pers. comm.; R. A. Beaver, pers. comm.; J. Hulcr, unpublished data).

Independently originated ambrosia lineages often display convergence in behaviour and ecological strategies (Farrell *et al.*, 2001). Multiple transitions from phloeophagy to xylomycetophagy or to mycetophagy offer an opportunity to examine the evolutionary association between host range and feeding mode in bark and ambrosia beetles.

There is no host specificity study, based on quantitative data obtained by standardised sampling, available for bark and ambrosia beetles in the humid tropics. For ambrosia beetles, quantitative data on host selection are missing for all biomes. Some temperate phloeophagous species have been shown to depend on one or a few host species (Atkinson & Equihua, 1986; Kelley & Farrell, 1998; Jordal *et al.*, 2004). Beaver (1979), Browne (1958b), and Atkinson and Equihua (1986) concluded that in the tropics, most phloeophages are specialised to a single plant genus or a family whereas ambrosia beetles are family specialists or generalists. However, a large proportion of host records used in these analyses come from *ad hoc* observations and anecdotic records from hand-collecting (Browne, 1958b; Browne, 1961; Beaver, 1979; Atkinson & Equihua, 1986; Wood & Bright, 1992). Such collections are often biased towards common plant and beetle species, and are unevenly distributed among geographic areas, habitats, and sampling methods. For example, many host records of scolytines from Papua New Guinea have been inferred from catches by sticky traps placed on the studied tree species (Gray, 1974; Gray & Wylie, 1974; J. Dobunaba, pers. comm.). Such data do not record the ability of beetle species to develop in that particular tree species. It is important that information on host plants is based on feeding experiments or rearing of larvae, rather than inferred merely from insect distribution. Further, comparative studies of host specificity should be based on quantitative community data obtained by standardised sampling for all studied species of plants (Basset, 1992).

This study examines host specificity and species diversity of bark and ambrosia beetles from a lowland rainforest in Papua New Guinea. The present study tested whether host specificity differs between phloeophagous and ambrosia beetles, whether host specificity varies among species within the same strategy, and whether it differs between the studied beetles and other herbivorous insects. The study tested the effect of the hosts' phylogenetic distance on the similarity of their bark and ambrosia beetle faunas, and the effect of wood moisture content, wood density, and tree parts on the composition of the beetle assemblages. The study was designed to produce large quantitative samples. Beetles were reared from replicated wood samples of standardised size from trees belonging to both related and unrelated species spanning the angiosperm phylogeny. Rearing of beetles indicates their choice of host for oviposition and the survivorship of progeny to adulthood. Furthermore, it can distinguish true larval feeding from maturation feeding, which is often less specific (Pfeffer, 1943) and less relevant to the actual role of a species in herbivore assemblages.

## Methods

### *Study area and plant species*

The study was conducted in a mosaic of primary and secondary lowland humid rainforest near Ohu Village, Madang province, Papua New Guinea (146°40′E, 5°15′S; 150–200 m a.s.l., average annual rainfall 3558 mm with low seasonal variation). The diverse vegetation [152 woody species of diameter at breast height (DBH) $>5$ cm ha$^{-1}$, Novotny *et al.*, 2004] is classified as mixed evergreen hill forest (Paijmans, 1976). The study was completed during 2002–2005 with different individuals of each tree species investigated at different times of the year, in order to diminish any influence of seasonal climate changes.

Thirteen tree species were selected for the study so that they were locally abundant, represented all major lineages of dicotyledonous plants and included also some closely related (congeneric and confamilial) species. Three individuals were sampled from each of 11 tree species, and two individuals from the remaining two species (Table 1). Phylogenetic relationships and taxonomic nomenclature of the studied host species are from Soltis *et al.* (2000). All species were characterised by wood density and water content (J. Leps, unpublished) (Table 1).

**Table 1.** The studied tree species. Classification after Soltis *et al.* (2000). Replicates, the number of individual trees sampled; water content, % of weight (wood characteristics: J. Leps, pers. comm.; samples taken from other individuals than those used in the rearing experiment, values are averages from two tree individuals per species).

| Species | Family | Order | Division | Replicates | Water content | Wood density (g cm$^{-3}$) |
|---|---|---|---|---|---|---|
| *Pouteria* sp. | Sapotaceae | Ericales | Asterids | 3 | 0.49 | 0.58 |
| *Litsea timoriana* Span. | Lauraceae | Laurales | Base | 3 | 0.36 | 0.29 |
| *Cananga odorata* Hook. f. & Thomson | Annonaceae | Magnoliales | Base | 2 | 0.45 | 0.27 |
| *Myristica* sp. | Myristicaceae | Magnoliales | Base | 3 | 0.45 | 0.46 |
| *Alstonia brassii* Monachino | Apocynaceae | Gentianales | Euasterids1 | 3 | 0.44 | 0.54 |
| *Teismanniodenron* sp. | Verbenaceae | Lamiales | Euasterids1 | 3 | n/a | n/a |
| *Pterocarpus indicus* Willd. | Fabaceae | Fabales | Eurosids1 | 3 | 0.44 | 0.56 |
| *Macaranga aleuritoides* F. Muell. | Euphorbiaceae | Malphigiales | Eurosids1 | 2 | 0.41 | 0.29 |
| *Ficus nodosa* Teysm. & Binn. | Moraceae | Rosales | Eurosids1 | 3 | 0.46 | 0.35 |
| *Ficus subtrinervia* Laut. & K. Schumm. | Moraceae | Rosales | Eurosids1 | 3 | 0.38 | 0.54 |
| *Artocarpus altilis* Fosberg | Moraceae | Rosales | Eurosids1 | 3 | 0.48 | 0.41 |
| *Pterocymbium beccarii* K. Schum. | Sterculiaceae | Malvales | Eurosids2 | 3 | 0.59 | 0.34 |
| *Aglaia cuculata* (Roxb.) Pellegr. | Meliaceae | Sapindales | Eurosids2 | 3 | 0.45 | 0.60 |

### *Insect rearing and identification*

Trees with DBH ∼20 cm were used for the study. Each tree was girdled, killed by fire, and left standing dead to allow for the beetle colonisation to start. The girdling consisted of peeling an approximately 30 cm wide circumferential strip of bark and wounding an adjacent 30 cm wide strip with multiple cuts. Fire and girdling increase the attractiveness of a tree to ambrosia beetles (J. Hulcr, unpublished data). After 20 days, the already dead tree was felled and the following standard-size samples were taken and placed separately into rearing boxes: (i) the uppermost 20–30 cm section of roots with adjacent 10 cm of the trunk base, (ii) a 50 cm long section of the burned part of the trunk and a 50 cm long section of the non-burned part including the wounded surface, (iii) branches 2–10 cm in diameter filling $30 \times 50 \times 60$ cm space (90 000 cm$^3$) inside a rearing box, and (iv) twigs (diameter $<$ 2 cm) filling the same volume inside a rearing box. Each box had a single opening in the front to which a transparent bottle with ethanol was attached. Phototactic beetles flew towards the light coming through the bottle, and were killed and preserved by the ethanol. Beetle samples were removed twice a week for 10 weeks, after which emergence of beetles was rare. The beetles were sorted into morphospecies by trained parataxonomists, databased, and subsequently identified by J. Hulcr or R. A. Beaver (Chiang Mai, Thailand), using comparison with identified material, including holotypes, in major collections. Vouchers were deposited in the Natürhistorisches Museum in Vienna, Smithsonian Institution in Washington, DC, Forest Research Institute, Lae, Papua New Guinea, National Insect Collection, Port Moresby, Papua New Guinea, the Natural History Museum in London and the A. J. Cook Arthropod Collection of Michigan State University, East Lansing, U.S.A.

The phloeophagous subtribe Cryphalina was excluded from the analysis as the inadequate taxonomy made species delimitation impossible. This is an important omission since several thousands of cryphalines were reared. Cryphalina are one of the taxonomically least known groups of scolytines (Wood, 1986).

### *Data analysis*

Samples of tropical insect communities include numerous rare species. These species should be excluded from host specificity analyses as their apparent narrow host range can be an artefact (Novotny & Basset, 2000). Species with $<10$ individuals were excluded from the analysis of host specialisation. A beetle species was considered a specialist on a particular plant species or clade if at least 90% of all individuals were found on this species or clade (Novotny *et al.*, 2002a). Ten individuals represent the smallest sample permitting this classification.

Further, we tried to distinguish instances of successful and unsuccessful breeding. The smallest number of conspecifics reared from the same tree that included freshly eclosed individuals, which represent evidence of successful breeding, comprised seven individuals. Further, scolytines have typically a brood size of at least five individuals from a single pair (Jordal & Kirkendall, 1998). Based on this indirect evidence, $<5$ conspecific individuals reared from the same sample were assumed to represent depauperate brood or not feeding adults and were excluded from the analysis. Data filtering excluded 17 from the total of 72 species but only 1.1% of all individuals.

Species accumulation curves were derived using the Mao Tau function (an analytical analog of a rarefaction curve derived from randomised resampling) implemented in the EstimateS software (Colwell, 2005). The total number of local scolytine species was estimated using Chao 2 statistics in EstimateS. The Chao 2 index is based on species incidences, which are suitable for our dataset with pseudoreplicated numbers of individuals in most species. This estimator performs well for samples with a substantial proportion of rare species and with potentially many species not sampled (Colwell & Coddington, 1994). Complete data including singletons were used for construction of the species accumulation curves.

Host specificity was characterised as the effective specialisation calculated as $FT = ST/(STavg \times T)$ where ST is the total number of beetle species found on $T$ hosts studied, and STavg is the

average number of beetle species found on a single host-plant species (Ødegaard *et al.*, 2000).

Similarity of beetle assemblages was quantified as the average proportion of shared species between the assemblages, estimated by the Chao–Sørensen index, which provides robust results even for incomplete samples with numerous rare and unsampled species (Gotelli & Colwell, 2001; Chao *et al.*, 2005). The Chao–Sørensen index was based on raw abundance data and implemented in EstimateS software (Colwell, 2005).

The correlation between the pairwise similarity of ambrosia beetle assemblages and the phylogenetic distance of their host plants species was tested. First, the hypothesis that conspecific trees tend to harbour similar ambrosia beetle communities was tested by a Mantel test (1000 runs), where the faunal similarity matrix was compared with a binomial matrix with 1 for conspecific pairs and 0 for heterospecific pairs. Second, it was tested whether beetle assemblage similarity decreases with increasing phylogenetic distance of their hosts. The hypothesis that phylogenetically related trees tend to harbour similar bark and ambrosia beetle assemblages, i.e. that phylogenetic distances between trees are correlated with similarity of their faunas, was tested using a Mantel test (1000 runs), where the number of nodes between host species on the cladogram was used as an approximation of phylogenetic distance. Conspecific trees were assigned a phylogenetic distance of zero.

Each beetle species was classified as a monophage, a clade-specialist, or a generalist, based on two criteria. First, a species was considered specialised if more than 90% of individuals of a species were reared from a single tree species or from trees in a single clade (of any rank – genus, family, order, etc., Table 1). Further, for each beetle species a null hypothesis was tested that the beetles were distributed across the tree phylogeny non-randomly, that is, that the distribution was contingent on the phylogenetic relationships of the trees. Host-plant range of each species was characterised by the Net Relatedness Index (NRI) using the program Phylocom (Webb *et al.*, 2006). NRI measures the difference between mean phylogenetic distance among host species and among the same number of randomly selected plant species from the host phylogeny. This allows for testing whether or not the host range is phylogenetically clumped, random, or overdispersed. A tree phylogeny was used with tree individuals used as terminals with phylogenetic distance between conspecific trees set to zero, and with each internal branch assigned a length of 1. Only presence/absence data were used for beetle–host associations.

The hypothesis that beetles select their hosts at random was tested by correlating the number of reared individuals of beetle species with the number of hosts from which they were reared. An existing correlation would imply lack of host specificity, since the number of recorded hosts is simply a function of the number of the particular beetle species records. A lack of correlation would imply that beetles are confined to a limited number of their hosts.

Correspondence analysis (CA) was used to search for patterns in the beetle species distribution, and canonical correspondence analysis (CCA) with subsequent variation partitioning was used to compare explanatory power of individual tested variables. Ordination methods based on unimodal distribution of species along environmental gradients (weighted average methods) were used. Most of the tested variables (host species and tree parts) are categorical variables, and it was expected that beetle species would prefer some tree parts over others, rather than respond linearly. Second, the initial exploratory detrended correspondence analysis (DCA) detected *gradient lengths* in the data over 4.0, which is a signal of unimodal species distribution along the gradients of the studied variable (Smilauer & Leps, 2000). The abundance of scolytine species was $\log_{10}(x+1)$ transformed. Only ambrosia beetles were included in the analysis as phloeophagous beetles were too species poor. Ordination analyses were performed using CANOCO (ter Braak & Smilauer, 2003).

The variation explained by all canonical variables ($v_{var}$; ratio of canonical eigenvalues to all eigenvalues), by host tree species ($v_{sp}$; tree part held as a covariable), and by tree parts ($v_{part}$; tree species held as a covariable) was estimated. The total variation

**Table 2.** Taxonomic groups represented in the samples and their host specificity. Taxonomy is following Arnett *et al.* (2002) and Kuschel (2006). The average number of nodes between all hosts in the analysis = 5.70. NRI is the Net Relatedness Index, a measure of phylogenetic clustering of host range; high values indicate high specificity. Species with non-random host selection: number of species occurring on a single species or a single host clade with statistical significance, see text.

| Feeding habit | Subfamily | Subtribe | No. of species | No. of individuals | Average no. of nodes between hosts | Average NRI | Species with non-random host selection |
|---|---|---|---|---|---|---|---|
| Ambrosia beetles | Scolytinae | Xyleborina | 45 | 33766 | 5.51 | 0.82 | 3 |
| | Platypodinae | Diapodina | 2 | 1967 | 5.81 | –0.43 | 0 |
| | | Tesserocerina | 5 | 1136 | 5.05 | 0.54 | 0 |
| | | Platypodina | 8 | 20681 | 5.52 | 0.86 | 0 |
| Bark beetles | Scolytinae | Hylesinina | 2 | 9359 | 2.67 | 4.74 | 1 |
| | | Diamerina | 1 | 94 | Reared from a single tree | n/a | — |
| | | Phloesinina | 2 | 8075 | 0 | 3.61 | 2 |
| | | Dryocoetina | 3 | 213 | 2.14 | 2.35 | 1 |
| | | Xyloctonina | 2 | 3696 | 0 | 3.51 | 2 |
| | | Ipina | 2 | 2 | <10 individuals | n/a | — |
| | | Cryphalina | ? | 2752 | ? | n/a | ? |

 

explainable by canonical variables is given by $v_{var} = v_{sp} + v_{part} + v_{res}$, where $v_{res}$ is the variation explained by interactions among the variables. Resulting ordination diagrams were rescaled to display inter-species distances. The effect of wood density and water content on beetle communities was tested by CCA of tree species (not tree individuals, as in the above analysis) as the wood properties were known for tree species, rather than individuals. Statistical significance of the effect of the tested variables was assessed using Monte Carlo permutation test implemented in CANOCO, with 499 permutations. Statistical significance of associations between species and tree parts were tested using *T*-value biplots with Van Dobben circles as implemented in CANOCO. These diagrams are a graphical approximation of *t*-value statistics of regression coefficients of multiple regression between individual species and all environmental variables (Smilauer & Leps, 2000).

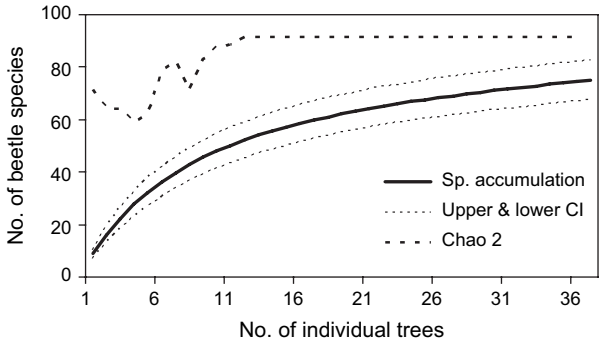


**Fig. 1.** Species accumulation and an estimate of total species richness. Complete data for all ambrosia and bark beetle species and all 13 tree species were included. Solid line: species accumulation curve derived analytically, Mao Tau function; dotted lines, 95% confidence intervals; dashed line, Chao 2 estimate of the total number of species.

## Results

*Species richness and taxonomic composition*

In total, 81 742 individuals from 73 scolytine species were reared, including 67 identified to known species (Table 2). The species accumulation curve for the entire data set has not reached an asymptote, but is approaching the Chao 2 estimate of the total number of species (Fig. 1), suggesting that the majority of the local species were represented in the analysis. This estimate of 92 (SD = 8.91) species was independent of sample size for data sets larger than 50% of the actual sample size.

*Host specificity of ambrosia beetles*

Ambrosia beetles were represented by 62 species in the samples (Table 2).

There was no statistically significant difference between the between-host-species and within-host-species faunal similarity indexes (average Chao–Sørensen index 0.636 and 0.657 respectively; $r^2 = 0.048$, Mantel test $P > 0.05$). Therefore, the identity of a host tree species does not influence its ambrosia beetle community. There was also no correlation between similarity of beetle communities and phylogenetic distance of host tree species ($r^2 = 0.017$, Mantel test $P = 0.697$; Figs 2 and 3). The effective host specificity of the ambrosia beetle community was 0.089.

Two ambrosia beetle species seem to be specialised on a single tree species: *Platypus excedens* on *Aglaia cuculata* (14 437 out of 14 927 total individuals; 97%) and *Xyleborus fallax* on *Ficus subtrinervia* (15 out of 15 individuals; Table 3). Further, comparison of the NRI of the diet of each species with its null model showed that one more species was significantly often associated with a single host (*Amasa resectus* with *Pouteria* sp.). However, more than 10% of individuals of *A. resectus* were

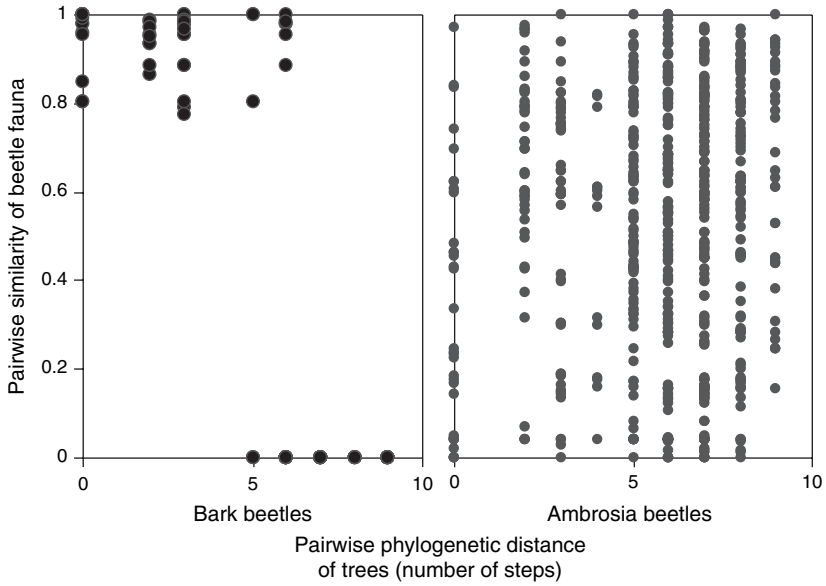


**Fig. 2.** Correlation between pairwise phylogenetic distances between host tree individuals and pairwise similarity of assemblages of bark beetles (left) and ambrosia beetles (right). Phylogenetic distance measured as number of nodes on the plant cladogram (Fig. 5). The relationship between the phylogenetic distance of plant species and the similarity of their beetle communities was significant for bark beetles (Mantel test, $P < 0.001$), but not for ambrosia beetles (Mantel test $P > 0.70$).

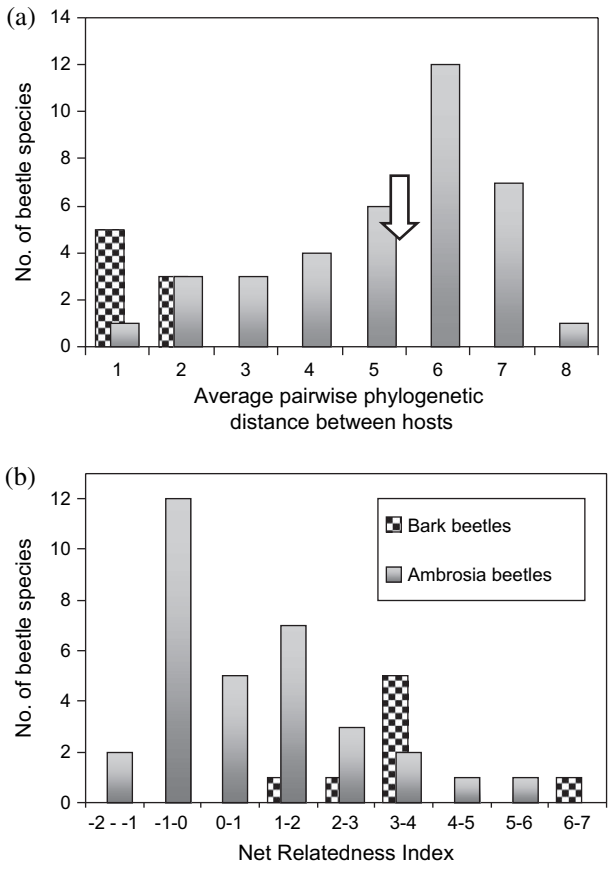


**Fig. 3.** (a) Distribution of average pairwise phylogenetic distances (number of nodes) between hosts in species of xylomycetophages (grey) and phloeophages (chequered). The arrow marks the average pairwise number of nodes between host trees in the dataset (5.7). (b) Distribution of Net Relatedness Index (NRI) among species of xylomycetophages (grey, $n = 33$) and phloeophages (chequered, $n = 8$). NRI, when used as a measure of host specificity, measures the difference between mean phylogenetic distance among host species and among the same number of randomly selected plant species from the host phylogeny. Values around zero indicate no specificity to any host clade, high values indicate that the herbivore species is associated with related host species.

found on two other unrelated trees, thus the species cannot be considered a monophage. A further six ambrosia beetle species (all Xyleborina) of 42 tested were statistically significantly confined to a phylogenetic clade of hosts higher than a species (Table 3, Fig. 3b). One species was confined to the genus *Ficus*, one to the family Moraceae, three to various suprafamilial clades. No other ambrosia beetle species showed any significant host preference. Three ambrosia beetle species were overdispersed on the cladogram (*Xyleborus perforans*, *Xyosandrus crassiusculus*, *Xylosandrus morigerus*; Table 3). Detailed results pertaining to individual species are available from the authors on request.

The average number of hosts utilised by an ambrosia beetle species was 3.76 out of the 13 studied, excluding beetle species that were found on a single tree individual. The average phylogenetic distance, expressed as the number of nodes between two hosts on the host cladogram, was 4.7 (SD = 2.9), not significantly different from the average pairwise distance among all hosts in the analysis (5.70, Fig. 3). The number of recorded host plant species ($y$) was a logarithmic function of the species abundance ($x$): $y = -1.564 + 2.311 \log_{10} x$ ($n = 44$, $r^2 = 0.442$, $P < 0.0001$, Fig. 4). Thus, the number of reared individuals explained over 60% of variability in beetle diet breadths. Examples of typical distribution of ambrosia species among hosts are given in Fig. 5.

### *Host specificity of phloeophagous bark beetles*

The 12 phloeophagous species (excluding Cryphalina) were more host specific and had a different community structure from ambrosia beetles (Table 3, Fig. 3). The similarity between phloeophagous communities was negatively correlated with the phylogenetic distance of their hosts ($r_s = -0.84$, Mantel test $P < 0.001$).Congeneric trees shared many phloeophages, while phylogenetically more distant trees hosted different phloeophage communities (Fig. 2). The effective host specificity of the phloeophagous guild was 0.289 and the average number of tree species utilised by a phloeophage was 1.6 out of the studied 13. The average phylogenetic distance among hosts of a phloeophage was 0.86 nodes (SD = 1.2; Fig. 3).

Four phloeophage species belonging to two separate subtribes were reared repeatedly from a single host species (Table 3). In these cases, however, no congeneric or confamilial host tree species were present in the study, therefore no conclusion about the level of their host specificity can be made. Two other species were abundant in all species of the family Moraceae, but not found elsewhere (Table 3, Fig. 5). The remaining four abundant phloeophagous species were reared from one or two host trees only, which is not sufficient for statistical testing.

### *Importance of tree parts and wood characteristics*

Cumulative percentage variance explained by the first four ordination axes in the CA analysis did not surpass 30%, suggesting little correlation among the distributions of individual ambrosia beetle species. Both tree part and tree species had statistically significant influence on the species distribution in the CCA analysis (Monte Carlo test, $P = 0.02$ for both variables). The tree part explained 6.1%, the tree species 18.3%, and their interaction 0.3% of the total variance as captured by the CA ordination axes unconstrained by the tested variables. The remaining 75.1% remains unexplained.

The CCA ordination where tree parts were used as explanatory variables identified an assemblage of five ambrosia species statistically significantly preferring roots and trunk bases, four species preferring trunks, and four species preferring branches and twigs, while the remaining 32 species showed no preferences (Fig. 6). Twigs and roots were least attacked as only 15 out of 55 species were successfully reared from twigs, and only 29 species were reared from tree bases and roots.

**Table 3.** Species for which various levels of host specificity were detected. Species marked with (?) were reported also from other clades in the literature, thus their specificity is uncertain. NRI, Net Relatedness Index, is the difference between the average pairwise phylogenetic distance among host plants and the average pairwise phylogenetic distance among hosts in a randomised diet.

| | | Level of specificity | Specialised to | NRI |
|---|---|---|---|---|
| Mycetophages | *Platypus excedens* Chapuis | Species | *Aglaia cuculata* | 2.84 |
| | (?) *Xyleborus fallax* Eichh. | Species | *Ficus subtrinervia* | * |
| | *Xyleborus pumilus* Eggers | Genus | *Ficus* | 5.06 |
| | *Euwallacea fornicatus* (Eichh.) | Family | Moraceae | 3.68 |
| | *Amasa resectus* (Eggers) | Higher clade | Asterids | 2.73 |
| | (?) *Euwallacea piceus* (Motsch.) | Higher clade | Rosids | 4.37 |
| | (?) *Euwallacea bicolor* (Blandford) | Higher clade | Rosids | 3.02 |
| | 24 species | Generalists | | 0.43† |
| | *Xyleborus perforans* (Walk.) | Overdispersed | | –0.99 |
| | *Xylosandrus crassiusculus* (Motsch.) | Overdispersed | | –1.81 |
| | *Xylosandrus morigerus* (Blandf.) | Overdispersed | | –1.62 |
| Phloeophages | *Hyledius nitidicollis* (Motsch.) | Genus | *Myristica* sp. | 3.56 |
| | *Hyledius cribratus* (Blandford) | Genus | *Myristica* sp. | 3.67 |
| | *Scolytomimus phillippinensis* (Eggers) | Genus | *Pouteria* sp. | 3.46 |
| | *Scolytomimus pusillus* (Eggers) | Genus | *Pouteria* sp. | 3.58 |
| | *Ficicis despectus* (Walker) | Family | Moraceae | 7.28 |
| | *Cyrtogenius brevior* (Eggers) | Family | Moraceae | 3.34 |

*Single host species, NRI not applicable.
†Average NRI.

The overall variability explained by tree species was low (18%), confirming previous analyses that showed little effect of tree species.

The wood density and water content showed no influence on the xylomycetophagous assemblages (Monte Carlo test of both canonical axes; $P = 0.920$). Both variables together accounted for no more than 13% to the variation detected by the ordination analysis. Testing the effect of these variables on individual species by *T*-value biplots showed that the distribution of two species was negatively correlated with wood density (*Xylosandrus crassiusculus* and *Xyleborinus perexiguus*). However, even though the distribution of their abundance was slightly skewed towards soft-wood trees, both were successfully reared from some of the hardest trees in the analysis. There was no correlation between the wood characteristics (wood density and water content) and either the number of scolytine species or the number of reared beetle individuals (for all combinations, $r_s < 0.3$, $P > 0.19$).

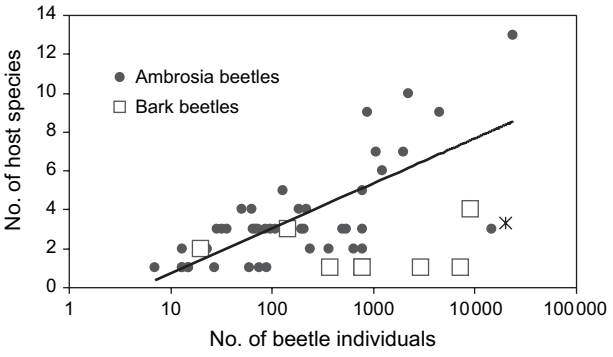


**Fig. 4.** Correlation between the number of reared individuals and the number of host species recorded for each beetle species. ●, ambrosia beetles ($n = 44$); □, bark beetles ($n = 8$). The trendline illustrates the increase of the number of host species with logarithm of the reared ambrosia beetle individuals ($y = -1.5645 + 2.3113 \log_{10} x$, $r = 0.675$, $P < 0.0001$); the regression does not refer to bark beetles. The asterisk marks *Platypus excedens*, an exceptional host-specific ambrosia beetle. Only beetles breeding in more than one tree were included.

## Discussion

The estimated local number of species is much lower than in studies on Neotropical scolytines (S. A. Dole & T. L. Erwin, unpublished data). At a single site in Ecuador, 61 scolytine species were collected by canopy fogging and the estimated total number of local species was 165. However, neither the species accumulation curve nor the richness estimator in the Ecuadorian dataset have reached an asymptote. This comparison indicates thorough sampling and a lower alpha diversity of scolytines in Papua New Guinea.

The effective specialisation of the ambrosia beetle guild, i.e. the proportion of beetle species restricted to an average host species, (0.089) was markedly lower than in phloeophages (0.289), or in leaf chewing beetles in the same rainforest (0.24; Novotny *et al.*, 2002b).

Of all the 62 species of ambrosia beetles, only four species displayed any host specialisation: *Euwallacea fornicatus* (on Moraceae, predominantly on *Artocarpus altilis*), *Platypus excedens* (on *Aglaia cuculata*), *Xyleborus pumilus* (*Ficus* spp.), and *Amasa resectus* (asterids clade *sensu* Soltis *et al.*, 2000). Only in the first two species are the associations supported by large numbers of reared individuals. Three other species exhibited specificity in the present study (*Euwallacea bicolor* and *E. piceus* on rosids and *Xyleborus fallax* on *Ficus*, Table 3), but are reported also from other hosts elsewhere (Wood &

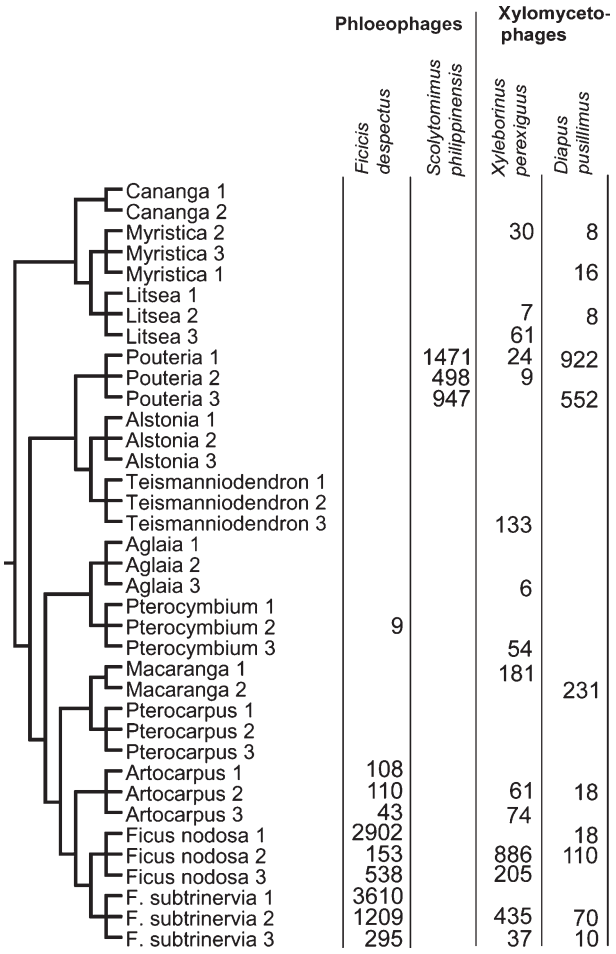


**Fig. 5.** Examples of distribution of reared bark and ambrosia beetles on the cladogram of host trees and the difference between the diet of typical bark beetles (left two columns) and ambrosia beetles (right columns). Numbers indicate reared beetle individuals from a particular tree individual.

Bright, 1992). Both Xyleborina and Platypodinae, each of which has evolved the ambrosia habit independently, show equal lack of host specificity. At least 11 of the ambrosia species in the present study are xylomycetophagous. None of these species showed any host specificity. Feeding on symbiont-predigested xylem does not appear to impose constraints on the host range of a beetle species; in contrast, feeding on near-fresh host phloem does.

The composition of the ambrosia beetle guild is not determined by the species composition of the local tree flora. Ambrosia beetle assemblages on different tree species are not significantly different, and beetle assemblages on trees belonging to the same species tend to be equally similar to assemblages on trees from different species. The only exception in the analysis was the fauna associated with *Aglaia cuculata*, which is strongly dominated by *Platypus excedens*, a species rare elsewhere. The fact that the observed diet breadth of a beetle species is a function of the abundance of that species in the sample lends further support to the conclusion that a majority of ambrosia beetles do not distinguish the identity of their host tree and that further sampling would probably extend the observed host ranges for rarer species. The same increase of host range with increased sample size was shown for tachinid parasitoids (Memmott *et al.*, 1994), but only to a much lesser extent for herbivores (Novotny *et al.*, 2002a).

Even though the number of specialised ambrosia beetles documented in this study was small, it may still be an overestimate. Bark and ambrosia beetles use species-specific olfactoric communication for orientation during host and mate search, making their spatial distribution more aggregated than random (Thunes, 1998). The active aggregation of ovipositing adults on certain tree individuals, together with the rearing of multiple individuals as progeny of a single female, contributes to the aggregated and pseudoreplicated distribution of reared individuals among individual trees. This aggregation contributes to bias in the measures of host specificity.

The low host tree specificity of ambrosia beetles may differ from their specificity with respect to their immediate food resource, represented by the ambrosia fungi. Specificity of this association may be high (Beaver, 1979), however empirical data are scarce and inconclusive (Batra, 1966; Beaver, 1989; Kinuura, 1995; Gebhardt *et al.*, 2004). Atkinson and Equihua (1986) concluded that polyphagy is associated with an inbred polygynous mating system, such as that in Xyleborina. The hypothesis is not confirmed here, as most Platypodinae, a monogamous and outbreeding group, displayed the same lack of host specificity as xyleborines.

Beaver (1979) indicated that 21–34% of xylomycetophages are family specific or genus specific. A significant portion of these data came from hand-collecting on an extensive but random selection of hosts with little or no standardisation of the collecting effort (Browne, 1961; Roberts, 1977; Beaver & Browne, 1978). This may have skewed the conclusions towards greater host specificity as some hosts may have been sampled more than others. The second explanation of the discrepancy may stem from numerous observations from non-Malesian SE Asia, suggesting specialisation of some ambrosia beetle taxa on Dipterocarpaceae and tropical Fagaceae. Some genera (*Cryptoxyleborus*, *Schedlia*, *Webbia*) are found almost exclusively on Dipterocarpaceae or Fagaceae (Browne, 1961; Beaver, 1979). Hand-collecting records (J. Hulcr, unpublished data) suggest that these groups exhibit the same patterns of host specificity in New Guinea, but are markedly underrepresented. In addition, species of Dipterocarpaceae are rare in the lowland forests of New Guinea. Accordingly, the overall host specificity of the Papua New Guinean ambrosia beetle fauna may be lower than that of the South-East Asian fauna.

The present study shows that 13 out of the 45 tested species (29%) are associated with a particular tree part. The spatial distribution of tropical scolytines in flight has been reported to be the same in both the understorey and canopy levels (Simon *et al.*, 2003; Leksono *et al.*, 2005), or greater in lower forest strata for all species (Chung, 2004), but no species-specific preferences have been shown. It is most likely that it is the diameter of the tree part, not the height stratum, that determines the distribution of beetles specialised to a particular part of the tree.

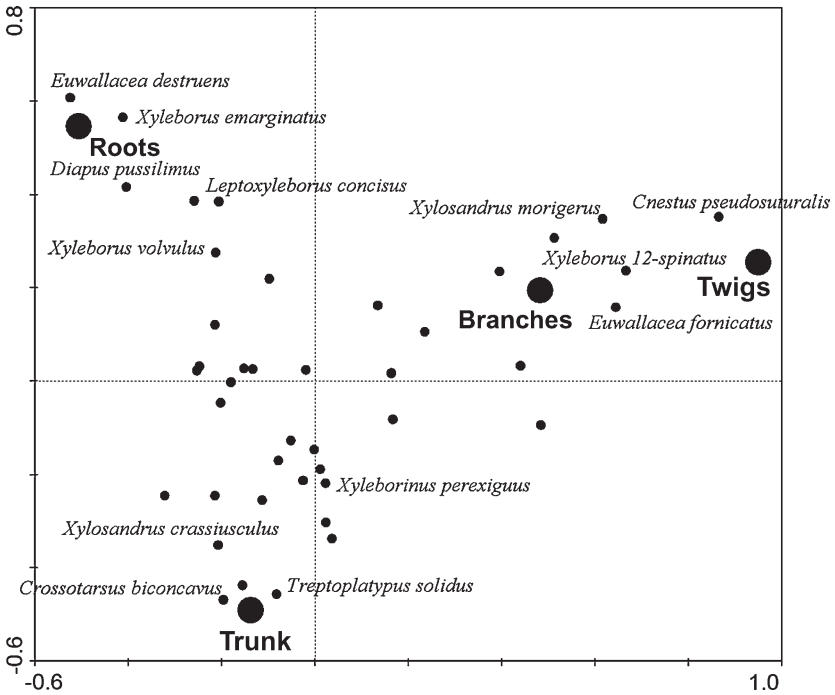


**Fig. 6.** Canonical correspondence analysis (CCA) of the distribution of ambrosia beetles among tree parts. Small dots represent individual species; species indicated by name were statistically significantly associated with a tree part. Tree parts used as the explanatory variable, tree species and wood characteristics as covariates.

Neither wood density nor water content seems to have any structuring effect on the ambrosia beetle assemblages. The selection of tree species covered most of the local range in wood density. It ranged from 0.25 to 0.68 g cm$^{-3}$ (*Cananga odorata* and *Aglaia cuculata* respectively), whereas the local tree flora ranges from 0.24 g cm$^{-3}$ in some Albizzia and Erythrina, to 0.75 in Intsia and Terminalia (Brown, 1997).

Some of the host associations of phloeophages found in this study confirm previously published results. For example, *Scolytomimus* was reported from Sapotaceae (Browne, 1958a); both species of *Scolytomimus* in this study were exclusively reared from *Pouteria* sp. (Sapotaceae). *Ficicis despectus* was common on Moraceae in this study, and only rare on other hosts, a pattern reported by Wood and Bright (1992). Host lists of *Hyledius nitidicollis* and *Hyledius cribratus*, reared only from *Myristica* sp., are dominated by Myristicaceae elsewhere (Wood & Bright, 1992). Results from the present study, along with those of others (Beaver, 1979; Atkinson & Equihua, 1986; Jordal, 1998; Kelley & Farrell, 1998; Jordal *et al.*, 2004), show that narrow host specificity is a universal feature of phloeophages regardless of the biogeographic area or taxonomic group, although data for one large group, Cryphalina, are not available. Host specialisation of phloeophages to several related hosts is comparable to that of herbivorous insects (Novotny & Basset, 2005).

The communities of xylomycetophagous and phloeophagous beetles show other differences in addition to different host specificity. While only a few species of phloeophagous bark beetles were encountered in the sample in the present study, they represent a substantial portion (30%) of the total number of individuals. Phloeophage species from both major scolytine clades, Hylesininae and Scolytinae (*sensu* Wood & Bright, 1992) exhibited this pattern. In contrast, both groups of ambrosia beetles, Xyleborina and Platypodinae, are species rich (83 species), but few individuals were encountered for the majority of species. A similar pattern was observed in a dryer deciduous tropical forest in Mexico (Atkinson & Equihua, 1986).

Host-plant diversity has been identified as the single most important factor in supporting and perhaps generating the conspicuous diversity of tropical herbivorous insects (Novotny *et al.*, 2006). The diversity of host trees, however, does not provide a diversified feeding niche for ambrosia beetles, since this guild displays virtually no fidelity to any host clade. Thus, unlike in the case of herbivores, we do not consider tree diversity to be a significant factor for generating and maintaining the diversity of ambrosia beetles. This is not surprising as xylomycetophages and mycetophages should not be expected to exhibit features found in phytophages, as their foraging strategy is closer to detritivory than to herbivory (Hanski, 1989; Basset, 1992).

Also the diversity of phloeophagous bark beetles does not seem to be correlated with plant diversity. Phloeophages feed solely on host tree tissues and thus may be expected to display patterns of diversity typical of other herbivores, such as a latitudinal increase in diversity tracking increase of plant diversity (Novotny *et al.*, 2006). However, according to Beaver (1979), the palaeotropical community of phloeophagous scolytines is rather depauperate compared with temperate assemblages, in contrast to the opposite trend in plant diversity. The present study also showed low diversity of phloeophages in the humid tropics, as phloeophages were successfully reared from less than 50% of tree individuals, and the number of phloeophagous species excluding cryphalines was lower than the number of

studied tree species. The composition of a scolytine assemblage of both bark and ambrosia beetles in a dry deciduous tropical forest in Mexico seems to fall in the middle of the temperate–tropical gradient, and differs by a greater percentage of species with alternative feeding strategies such as xylophagy and myelophagy (feeding on pith of twigs) (Atkinson & Equihua, 1986). The absence of an increase of phloeophage diversity in the tropics suggests either underutilisation of the resource, or a resource difficult to exploit, but does not support the hypothesis that the true bark beetle species diversity is a function of plant diversity. A possible explanation of this pattern may be that temperate floras have larger proportions of conifers, which are the ancestral habitat of phloeophagous scolytines (Marvaldi *et al.*, 2002), whereas the tropics are dominated by angiosperms with more sophisticated chemical defences, less prone to colonisation by phloeophages (Ohmart, 1989).

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