



Low beta diversity of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae) in lowland rainforests of Papua New Guinea

Jiri Hulcr, Vojtech Novotny, Brian A. Maurer and Anthony I. Cognato

J. Hulcr (*hulcr@msu.edu*) and A. I. Cognato, Dept of Entomology, Michigan State Univ., 243 Natural Sciences Building, East Lansing, 48824 MI, USA. – JH and V. Novotny, Faculty of Science, Univ. of South Bohemia and Biology Center of Czech Academy of Sciences, Branisovska 31, 37005 Ceske Budejovice, Czech Republic. VN also at: New Guinea Binatang Research Center, Madang, Papua New Guinea. – B. A. Maurer, Dept of Fisheries and Wildlife, Michigan State Univ., 13 Natural Resources Building, East Lansing, 48824 MI, USA.

We assessed the effect of geographical distance on insect species turnover in a situation where other major environmental factors, including host plant species, altitude, and climate, were constant. We sampled ambrosia beetles (Coleoptera, Curculionidae: Scolytinae and Platypodinae) from four tree species: *Artocarpus altilis*, *Ficus nodosa*, *Leea indica* and *Nauclea orientalis*, at three sites forming a 1000 km transect in lowland rainforests of northern Papua New Guinea. A standardized volume of wood from trunk, branches and twigs was sampled for ambrosia beetles from three individuals of the four tree species at each site. Each tree was killed standing and left exposed to beetle colonization for 20 days prior to sampling. We obtained 12 751 individuals from 84 morphospecies of ambrosia beetles. We surveyed most of the local species richness at each site, predicted by Chao 2 species richness estimates. The similarity of ambrosia beetle communities, estimated by Chao-Sorensen index, was not correlated with their geographical distance. Likelihood analysis and Q-mode analysis using Monte Carlo-generated null distribution of beetles among sites supported the hypothesis that the assemblages of ambrosia beetles at different sites are drawn from the same species pool, regardless of their geographical distance. Tree part (trunk, branch, or twig) was more important predictor of the composition of ambrosia beetle communities than was the host species or geographical location. All three variables, however, explained only a small portion of variability in ambrosia assemblages. The distribution of ambrosia beetles among tree parts, tree species and study sites was mostly random, suggesting limited importance of host specificity or dispersal limitation.

One of the major questions of contemporary community ecology is whether patterns in species diversity are determined by environmental factors, inter-specific interactions or emergent properties of complex stochastic systems (Hubbell 2001, O'Neill 2001). A crucial concept describing the patterns of species spatial distribution is beta diversity, the turnover of species composition of communities in space (Bell 2001). However, the actual rate of species turnover in space is disputed, as well as the roles of mechanisms that cause it.

The classical target of studies of spatial patterns in organismal distribution is the correspondence of species distribution with environmental discontinuities and gradients (Begon et al. 1996). An alternative approach is to deem species ecologically equivalent and study non-deterministic processes driving their distribution (Novotny and Weiblen 2005). Some of the most important dynamic factors in species distribution are dispersal, speciation and extinction, and the changes of distribution in time caused by geological processes. Dispersal is expected to lower the differences between communities, although the link between dispersal mode or capacity and the species distribution is missing

(Soinien et al. 2007). Speciation and extinction are expected to increase variability among distant communities, but the resulting rate of community diversification is unknown and likely variable between different kinds of organisms. Geographical barriers, or their historical legacies, are known to drive speciation, extinction, and community differentiation (Brooks and McLennan 2002).

These biological processes influencing species distribution often depend on environmental determinants, but also introduce a large stochastic component (Hubbell 2001). For example, in a large homogeneous habitat such as tropical lowland rainforests, even groups with different life histories such as tropical trees and insects, exhibit similar patterns of species turnover associated with distance. Both groups show aggregate distribution on smaller scales, but low species turnover on large scales (Condit et al. 2002, Beck and Chey 2006, Novotny et al. 2007).

Measures of beta diversity also crucially depend on methodological assumptions. Spatial beta diversity can be understood either as a turnover of species along a geographical vector, or as a dimension-less difference between local and regional diversity. The relationship between the two

concepts is debated (Legendre et al. 2005, Tuomisto and Ruokolainen 2006); this study is concerned only with the first, spatially explicit concept. Observations of species spatial distribution are highly influenced by the chosen geographical scale (Levin 1992). Organismal communities typically show patchiness of populations on small geographical scales (less than tens of kilometers) but more even distribution on larger scales (Lucky et al. 1998, Koleff and Gaston 2002). Comparison of communities also depends on the completeness and evenness of sampling, especially in species-rich communities with highly uneven abundance distribution. For example, insect samples from the canopy of Amazonian rainforest suggest large differences between localities no more than 30 km apart (Erwin et al. 2005). However, the samples were dominated by species encountered as single individuals, thus it is unclear whether the apparent high beta-diversity reflects high species turnover, or is an artifact of omission of many rare species. On the other hand, rare species often have limited distribution and may be a source of genuine dissimilarity (Brown 1984). To distinguish between rare species unsampled by error and species genuinely absent, thorough sampling is necessary.

To study the effects of non-deterministic factors on beta diversity, we used a model system where all determinants of species distribution except distance, geological history, and stochastic biological processes, could be factored out, and where near-exhaustive species sampling is possible. The model system used was a community of tropical wood-boring ambrosia beetles (Col., Curculionidae, Scolytinae and Platypodinae) in lowland rainforests of Papua New Guinea. Ambrosia beetles colonize dying trees and feed on symbiotic xylophagous ambrosia fungi that they introduce into the trees (Beaver 1989, Farrell et al. 2001). Exploitation of the fungi as a food source have allowed ambrosia beetles to utilize a wide variety of host trees (Beaver 1979, Hulcr et al. 2007), thus eliminating the local tree community composition as a factor influencing geographical distribution of species. Many ambrosia beetle species are capable of quick dispersal and establishment in new habitats, and belong among the most widespread invasive species (Allen and Humble 2002, Haack 2006). Some species of Scolytinae can fly distances up to 50 km per generation (Forsse and Solbreck 1985), and effectively track their hosts over large geographical areas following major changes in geography and climate (Sallé et al. 2007).

Studies focused on spatial distribution of scolytine beetles are mostly concerned with individual temperate phloem-feeding (non-ambrosial) pest species (Byers 1992, Logan et al. 1998, Cognato et al. 2005, Sallé et al. 2007). Studies on spatial structure of entire scolytine communities are rare, and have been also limited to temperate phloem feeders (Peltonen et al. 1998, Jordal and Hewitt 2004). Thunes (1998) studied ambrosia beetles in a neotropical rainforest in Costa Rica and found an uneven spatial distribution on a scale of less than 4 km², but was unable to distinguish between its causes, such as patchiness of resources or aggregation based on chemical communication. Deyrup and Atkinson (1987) showed substantial dissimilarity between distant communities of neotropical ambrosia beetles; however, variation in environmental conditions between the localities confounded the effect of environmental variation and that of distance.

Papua New Guinea (PNG) is one of the few remaining regions with extensive continuous lowland rainforests. PNG has a complex and recent history of geological changes. These processes may cause faunal dissimilarity or promote endemism in different parts of apparently homogeneous lowland rainforests (Polhemus and Polhemus 1998, Turner et al. 2001).

Our study quantified beta diversity of communities of tropical ambrosia beetles and examined the processes that have influenced it. We compared thoroughly sampled ambrosia beetles assemblages between sites up to 1000 km apart while keeping constant major environmental variables including host plant, forest type, elevation and climate. Given the spatial scale of our sampling, we predict that low species turnover among sites would indicate unlimited dispersal as the most important factor in species distribution, while high species turnover would point to recent geological separation of sites or local speciation or extinction.

Methods

Beetles were collected from three study sites that formed a 1000 km transect through a continuous lowland rainforest on the northern side of Papua New Guinea (Fig. 1, Table 1). All three sites were at a similar altitude (between 100–200 m above the sea level), with minimal seasonal variation, and similar amounts of annual rainfall (3000–4000 mm) (Parsons 1999). The mosaic of primary and secondary lowland humid rainforest at each site is classified as mixed evergreen hill forest (Paijmans 1976) with very diverse vegetation (152 woody species of diameter at breast height (DBH) > 5 cm per ha in Ohu village; Novotny et al. 2004). The sampling was conducted between February and June of 2006. Two independent periods of sampling were completed in the Madang site (Madang 1 and Madang 2; Table 1) to examine the effect of increased sample size on diversity estimates.

Ambrosia beetles were sampled from four tree species at each site: *Artocarpus altilis* (Moraceae), *Ficus nodosa* (Moraceae), *Leea indica* (Leeaceae) and *Nauclea orientalis* (Rubiaceae). These tree species were selected because they were abundant at all sites and represented both closely and distantly related species. The low number of sampled tree species was due to logistic reasons, and is considered sufficient for obtaining representative proportion of local species. Ambrosia beetles display little or no host specificity, and neither abundance nor phylogenetic position of a host tree has a significant effect on the composition of the colonizing ambrosia beetle assemblage (Hulcr et al. 2007). At each site, three individuals of each tree species of a breast height diameter (DBH) 20–25 cm (15–20 cm for *Leea indica*) were selected as in situ bait trees. Trees from both primary and secondary forest were used.

Bait trees were killed standing by girdling and burning at the trunk base, which triggered colonization by the beetles. Trees were girdled by first removing an approximately 30 cm wide circumferential strip of bark and creating a 30 cm wide wounded strip with multiple cuts. After 20 days, the bait tree was felled and the following samples were taken: 1) a 1 m long portion of trunk base including burned, girdled,

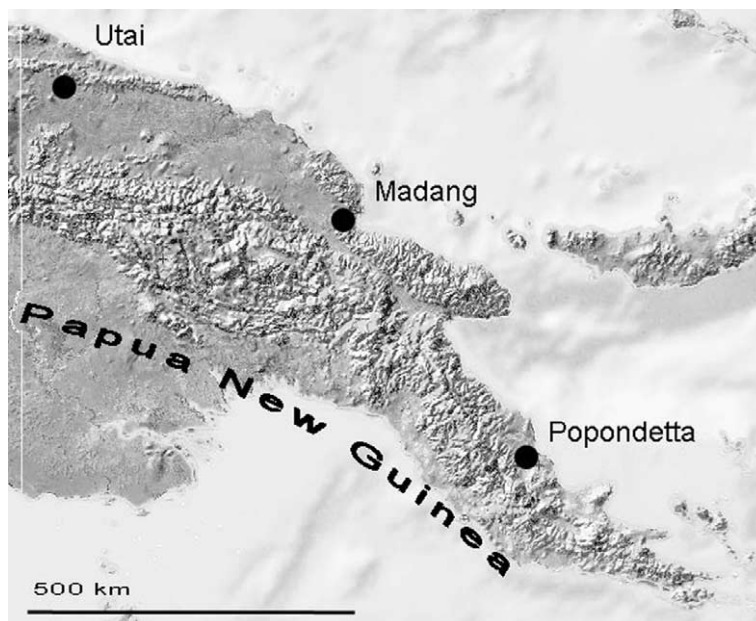


Fig. 1. Sampling sites in northern Papua New Guinea, South Pacific.

and untreated surface, 2) a combined 2 m length of branch pieces (diameter 2–10 cm), and 3) a total of 2 m of pieces of twigs (diameter less than 2 cm) with apparent beetle infestation. The trunk base was cut into 5 cm thick slices to facilitate dissection of beetles. All timber samples were dissected by hand; all adult ambrosia beetles of the parental generation were removed and stored in ethanol. The tree preparation, dissection, and beetle sampling were performed with the help from parataxonomists and local villagers (Basset et al. 2000). Voucher specimens were deposited in the A. J. Cook Arthropod Research Collection, Michigan State Univ., the Forest Research Inst. Insect collection in Lae, Papua New Guinea, the Natural History Museum, London, the Smithsonian Inst., Washington, D. C., and the Naturhistorisches Museum, Vienna.

To estimate the completeness of sampling at a single site, we compared the sample Madang 1 with both samples Madang 1 and Madang 2 combined, i.e. with doubled sampling effort at the same site. That allowed us to assess the precision of analytical estimates of the total species richness derived from our typical sample size.

There are a number of estimators of total local species diversity, mostly utilizing the asymptotic relationship between the increase in sample size and the cumulative number of species. Of the seven indices used to estimate the total number of species from the combined sample of Madang 1 and Madang 2 (Chao 1, Chao 2, Bootstrap, 1st order Jackknife, 2nd order Jackknife, ACE, and ICE; Colwell 2005), most converged on similar total number of estimated species. Chao 2 was selected for the subsequent estimates of species richness, as it was least dependent on

the sample size compared to other indices (Fig. 2) and was reported to give robust estimates even when a large portion of species is missing from samples (Colwell and Coddington 1994). EstimateS software was used to calculate diversity statistics (Colwell 2005).

Between-site pair-wise similarity was measured by the Sørensen index modified by Chao for raw data (Chao et al. 2005). The probability that two individuals randomly sampled from sites A and B belong to the same species was calculated as $p_c = (n_{iA}/N_A)(n_{iB}/N_B)$, where n_{iA} is the number of individuals of species i collected at site A, and N is the abundance of all ambrosia beetles collected at that site (Novotny et al. 2007). To test whether ambrosia beetle community similarity decreases with distance, we performed linear regression of pair-wise Chao-Sørensen community similarities between sites vs pair-wise geographical distances, and regression of the probability that two beetles randomly drawn from two sites are conspecific (p_c) vs pair-wise log-distance. The latter model was tested since it was shown to approximately fit the similarity decay in Neotropical tree communities (Condit et al. 2002). Each regression analysis was applied to two types of similarity data – pairwise similarities between whole communities at different sites, and pairwise similarities between communities on individual conspecific trees. Significance of each correlation was assessed with a Mantel test. The two samples from Madang were used independently with mutual geographical distance of zero. Where multiple tests of the same hypothesis were conducted, the level of statistical significance was adjusted by Bonferroni correction.

Table 1. Study sites in northern lowlands of Papua New Guinea.

Site	Province	Latitude	Longitude	Altitude (m)	Date (2006)
Utai village	Sandaun	3°23'S	141°35'E	210	April
Madang (Ohu village)	Madang	5°15'S	146°40'E	120–200	February (Madang 1), May (Madang 2)
Popondetta (Ohiki village)	Oro	8°48'S	148°13'E	200	May

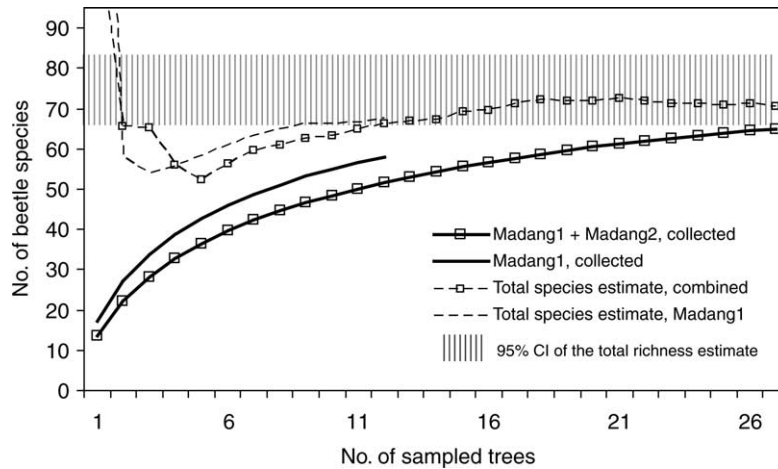


Fig. 2. Species accumulation curves and total species richness estimates for Madang 1 sample and for the combined samples Madang 1 and Madang 2. A single sample (Madang 1) does not reach the estimated total number of species, but is sufficient for a robust estimate. Doubling the sampling effort yields species richness falling within the 95% CI of the total estimate (shaded area). Accumulation curves were derived with Mao Tau algorithm in EstimateS (Colwell 2005). Independent analysis of Madang 2 gave nearly identical result as Madang 1 (not shown).

We tested the hypothesis that the samples from the three study sites were randomly drawn from a single regional pool of species. We used a likelihood approach to test the uniformity of abundance distribution and a Q-mode analysis of community similarity. We compared the likelihood of three models of abundance distribution: 1) each locality is characterised by different abundance distributions, 2) Madang 1 and Madang 2 have the same abundance distribution (individuals per each species summed up), while Popondetta and Utai each has a unique abundance distribution, and 3) all samples are drawn from a single community and thus have a similar abundance distribution (beetle individuals were summed within species across all sites). Assuming that the sampling distribution of species is a multinomial distribution, the likelihood function for s species distributed among J individuals is:

$$L(x, \rho, J) = -\sum_i x_i \log_e \rho_i$$

where x_i = the number of individuals of species i and $\rho_i = x_i/J$. The right side is equal to H' (Shannon diversity index). The likelihood of each of the three models described above was determined by estimating unique parameters for each species abundance distribution implied by the model. The likelihoods were adjusted for overfitting with the Akaike information criterion (AIC)

$$AIC_A = 2L_A + 2(K_A - 1)$$

where L_A is the likelihood and K_A is the number of parameters of model A (Burnham and Anderson 2002). The model with the lowest AIC was chosen as the preferred model of abundance distribution across the sites.

To test the hypothesis that samples from different localities represented a single community, we compared the average observed pairwise similarity between sites to a null model of distribution of similarity (Gotelli and Graves 1995). To obtain the null model, abundance values of beetle species at individual trees were redistributed randomly among all sites. We explicitly assumed a uniform abundance distribution across sites, and tested the assumption by the likelihood test above. The redistribution of

species records was constrained to within tree species since different tree species accumulated different numbers of beetle individuals and species. The randomization was repeated 1000 times, and the resulting model distribution of average pairwise similarities was used for a one-tailed test of non-randomness of the observed average pairwise similarity between sites. Chao-Sørensen index for raw data was used as the similarity measure. Sample Madang 2 was not used in this analysis, since the randomization procedure assumes equal sample size for each site.

To compare and visualize the effects of site, tree species, and tree parts on the composition of beetle communities, we performed multivariate ordination analysis using Canoco 4.5 (ter Braak and Smilauer 2003). The highly uneven abundances of scolytid species were $\log_{10}(x+1)$ transformed. States of each variable were used as independent complementary variables, i.e. sites represented three variables, tree parts represented three variables, and tree species represented four variables. Correspondence analysis was used to determine the amount of correlation in distribution of individual species within the beetle community. Canonical correspondence analysis was used to explore the effect of tree species, tree part and locality on the distribution patterns in the beetle species distribution. The differential contributions of individual variables to the overall explained variance was calculated by variation partitioning:

1) we measured the proportion of variation explained by all canonical axes (constrained by the variables) when all variables are used in the analysis (v_{total});

2) we measured the proportion of the total variance explained by each of the three subsets of variables individually (tree parts = v_{parts} , tree species = v_{trees} , sites = v_{sites}). For each variable, we calculated the ratio of the sum of all canonical eigenvalues when the two remaining variables were held as covariates to all eigenvalues from unconstrained CA

3) the effect of interactions between variables v_{inter} was calculated as:

$$v_{inter} = v_{total} - (v_{parts} + v_{trees} + v_{sites})$$

Rarity or absence of a species in a sample may be a result of true rarity/absence at a site, or of undersampling. The probability that a species is present at a particular site when N individuals are randomly distributed among n sites is $p = 1 - (1 - 1/n)^N$. For our three sites, $p > 0.95$ when $N \geq 8$. Thus, to examine the influence of rare species on our analyses of community similarity, we calculated selected analyses twice: once with all species included and once with dataset containing only species of which more than seven individuals were encountered. This process excluded 36 species from the total of 86, which represented less than 1% of individuals.

We excluded one ambrosia beetle species, *Xylosandrus crassiusculus* from analyses of site similarity. *X. crassiusculus* is most likely a non-indigenous species recently introduced to New Guinea (R. A. Beaver pers. comm.; Hulcr unpubl.). It is very abundant near the town of Madang, but has apparently not yet spread to other sites.

Results

In total, 12751 ambrosia beetle individuals representing 84 morphospecies were collected from all three sites. All species belonged to one of two distinct taxa, Platypodinae (5467 individuals) or Xyleborina (7284 individuals). Sixty eight (81%) of these morphospecies have been already taxonomically described (see Supplementary data).

Although the number of species we collected in a single sample did not reach the estimated total number of local species, it was sufficient for calculating robust diversity estimates (Fig. 2). For example, the total number of species in the Madang area was estimated to 68, based on the sample Madang 1 with 58 actually collected species. With the inclusion of Madang 2, the number of collected species reached 65, and the estimate increased to 70. The total local diversity estimate derived from the single Madang 1 dataset falls within the 95% confidence interval of the estimate derived from both samples (67–83, Fig. 2), and is independent of sample size for samples of more than 60% of our actual sample size.

The total number of ambrosia beetle species occupying the lowland rainforests of northern PNG was estimated to be 98 by Chao 2 (SD = 7.03, Fig. 3). The estimate was calculated with all tree samples combined, regardless of the site. The estimate was only slightly dependent on the sample size for datasets larger than 1/3 of our actual sample size.

Forty-four of the 48 species that were sufficiently abundant for the analysis were present in more than one site, while only four species were restricted to a single site (Fig. 4). The average proportion of species shared between sites was 72.6%, and the average community similarity measured by Chao-Sørensen index was 0.948 (SD = 0.028). When undersampled species were included in the analysis, the average proportion of shared species dropped to 63%, but the average Chao-Sørensen similarity remained nearly identical (0.940, SD = 0.024). Similarity of the two samples Madang 1 and Madang 2 approached unity (Chao-Sørensen = 0.998, SD = 0.002). The number of sites occupied by a species was correlated with the logarithm of

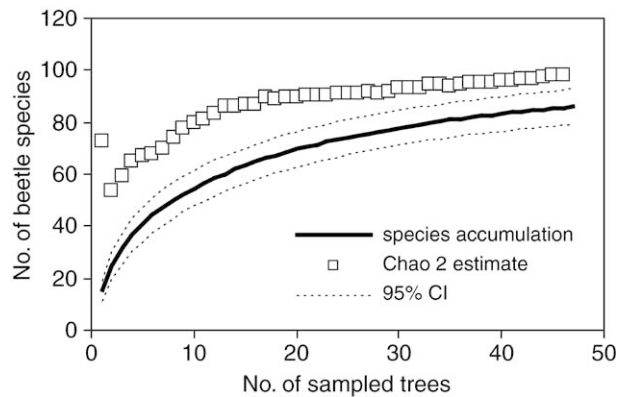


Fig. 3. Species accumulation curve for all samples combined and the estimate of total species richness of ambrosia beetles in northern lowlands of Papua New Guinea. The solid line represents the species accumulation curve derived analytically with the Mao Tau function in EstimateS. Dashed lines indicate 95% confidence intervals. Squares – Chao 2 estimate of the total number of species as it varies with the number of tree samples included. Complete data for all 48 tree individuals regardless of site were included.

its total abundance (for species of $N > 7$, $n = 48$; $r = 0.523$, $p < 0.001$).

Pairwise similarity of samples from different sites was similar to pairwise similarity of two independent samples from the same site (Madang 1 and Madang 2; Table 2). There was no significant correlation between pairwise similarities of beetle assemblages and pairwise distances between localities (mean Chao-Sørensen index of similarity = 0.955; $n = 6$; $r = -0.109$, Mantel test $p = 0.40$; Fig. 5). Also, there was no significant correlation between similarities of samples from individual conspecific trees and the distances between the trees (*A. altis* $r = 0.002$, $p = 0.495$; *F. nodosa* $r = -0.266$, $p = 0.100$, *L. indica* $r = 0.244$, $p = 0.894$, *N. orientalis* $r = 0.287$, $p = 0.055$; in *L. indica* $n = 55$, in other cases $n = 66$). The probability that two beetles randomly sampled from two different sites would be conspecifics did not decrease

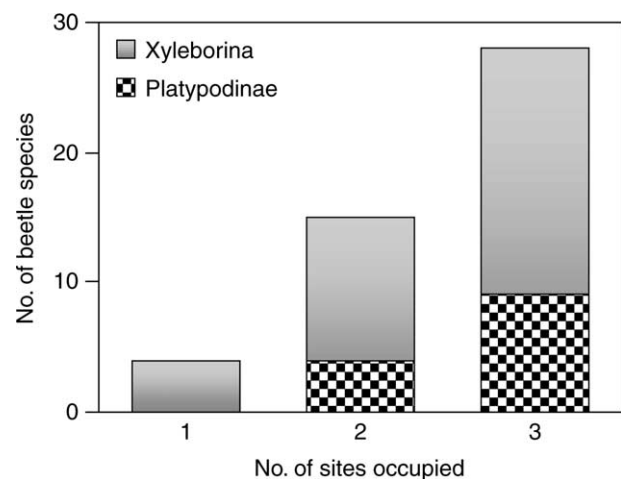


Fig. 4. Distribution of ambrosia beetle species among the three study sites in northern Papua New Guinea. Sample Madang 2 was not included. Only sufficiently abundant species were included to prevent inflation of the first category.

Table 2. Pairwise comparisons of ambrosia beetle community similarity between sites (Chao-Sørensen index). Madang 1 and Madang 2 are two independent samples from the same site.

	Utai	Madang 1	Madang 2
Madang 1	0.978		
Madang 2	0.977	0.998	
Popondetta	0.983	0.918	0.924

significantly with log-distance ($n=6$, $r = -0.762$; Mantel test $p=0.08$; Fig. 5). Also the probability that two beetles randomly sampled from two conspecific trees would be conspecifics did not decrease with log-distance (*A. altilis* $r=0.061$, $p=0.329$; *F. nodosa* $r = -0.270$, $p=0.052$, *L. indica* $r=0.019$, $p=0.433$, *N. orientalis* $r=0.217$, $p=0.085$; in *L. indica* $n=55$, in other cases $n=66$). When undersampled species were included in the analysis, all the above correlations of community similarity with distance remained insignificant at the level of $\alpha=0.05$, except the distance decay of community similarity on *F. nodosa* ($r = -0.289$, $p=0.045$) which was however insignificant under Bonferroni correction ($\alpha=0.0125$).

Of the four models of abundance distribution tested by the likelihood test, the model assuming that all samples come from a single distribution had the best (lowest) AIC-corrected likelihood score, and was thus selected as the model that best fit the data. The AIC-corrected likelihood scores were 343.6 for the model of all samples pooled together, 898.3 for the model pooling two Madang samples and keeping Utai and Popondetta separately, and 1134.4 for the model treating all four samples separately.

The hypothesis that samples from all three sites are no more different than three random samples from a single population was upheld (mean Chao-Sørensen index of pairwise similarity = 0.948, median of the modeled distribution of mean pairwise similarities = 0.973, Monte Carlo test $p=0.069$). When undersampled species were included in the analysis, the similarity among communities was marginally lower than random (mean Chao-Sørensen

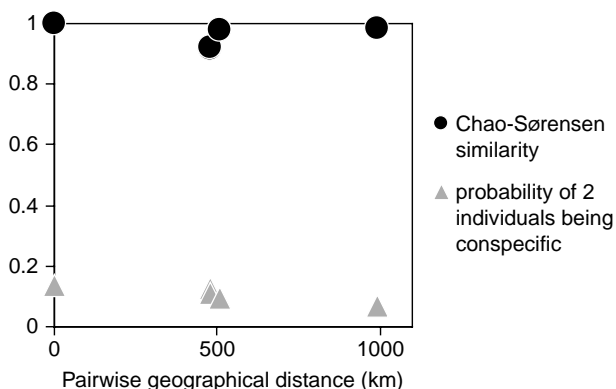


Fig. 5. Similarity decay of ambrosia beetle communities over geographical distance (Chao-Sørensen index and the probability that two individuals randomly sampled from two different sites in northern lowlands of PNG would be conspecifics. Both relationships are statistically not significant (similarity decay: $r = -0.109$, Mantel test $p=0.40$; probability of random individuals being conspecific: $r = -0.762$, Mantel test $p=0.08$). The two independent samples from Madang (Madang 1 and Madang 2), treated as independent data sets with a geographic distance of zero.

pairwise similarity = 0.935, median of the modeled distribution of mean pairwise similarities = 0.959, $p=0.02$)

The Correspondence analysis revealed weak correlations among the distribution patterns of individual species. The first ordination axis explained 10.4% of the total variation; the first four axes together 34.5% of the variation. The Canonical correspondence analysis showed significant, differential, and uncorrelated influence of the tested variables on ambrosia beetle distribution (Fig. 6). The variables most strongly correlated with the first, second, and third ordination axes were, respectively: (1) all three hosts parts, (2) the host species *L. indica* and *A. communis*, and (3) all three sites. The correlation between environmental variables and the beetle species distribution was highly significant (Monte Carlo test, 999 permutations, $p=0.001$). However, the canonical axes (constrained by the environmental variables) explained only 18% of the total variation (sum of all eigenvalues from Correspondence analysis = 6.993, sum of all canonical eigenvalues = 1.248).

Variation partitioning revealed low and mutually uncorrelated contribution to the explained variability by all three sets of variables. The most important variables for the species distribution in our sample were the tree parts (9.0% of the variation), slightly less important were tree species (7.2%), and the least important was the site (4.2%). Interactions between the variables were negligible (0.2% of the variation), showing a lack of interdependence among the variables.

The average number of beetle species colonizing an individual tree was approximately equal for all tree species (17.5, *A. altilis*; 19.8, *F. nodosa*; 15.7, *N. orientalis*) except *Leea indica*, where the numbers of colonizers were substantially lower (7.8 beetle species per tree individual). However, the beetle community on *L. indica* was no less species rich than communities on other hosts when these are computationally rarefied. In *L. indica*, 484 beetle individuals yielded 31 spp., compared to >1800 individuals necessary to yield 31 spp. in *A. altilis*, >1200 in *N. orientalis*, and >1000 in *F. nodosa* (rarefied using MaoTau function in EstimateS).

Discussion

Most of the 84 morphospecies were species known to science ($n=67$; 78%), while the remaining had uncertain or undescribed status. The high proportion of known species reflects extensive collecting and descriptive work on New Guinea ambrosia beetles (Schedl 1969a, 1969b, 1972a, 1972b, 1975, Gray and Wylie 1974, Roberts 1986, 1989) combined with broad distribution of many species documented in this study. This is in agreement with several other studies showing that many non-cryptic or economically important insect groups from Papua New Guinea may be known to larger extent than often assumed (Novotny and Missa 2000, Miller et al. 2003). On the other hand, identification of most of the species required a several-year-long effort, which illustrates the contemporary 'taxonomic impediment' (Wheeler et al. 2004). Despite the fact that most species have been described, their identification is extremely difficult since the type material is scattered

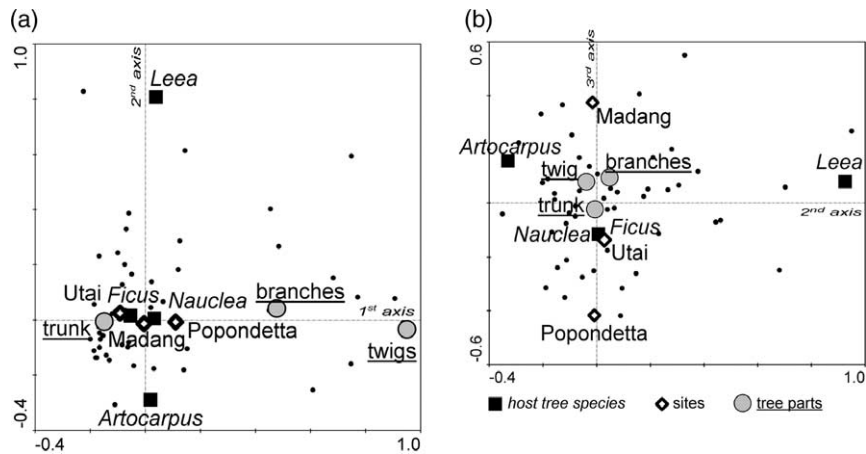


Fig. 6. CCA ordination diagrams of explanatory variables with the (a) 1st and 2nd canonical ordination axes and (b) 2nd and 3rd canonical ordination axes. From the explanatory variables, tree parts (circles) are most correlated with the first canonical axis, hosts (*L. indica* and *A. communis*, squares) with the second axis and sites (diamonds) with the third axis, rather weakly. Dots represent ambrosia beetle species.

in museums worldwide, the published information is inadequate for species diagnosis, and within-species variability has never been sufficiently studied.

The tree species *Leea indica* proved to host a comparatively depauperate ambrosia beetle community. It is unclear whether this is due to chemical components of the tree's tissues, the small size of the tree, or other factors. Although nearly all ambrosia beetles in Papua New Guinea are host generalists (Hulcr et al. 2007), some tree species are more attractive than others to the whole beetle assemblage. Subsequently, the more frequent colonization of these trees by all species result in higher species richness.

Even though our sampling at each study site was not exhaustive, it permitted a robust estimate of the total species richness and similarity between sites. The total number of species recorded in two combined samples from Madang approached the estimated total richness, suggesting that there were probably few unsampled species.

The rate of species turnover of ambrosia beetles in lowland New Guinea proved to be extremely low, as the decrease of community similarity with distance was insignificant. Both xyleborines and platypodines displayed the same lack of site fidelity. Low species turnover at distances up to 500 km was shown also for the communities of moths from the same area region (Novotny et al. 2007). Our study shows that even doubling the geographical scale does not decrease similarity of the studied insect communities.

The number of sites occupied by a species is correlated with its total abundance. This suggests that failure to collect a species at all sites might have been due to undersampling. However, rare species often have restricted ranges (Rosenzweig 1995). Although we are unable to distinguish between incomplete sampling and actual range restriction, we believe that the observed high similarity among sites was not a result of omission of rare endemic species. Inclusion or exclusion of undersampled species had only marginal effect on the results. Although their inclusion made the between-site similarity appear slightly lower than random, it was caused by the increase of similarity in the resulting null model, not by the decrease in the observed similarity, and the effect was not correlated with distance. Further, our

sampling strategy allowed for collecting most of the species present at a locality, as can be seen in the case of two samples from a single site, which were nearly identical.

The neutral model of beta diversity by Hubbell (2001) predicts a linear decrease in faunal similarity with the logarithm of distance. This model has been supported by data from Neotropical tree communities on scales of tens of kilometers, but the decay of community similarity on larger geographic scales was slower than the model predicted (Condit et al. 2002). Other models of rainforest tree communities are based on dispersal, rather than on niche-based processes, and predict slower species turnover rate than is observed in the field (Duivenvoorden et al. 2002). In our samples spanning a 1000 km distance, the similarity between communities does not decrease linearly with log-distance.

This study showed the importance of controlling environmental variables for beta diversity estimates. Separating the effects of host and habitat availability from that of geographical distance has been an important issue in studies of beta diversity of insects, and has required a posteriori statistical tools to estimate the effect of each variable (Beck and Chey 2006, Novotny et al. 2007). Ambrosia beetles are host generalists, therefore in most cases the presence or absence of an ambrosia beetle species at a particular site is independent of the composition of the local tree community.

Insect dispersal propensity ranges from slow migrants that, despite their capacity for flight, can remain on a single patch of suitable habitat for many generations (Spitzer and Danks 2006) to efficient migrants that are often the first organisms to colonize new habitats (Thornton et al. 2001). Ambrosia beetles are moderate to good dispersers, as each new generation seeks new breeding trees, and the distances between suitable dead trees can be substantial. Our study showed that unlimited dispersal results in community homogenization over large distances, provided the studied habitat and niche availability are uniform.

Although each of the three sites sampled in this study is characterized by a similar forest type, each of the sites lies on a geologically independent Pacific terrane. Polhemus

and Polhemus (1998) suggested that this has affected the present day distribution of New Guinea aquatic Heteroptera, a group with limited dispersal propensity and strict habitat requirements. However, accretion of these terranes to the New Guinea island and the collision-related uplifting took place at least 5 million years ago (Hall 2002), making its effect on contemporary ambrosia beetle population separation extremely unlikely. More recent events led to the separation of the northern (Utai) and the two southern sites (Madang and Popondetta) by a sea incursion in the Sepik and Ramu floodplains around 6000 years ago, and, perhaps more importantly, the climate and vegetation cover of parts of the lowlands was different during the colder and drier periods of the Pleistocene (Nix and Kalma 1972). However, even if these dispersal barriers and habitat changes had previously influenced the geographical structure of the lowland ambrosia beetle community, our data suggest that the effect apparently disappeared within the last several thousand years. The results of this and previous analyses (Hulcr et al. 2007), aimed at discerning the factors correlated with ambrosia beetle diversity, suggest that, host specificity, microhabitat specificity and separation by distance do not isolate ambrosia beetle populations and thus do not promote speciation. This adds credibility to alternative hypotheses, suggesting that it is a separation by major habitat differences, such as those associated with altitude, or major barriers to dispersal, such as sea, that generate the diversity of tropical ambrosia beetles.

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