

# Tree species distributions across five habitats in a Bornean rain forest

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**Abstract.** We examined the distribution of tree species across five habitats in 69 small plots within a single watershed of the Gunung Palung National Park, West Kalimantan, Indonesia (GPNP). The spatially complex distribution and close proximity of habitats provided an opportunity to test habitat specificity of tree species across strong environmental gradients, in a situation where dispersal into 'inappropriate' habitat should not be a rare event. Habitat had a weak influence on community structure, although species diversity was lower in the alluvium and peat habitats. Association tests based on two randomization models (spatially independent and explicit) were used to examine habitat distribution of 55 'common' and 142 'frequent' taxa. The general patterns were similar in the two models but the interpretation of specific patterns depended greatly on assumptions about dispersal ability. A majority (67%) of the common species was significantly associated with a single habitat, while few were restricted to one habitat. A small proportion (16%) of the species appear to be habitat generalists. The peat habitat had the most profound effect on species distribution. Overall, a large amount of variation was found in the degree of habitat specificity, even within speciose groups. No obvious evolutionary or ecological correlates with degree of habitat specificity were found. These results suggest that a mixture of stochastic and deterministic processes determine species distribution even across strong environmental gradients.

**Keywords:** *Dipterocarpaceae*; Gunung Palung National Park; Indonesia; Kalimantan; Monte Carlo procedure; *Myrtaceae*; Species diversity.

**Abbreviations:** GPNP = Gunung Palung National Park.; SEMI = spatial dependence; SPI = spatial independence.

**Nomenclature:** Ng (1978, 1989); Soepadmo & Wong (1995); Soepadmo et al. (1996); Whitmore (1972, 1973b).

## Introduction

Tree species composition varies with habitat in tropical rain forest (Richards 1952) and their distributions are often associated with environmental factors (Baillie et al. 1987; Clark et al. 1998; Duivenvoorden 1996; Hall & Swaine 1981; Hubbell & Foster 1983; Lieberman et al. 1996; Newbery & Proctor 1984; Pendry & Proctor 1997; Phillips et al. 1994; Sollins 1998; Swaine 1996; Veenendaal 1998; Whitmore 1973a) but tests of association are often confounded by the naturally clumped distributions of trees (Hubbell 1979; Plotkin et al. 2000; Tilman 1994), thus reducing the spatial independence of individual samples (Mueller-Dombois & Ellenberg 1974) and violating the assumptions of standard statistical tests (Legendre & Legendre 1998). Spatially-limited seed dispersal is often suggested as the process leading to species clumping (Condit et al. 2000) but the degree of dispersal limitation observed in among most Bornean tree species was not sufficient to maintain strong aggregations over many generations, given intact faunal communities (Webb & Peart 2001). Clumping of individuals, due to this process, will not be broken down by shallow environmental gradients, reducing the power of tests to distinguish between association and aggregation. Embedded small patches of different habitat may also show more similarity to the surrounding forest than would be otherwise expected because of a limited source pool of 'appropriate' species (Butaye et al. 2001). Our 15-km<sup>2</sup> research site in the Gunung Palung National Park (GPNP) provided an opportunity to examine species-habitat associations in a situation where tree species could easily disperse across strong environmental gradients, without major disparities among habitats in the size of source and sink populations.

The complex geological history of Borneo (Audley-Charles 1987), the limited amount of volcanic activity (Hall & Holloway 1998) and climate change over past millennia (Morley 2000) has created mixed tree communities that vary in a fine-grained mosaic pattern (Ashton 1995). Across the island of Borneo, the dominant families are consistent within habitats but dominant

species vary in different locations (Kartawinata et al. 1981; Newbery & Proctor 1984; Slik et al. 2003; Suselo & Riswan 1987), even when habitats are basically identical (Baillie et al. 1987; Brunig 1969; Newbery 1991). Such evidence suggests rain forest trees have limited seed migration capacity across complex landscapes and distant communities evolve independently of one another, resulting in high levels of  $\gamma$ -diversity. High levels of genetic endemism were found across Borneo in *Lithocarpus*, indicating that most communities here are >> 1 million yr old and did not disappear during the last glacial period (Cannon & Manos 2003).

Recently, different types of randomizations tests have been applied in single forest sites to examine community level distribution of species (Harms et al. 2001; Sri-Ngernyuang et al. 2003; Webb & Peart 2000). In this study, we apply similar randomization tests based upon spatially-independent and spatially-explicit models. The questions we addressed were: 1. Does forest habitat significantly affect community structure and diversity? 2. Do different randomization models have an effect on the outcome of the species-habitat association tests? 3. What proportion of the common species was significantly associated with a habitat? 4. Were families associated with habitats? 5. Can degree of habitat association be correlated with overall congeneric diversity, local abundance of congenics, and seed dispersal strategy?

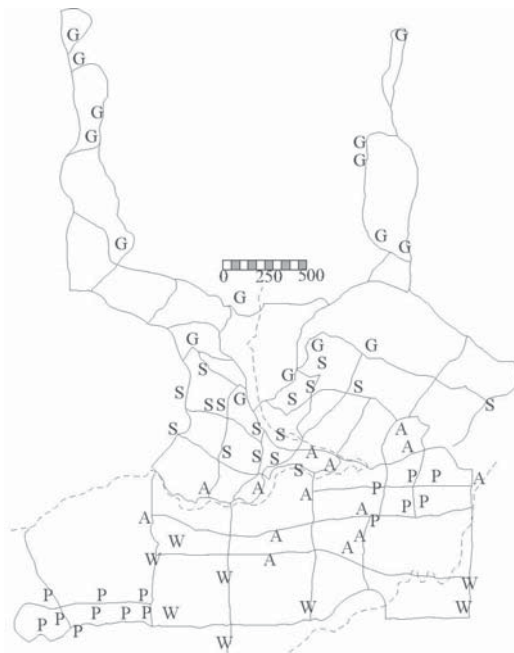
## Methods

### Study site and data collection

The Gunung Palung National Park (GPNP, West Kalimantan, Indonesia; 1°15' S, 110°10' E; 90 000 ha) contains a small coastal mountain range (Mt. Palung reaches 1110 m a.s.l) surrounded by well-drained lowland and seasonally-flooded forests. The study site (ca. 1500 ha) is located in the western watershed, drained by the Air Putih (Fig. 1). Little evidence of human disturbance was apparent at the time of the study, although gaharu poachers (Paoli et al. 2001) and illegal loggers (Jepson et al. 2001) have been active recently. The presence of a large number of endemic chloroplast haplotypes, encompassing a large relative amount of genetic variation, found in a Southeast Asia wide study of one tree genus, *Lithocarpus* (*Fagaceae*), suggests that GPNP has been isolated from other Bornean tree populations for potentially millions of years (Cannon & Manos 2003).

Five main habitat types are found within the study site and were identified by elevation, soil parent material, amount of accumulated organic material, and drainage conditions: (A) alluvium: rich soils of a recent origin from both sandstone and granite parent material within the floodplain of the Air Putih, at 0 to 50 m elevation, generally well-drained but inundated frequently; (S) sandstone: well-drained sedimentary soils at 20-200 m elevation, high in clay content with occasional presence of shale; (G) granite: well-drained granite soils above 300 m elevation (see Webb & Peart 2000 for a more detailed analysis of this habitat), including submontane forest above 700 m along the two major ridge systems; (W) freshwater swamp: seasonally flooded and poorly drained gleyic soils; and (P) peat: bleached white sands with various amounts of accumulated organic matter, often several meters deep, at 5 - 10 m elevation.

Tree plots were placed using a stratified random design so that each habitat type was well represented in the study (sample sizes: A = 14, S = 16, G = 16, W = 8, P = 15). All 69 plots were 0.1 ha in size; 20 measured 10 m × 100 m and 49 measured 20 m × 50 m. All trees ≥ 15 cm DBH were measured and mapped in the plots, bark and leaf arrangement descriptions were made, and fallen leaf samples were collected. Leaf samples and descriptions were matched against one another to identify unique morphotypes across the entire sample. Common taxa were identified to the species level by matching with collections in the Harvard Herbaria and assistance from P.S. Ashton and P.F. Stevens.



**Fig. 1.** Map of the study site. Soil lines show the trail system while the dashed lines indicate the position of rivers. Plots are indicated by habitat type. A = alluvium; G = Granite; P = Peat; S = Sandstone; W = Swamp.

Randomization tests

The spatial and habitat-related patterns in community structure and species distribution were examined using randomization tests (Fox 1987; Harms et al. 2001; Manly 1997; Webb & Peart 2000), modified to assume spatial independence (SPI) and spatial dependence (SEMI) of seed dispersal. In both models, plot samples were treated as a single unit (abundance of individuals was used but individuals in a plot were randomized together). To perform the SPI test, habitat designations of plots were randomly shuffled during each randomization, regardless of their starting position. For the SEMI test, an attempt was made to impose the spatial reality of habitat distribution. To create a much larger simulated landscape, reflections of the plot system were added along each edge of the sampled area. During each randomization, the entire network of plots was moved a random distance, drawn from a  $\gamma$ -distribution, across this simulated landscape. This technique should be an improvement over ‘wrapping’ (Sri-Ngernyuang et al. 2003) or torus-translations (Harms et al. 2001) because it is unrealistic for seasonally flooded peat swamp at

sea-level to be adjacent to upland granite soils at 1000 m in elevation. Using mirror images to simulate landscapes should avoid abrupt and unnatural changes in habitat distribution. For both tests, plot location was randomized 1000 times and the habitat abundance of each species was counted for each replicate, generating null species-habitat distributions.

These tests were performed on 55 ‘common’ species and 36 families that were observed in more than seven plots in the entire sample (see Table 1 and App. 1) and on 142 ‘frequent’ species observed in four to seven plots. Additionally, the results from these randomization tests were compared to a  $\chi^2$  test and a principal components analysis. These tests generally agreed but we present only the randomizations because these provided more definitive results and better contrasted the important spatial aspects of habitat and species distribution.

Significance in these randomization tests was determined in two ways: (1) ‘local’ significance was noted if the observed number of individuals in a particular habitat lay beyond 97.5% of the randomized values, along either tail; (2) ‘global’ significance was noted if the total observed deviation value, based upon the summation of

**Table 1.** Significant species-habitat associations in the Gunung Palung National Park, Indonesia. Observed number of individuals in each habitat (OBS) is shown in the left series of columns. Column headings: A = alluvium; S = sandstone; G = granite; W = swamp; P = peat. The results of the two randomization tests (discussed in the Methods) are shown to the right. All species shown were ‘globally’ significant in the SPI test while asterisks in the middle column indicate significance in the SEMI test. Results for all 55 common species are shown in App. 1. Plus and negative signs indicate ‘locally’ significant results between each species/habitat combination (see Methods). One sign =  $p < 0.975$ ; two =  $p < 0.99$ ; three =  $p < 0.9999$ .

	OBS					SPI					SEMI				
	A	S	G	W	P	A	S	G	W	P	A	S	G	W	P
<i>Popowia tomentosa</i> (Annonaceae)	1	1	0	12	0			+++	*			+++			
<i>Bhesa paniculata</i> (Celastraceae)	0	1	1	0	7					++					
<i>Atuna racemosa</i> (Chrysobalanaceae)	2	9	1	0	0	+++					+++				
<i>Dactylocladus stenostachys</i> (Crypteroniaceae)	2	0	0	1	40		-	-		+++	*			+++	
<i>Dipterocarpus sublamellatus</i> (Dipterocarpaceae)	38	26	15	0	0	++			-		+++++++				
<i>Shorea crassa</i> (Dipterocarpaceae)	0	0	26	0	0			+++			*		+		
<i>Shorea quadrinervis</i> (Dipterocarpaceae)	0	0	18	0	0			+++			*		+++		
<i>Fahrenheitia pendula</i> (Euphorbiaceae)	1	9	3	0	0		++					+			
<i>Pimeleodendron griffithianum</i> (Euphorbiaceae)	0	2	5	0	13	-				+++				+++	
<i>Archidendron</i> sp. 1 (Fabaceae)	0	0	0	3	7					+				++	
<i>Dialium</i> spec. 1 (Fabaceae)	3	2	0	3	0				+						
<i>Sindora</i> spec. 2 (Fabaceae)	0	0	0	2	6					++				+	
<i>Stemonurus</i> spec.1 (Icacinaeae)	1	0	0	1	13		-			+++				+++	
<i>Stemonurus secundifolius</i> (Icacinaeae)	0	3	0	0	24			-		+++	*			+++	
<i>Eusideroxylon zwageri</i> (Lauraceae)	3	6	0	2	0		+					+			
<i>Pternandra coerluscens</i> (Melastomataceae)	5	1	2	30	1				+++		*			+++	
<i>Artocarpus kemando</i> (Moraceae)	2	0	0	7	0				+++						
<i>Syzygium</i> spec. 1 (Myrtaceae)	17	1	1	1	6	+++					+++				
<i>Syzygium</i> spec. 60 (Myrtaceae)	1	0	12	0	6		-	++						+	
<i>Strombosia ceylanica</i> (Olacaceae)	7	28	8	0	1	+++			-	-		+++			
<i>Ochanostachys amentacea</i> (Olacaceae)	9	8	0	6	0			-		-		+	+		
<i>Xanthophyllum</i> spec. 2 (Polygalaceae)	0	0	0	0	19					+++	*			+++	
<i>Nauclea</i> spec. 2 (Rubiaceae)	0	0	0	0	24					+++	*			+++	
<i>Palaquium leiocarpum</i> (Sapotaceae)	0	0	0	1	54	-	-	-		+++	*			+++	
<i>Palaquium</i> spec. 5 (Sapotaceae)	0	1	19	0	0			+++			*		+++		
<i>Scaphium macropodum</i> (Sterculiaceae)	0	2	7	2	1			++							
<i>Gironniera</i> spec.1-cc (Ulmaceae)	7	1	0	0	0	+++					+++				

the deviation from expectation for each habitat (Webb & Peart 2000), was greater or less than 97.5% of randomized total deviation values, along either tail. The SEMI model should provide a more rigorous test of the associations between forest habitat and tree species and family distribution by retaining the spatial relationships of the observations and help tease out the effects of dispersal limitation.

To examine whether (1) congeneric species diversity and (2) local congeneric abundance affected the strength of species-habitat associations, the mean difference between observed global deviation and each replicate of the SEMI model for each species was plotted against (1) the number of unique congeneric species within the entire sample and (2) the mean observed abundance of congeners (but not including conspecifics) present in each sample plot was also calculated. Non-parametric contingency tables were used for significance tests.

Structural differences among habitats were tested using only the SPI model, as the distribution of forest structure should not be spatially limited. Observed numbers of all stems and big stems (DBH > 30 cm) were compared to the results from the randomization of habitat designation, using standard tests for significance. Differences in species diversity among habitats were tested by comparing observed species diversity within each habitat to 100 random sets of plots, corresponding in sample size. If observed diversity fell outside the 97.5% quantile of the expected frequency distribution, the test was considered significant. The bias in  $\beta$ -diversity introduced by differences in spatial proximity among plots within habitats was examined by comparing the species-area accumulation curves for each habitat obtained from the series of randomizations from the SEMI model. If plots of a particular habitat were widely distributed across the landscape, they might be expected to inherently contain a higher diversity by encompassing a wider range of  $\beta$ -diversity in the community. This spatial bias was expressed as a ratio of mean total species diversity for each pairwise comparison of habitats (Table 2). All analyses were conducted in Mathematica 4 (Wolfram 1998).

**Table 2.** Values above the diagonal indicate the ratio of species diversity (row over column) among habitats (see Table 1) from the SEMI test. Values below the diagonal are species complementarity (unique/total spp.) among habitats.

	A	S	G	W	P
A	-	0.99	0.93	0.99	1.05
S	0.78	-	0.94	1.02	1.02
G	0.85	0.85	-	0.95	1.09
W	0.81	0.87	0.89	-	1.05
P	0.89	0.90	0.92	0.88	-

## Results

### *Taxonomic composition and diversity*

A total of 595 morphotypes were distinguished among 2328 trees, identified to 55 families and at least 145 genera; 81 samples were identified to family only and 23 individuals remain completely unidentified. The *Dipterocarpaceae* dominated the three well-drained lowland habitats in stem density (>20% in alluvium and granite) and in basal area (the single most dominant species comprised 16% and 23% in the alluvium and sandstone, respectively). The *Myrtaceae* (20% of stems in the peat) was the only other family to obtain such high levels of dominance. The *Melastomataceae* contributed 12% of the stand in the swamp but were rare or absent in all other forest habitats. The *Euphorbiaceae* were frequent in the swamp (12%), sandstone (10%) and alluvium (8%). Other common families included the *Sapotaceae* in the granite and peat (11 and 13%), the *Annonaceae* in the swamp and sandstone (10 and 7%), the *Myristicaceae* in the alluvium (9%), and the *Fabaceae* in the peat (6%).

In the alluvium, swamp and peat, a single species comprised a significant proportion of the stand density: *Dipterocarpus sublamellatus* (9% of total stand), *Pternandra coerulea* (11%), and *Palaquium leio-carpum* (10%), respectively, while 'dominant' species in the sandstone and granite were less common: *Strombosia ceylanica* and *Dipterocarpus sublamellatus* (both 5%) and *Shorea crassa* (5%), respectively. *D. sublamellatus* was the most common tree in the study site, frequent in three habitats and constituting almost 3% of the pooled sample. *Polyalthia sumatrana* was the most widespread species, being among the top ten in four separate habitats. Only two other species, *Strombosia ceylanica* and *Ochanostachys amentacea*, were common in more than two forest habitats. In all forest habitats, the percent contribution of the ten most common species dropped off rapidly so that the 11th ranking species represented less than 2%. In terms of species composition, the alluvium and sandstone forest habitats were the most similar (72% complementarity, 44 spp. shared), while the peat and granite were the most dissimilar (92% complementarity, 13 spp. shared). Overall, the peat was the most dissimilar in composition, being > 88% complimentary to all other habitats (Table 2).

None of the habitats contained significantly different densities of stems, for either all or only big (> 30 cm DBH) trees, although several trends were apparent: the alluvium contained lower densities of tree than expected for both size classes; lower densities of big trees were present in the swamp; the granite and peat

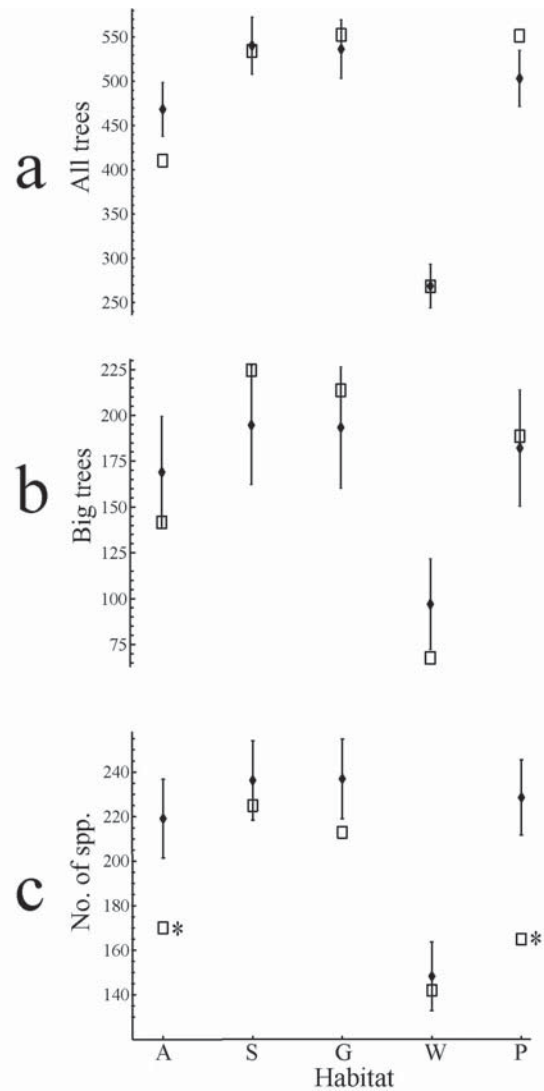
contained higher densities of trees for both size classes (Fig. 2a). The alluvium and peat were significantly less species diverse than other habitats (Fig. 2b). The spatial arrangement of plots in the peat had a slight effect on expected species diversity; with consistently fewer species being captured in the SEMI randomizations (Table 2), suggesting that the observed diversity was reduced slightly by the close proximity of plots. The granite on the other hand generally contained slightly more total species than other habitats (roughly 2.5%) due to the wide dispersion of plots.

### Species-habitat associations

In the spatially-independent model (SPI), the distributions of 15 common species (27%) were indifferent to habitat, 14 (25%) were 'locally' associated with a habitat, and the remaining 26 (45%) were 'globally' significant (Table 1 and App. 1). The peat habitat had the most profound effect on tree species distribution, with 12 positive and six negative associations, while the adjacent freshwater swamp had the least effect on species distribution (four positive and one negative associations). The granite had the greatest negative influence, with seven significant results. Overall, associations were more positive than negative (33 vs. 20). No species was positively associated with more than one habitat.

Four species were restricted to a single habitat, including *Shorea crassa* and *S. quadrinervis* in the granite and species of the genera *Xanthophyllum* and *Nauclea* in the peat. Four additional species were 90% restricted in their distribution (1: granite and 3: peat, Table 1), including both common *Sapotaceae* species: *Palaquium leiocarpum* was the second most frequent species in the study site. *Ochanostachys amentacea* was the only species that was 'globally' significant without being positively associated with any habitat: these trees avoid the granite and peat.

In contrast, no negative species-habitat associations were found in the SEMI test but a greater number of positive associations were found to be significant (Table 1 and App. 1). Overall, only ten species (18%) had 'globally' significant distributions, 29 species (52%) were 'locally' significant, and 16 species (29%) were indifferent to habitat. All species with a 'globally' significant result in the SEMI model were also 'globally' significant in the SPI model. Similar to the results from the SPI test, the peat had a profound impact on species distribution, with 13 positive associations, but in contrast, the sandstone now contained an equal number of positive associations. The number of significant positive results for the alluvium also increased from seven to 11 in the SEMI test (see App. 1).



**Fig. 2.** Habitat structure and diversity. Habitats are A = Alluvium; G = Granite; P = Peat; S = Sandstone; W = Swamp. Graphs show (a) the number of all trees; (b) the number of big trees (> 30 cm DB) and (c) number of species. Solid diamonds represent expected habitat means, assuming spatial independence. Error bars illustrate one standard deviation. Open boxes are observed means in each habitat. Significant deviation from random expectations is indicated by an asterisk ( $p < 0.05$ ). Shannon-Wiener values for each habitat were: A = 4.72; S = 5.00; G = 4.89; W = 4.53; P = 4.32.

Most positive associations with the peat were the same in both models, although *Bhesa paniculata* (*Celastraceae*) was indifferent while *Tetramerista glabra* (*Tetrameristaceae*) and *Syzygium* sp. 60 (*Myrtaceae*) were new associates in the SEMI test. All of the positive SPI results for the alluvium and sandstone were also significant in the SEMI test and several additional positive results were found, including

*Dipterocarpus sublamellatus* and *Ochanostachys amentacea* which were globally significant and positively associated with both habitats (Table 1).

Among the 142 frequent species, the impact of the randomization model was less profound. A small percentage of frequent species were globally significant in both models (SPI: 32%, SEMI: 12%) while the number of locally significant frequent species remained relatively unchanged (52 and 47%, respectively). The relative impact of the habitats on the distribution of frequent species was substantially different than the common species, particularly in the SEMI test. Fully a third of locally significant species were associated with the sandstone habitat while most of the remaining species were split equally between the granite and peat habitats. The deviation from expectations was proportional to the number of plots for specialist species, both common and frequent, while 'intermediate' species were largely absent from the study area (Fig. 3).

#### *Family-habitat associations*

Fully two-thirds of the 36 families tested in the SPI model were found to have 'globally' significant habitat associations, while none of them were significant in the SEMI model (App. 1). The alluvium had a strong negative impact on family distributions in the SPI model but none, once again, in the SEMI model. The *Ulmaceae*, on the other hand, was locally associated with the alluvium in both tests. Two families were associated with the sandstone in both tests (*Olacaceae* and *Chrysobalanaceae*) and the *Bombacaceae* were only significant in the SEMI test. The *Icacinaceae* and *Crypteroniaceae* were both strongly restricted to the peat in both tests. Several families found to be 'globally' significant in the SPI test were not significant, even 'locally', in the SEMI test (*Annonaceae*, *Clusiaceae*, *Dipterocarpaceae*, *Melastomataceae*, *Meliaceae*, *Rubiaceae*, *Sapotaceae* and *Sterculiaceae*; see App. 1).

#### *Degree of association and congeneric diversity*

The relationships of congeneric diversity and local abundance with strength of habitat association from the SEMI model were not significant, although congeneric diversity and local abundance both seem to be weakly correlated with habitat specificity. Several species in monotypic genera were also habitat specialists, with few intermediates present.

## Discussion

### *Habitat effects on community structure and diversity*

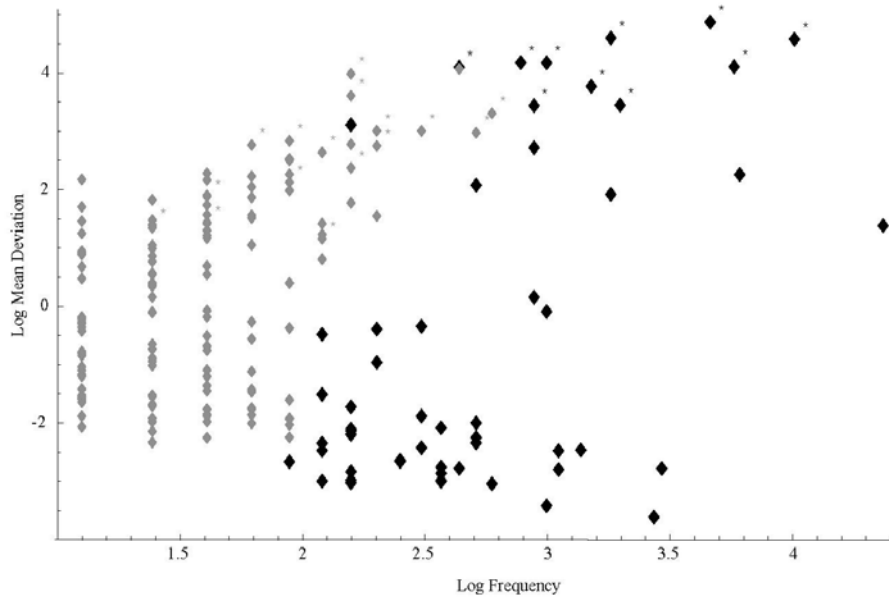
The spatial dispersion of plots within a habitat had only a small effect on expected species diversity (only the peat was consistently lower because of the close proximity of sample plots). The wide range of environmental conditions and evident species-habitat associations also meant that no one habitat was as diverse as the entire watershed. This bias should affect habitats equally and be more directly related to sample size. Although corresponding soil analyses have not been conducted across all habitats, extractable phosphorus levels in the alluvium, sandstone, and granite ranged across a 16-fold range with means of 48, 22, and 12 kg/ha P, respectively, in the top 20 cm of soil (Paoli 2003) while peat soils are famously poor in available nutrients. It is interesting that the poorest soils (peat) and the richest soils (alluvium) would possess fewer species, lending further support to the theoretical idea that intermediate habitats should be more species diverse.

The lack of a habitat effect on forest structure is somewhat surprising given the different 'feel' of these habitats and the well-established differences in the literature. The outcome in this study may be due to the small size of the sample plots and their wide dispersion within each habitat, encompassing a range of forest successional stages, resulting in large variance in stem density.

### *Effect of model assumptions*

Both randomization tests rejected many more tests of association than standard  $\chi^2$  tests, in agreement with a similar randomization procedure used by Harms et al. (2001), suggesting that the results from randomization methods are generally more conservative. Imposing a spatially-explicit randomization model (SEMI) further reduced the number of globally significant associations and completely eliminated locally significant negative associations. This implies that many species are not avoiding habitats but that they might actually have difficulty dispersing into them because of spatial constraints and the overall limited availability of some habitats. Also, the fact that all family results were not 'globally' significant suggests that the SEMI test might be too stringent, despite strong obvious patterns (see *Icasinaceae* in App. 1).

It is important to note that the SEMI model did not uniformly reduce the number of 'locally' significant association tests. Significant local results were found for several species only for the SEMI model, especially those associated with the alluvium and sandstone. Only



**Fig. 3.** Relationship of species frequency and deviation of habitat distribution from expectations. All values are natural logs. Frequency equals the number of independent plot observations for each species and ‘Mean Deviation’ equals the mean difference between the observed deviation and the deviation calculated for each randomization in the spatially-explicit test. Common species are shown by black diamonds while frequent species are shown by gray diamonds. Globally significant species indicated by an asterisk (see Table 1).

one example of contradictory results can be found: ‘*Syzygium spec. 60*’ was significantly associated with the granite in the SPI test but with the peat in the SEMI test. These differences are due to a combination of the spatial distribution of individuals and their unique local habitat setting. Ultimately, the spatially-explicit model more powerfully detected species-habitat associations in the complex mosaic of habitats among the alluvium, peat, and sandstone but rejected species associations with large contiguous blocks of habitat, like the granite.

The biological significance of the reduction in significant results between the tests (SEMI: 0 fam. and 10 spp. vs. SPI: 23 fam. and 27 spp.) depends a great deal on whether species are truly dispersal limited at the scale of a single watershed. Webb & Peart (2001) found little evidence of dispersal limitation within the granite for mostly animal dispersed species. Whether this result can be extrapolated to the entire watershed depends on the habitat specificity of animal feeding behaviour. The absence, in this study, of a relationship between seed dispersal strategy and degree of association implies that dispersal strategy is not important but the small number of independent contrasts limits this interpretation. The difference in globally significant results between the two models is caused by differences in the test statistics produced by each model: the SPI test generates a normal distribution of overall deviation values from expectations (see Methods) while the SEMI test can generate skewed distributions due to spatial heterogeneity.

The patterns of habitat specificity were similar between common and frequent species, although frequent species were generally less specific than common species. This difference between these two classes of species may largely be due to the inadequate number of independent observations of the frequent species. The spatially explicit model did appear to have an interesting effect on some of the frequent species, as the magnitude of mean deviation was not always a good indicator of global significance. The spatial position of the individual observations of these species within the study site obviously affected the outcome.

#### *Degree of association*

Most species were also observed on ‘inappropriate’ habitat, despite strong apparent preference. This habitat infidelity indicates a certain degree of neutrality in species distribution even in a situation where substantially different habitats are in close proximity. A sharp separation can be seen between peat specialists and avoiders and the presence of peat specialists in the granite demonstrates that these species were not dispersal limited but could establish in sites up to 2 km away and a considerable increase in elevation. The relative absence of strict habitat fidelity in this study emphasizes the potential difficulty in detecting associations across shallow gradients.

Ten common species were completely indifferent to

habitat in both tests (see App. 1). Given the broad range of habitats, particularly the differences in drainage condition, within the research site, this result is rather surprising. Most of these generalist species were widely distributed, found in at least six plots and frequently more than nine. No apparent evolutionary or ecological pattern explains these generalists: they come from a wide range of families and genera and produce several different types of fruit. The interpretation of habitat generalization among these species should not be strongly affected by source-sink population dynamics (Pulliam 1988) because of the wide dispersion of plots across the study area and the lack of clumping of stems.

The restricted distributions for the specialist species were probably due to differences in edaphic and elevation aspects of each habitat, as has been found elsewhere (Debski et al. 2002; Swaine 1996; Tuomisto & Ruokolainen 1997) and not dispersal limitation, particularly in the SEMI test. The close proximity of the habitats in this study allows abundant mixing of individuals between habitats. Additionally, the two patches of peat are separated by over a km of intervening swamp and alluvium and yet this did not limit the distribution of peat specialists. The alluvium is the most difficult habitat to define, based upon species distribution, particularly in the large degree of overlap in specialist distribution with the sandstone. These two habitats were the most intermingled geographically and were probably separated by the shallowest environmental gradients in the study. Because of the nature of alluvial soils, the parent material and nutrient content for these two habitats are probably quite similar. Paoli (2003) found an extremely wide range of extractable phosphorus in the sandstone, encompassing the entire range of values observed across the alluvium, granite and sandstone habitats.

Globally significant family level associations with habitat were strongest in families comprised mainly of few species and exclusively in the spatially-independent model, while several families were locally significant in both tests. The *Bombaceae* and *Olacaceae* were locally associated with the sandstone habitat in the SEMI but not in the SPI model. These results do not indicate a stronger level of specialization at this higher taxonomic level.

## Conclusions

Despite the fundamental difference in the assumptions of the two randomization models, the general level of habitat specialization detected remained relatively high. Contrasting the results from these two models can simultaneously reveal the effects of spatial distribution of habitats and begin to tease out the degree of dispersal

limitation within a single watershed. The fit of community structure to the expectations of a neutral model (Hubbell 2001) is probably not due to the overall neutrality of species distribution and interaction but to the variation in strength and broad scope of the mechanisms regulating relative densities through time (Van Valen 1992) and the spatially explicit and clumped nature of plant communities (Tilman 1994). Many of these mechanisms, whether deterministic or stochastic, are mutually compatible (Wright 2002) and have been functioning simultaneously throughout the long history of these forests. Additionally, long generation times of rain forest trees would further impede fine-tuned specialization of species to local habitat (Cannon 2001). Comparative research of clear specialists and generalists, at the community level, would greatly expand our understanding of the factors most strongly influencing habitat specialization and the process of competitive exclusion in rain forest trees.

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