Oecologia

10.1007/s00442-004-1525-3

Community Ecology

Habitat heterogeneity and niche structure of trees in two tropical rain forests

Matthew D. Potts[1], Stuart J. Davies[2] ✉, William H. Bossert[3], S. Tan[4] and M. N. Nur Supardi[5]

(1) Institute on Global Conflict and Cooperation, University of California San Diego, La Jolla, CA 92039, USA
(2) Center for Tropical Forest Science-Arnold Arboretum Asia Program, Harvard University, 22 Divinity Avenue, Cambridge, MA 02138, USA
(3) Division of Engineering and Applied Science, Harvard University, Cambridge, MA 002138, USA
(4) Forest Department, 93660 Kuching, Sarawak, Malaysia
(5) Forest Research Institute of Malaysia Kepong, 52109 Kuala Lumpur, Malaysia

✉ **Stuart J. Davies**
Email: sdavies@oeb.harvard.edu

Received: 28 July 2003 **Accepted:** 28 January 2004 **Published online:** 3 March 2004

Abstract Dispersal-assembly theories of species coexistence posit that environmental factors play no role in explaining community diversity and structure. Dispersal-assembly theories shed light on some aspects of community structure such as species-area and species-abundance relationships. However, species’ environmental associations also affect these measures of community structure. Measurements of species’ niche breadth and overlap address this influence. Using a new continuous measure of niche and a dispersal-assembly null model that maintains species’ niche breadth and aggregation, we tested two hypotheses assessing the effects of habitat heterogeneity on the ability of dispersal-assembly theories to explain community niche structure. We found that in both homogenous and heterogeneous environments dispersal-assembly theories cannot fully explain observed niche structure. The performance of the dispersal-assembly null models was particularly poor in heterogeneous environments. These results indicate that non-dispersal based mechanisms are in part responsible for observed community structure and measures of community structure which include species’ environmental associations should be used to test theories of species diversity.

Keywords Niche-assembly - Dispersal-assembly - Partitioning - Null model - Species coexistence

---

Introduction

The dichotomy of "neutrality versus the niche" (Whitfield 2002) effectively embodies the ongoing debate over the relative importance of niche- versus dispersal-assembly theories of species coexistence and community assemblage. Niche-assembly theories posit that environmental heterogeneity and biological interactions are responsible for species coexistence and community structure (Tilman 1982; Lieberman et al. 1985; Hubbell and Foster 1986; Denslow 1987; Kohyama 1994; Terborgh et al. 1996; Clark et al. 1998). In contrast, dispersal-assembly theories hypothesize that chance, history, and dispersal explain species coexistence and community structure (Hubbell 1997; Bell 2001; Hubbell 2001).

Theoretical and empirical studies have demonstrated that some aspects of community structure and diversity, including species-area curves and species-abundance distributions, can be explained without invoking biologically based mechanisms of species coexistence (Plotkin et al. 2000; Hubbell 2001; Chave et al. 2002). However, species-area relationships and species-abundance distributions provide little information on the arrangement of species within a community with respect to the environment or with respect to other species. Measures of community structure and diversity that account for species-environment and species-species associations should be used to assess the validity of niche and dispersal based theories of species diversity. Whether or not dispersal-assembly theories explain measures of community structure and diversity that incorporate environmental heterogeneity remains untested.

Species niche measurements implicitly provide information on species-environment and species-species associations. Recent studies in meadow communities (Silvertown et al. 1999, 2001) and arctic tundra communities (McKane et al. 2002) have demonstrated that niche-assembly theories in part explain plant community structure and diversity. Niche-assembly processes might be expected to play a role in defining community structure in tropical rain forest communities due to their exceedingly high local diversity, the co-occurrence of large numbers of closely related species, and their great variation in life-history strategies. In this study, we present empirical evidence that in tropical tree communities, dispersal-assembly based models cannot alone explain observed niche structure.

Niche-assembly theories posit that environmental factors account for observed species' niche measurements. Given empirical evidence of species-habitat associations (Plotkin et al. 2000; Harms et al. 2001), we hypothesized that dispersal-assembly models would not accurately predict species' niche breadth and pairwise species' overlaps in heterogeneous environments. In contrast, in areas with little environmental heterogeneity, we expected dispersal-assembly models to explain a greater proportion of the variation in observed species' niche measurements.

Species-specific ecological and environmental data were gathered for ca. 1,300 species of tropical rain forest trees in two tropical rain forest plots in Malaysia to test these hypotheses. The 50 ha spatial scale of these plots encompasses a local community of co-occurring tropical trees. The scale of the plots is larger than the scale of the common disturbance regime (gap formation through tree falls) as well as the vast majority seed dispersal events. Using data drawn from these plots, species' niche breadths and pairwise species' niche overlaps were measured for all species. These empirical niche measurements were compared to those expected under a dispersal-assembly null model. Comparing the empirical results to null model results enabled determination of the relative ability of dispersal-assembly theories to explain observed local community structure as well as to determine the factors influencing and controlling niche structure within tree communities.

Materials and methods

Study sites

The data for this study were drawn from two large-scale forest research plots in Malaysia. One plot is in the Pasoh Forest Reserve, Negri Sembilan in Peninsular Malaysia (2°59′N, 102°18′E, hereafter Pasoh) and is coordinated by the Forest Research Institute of Malaysia in collaboration with the Center for Tropical Forest Science-Arnold Arboretum Asia program (CTFS-AA). The other plot is in Lambir Hills National Park, Sarawak in Borneo (4°12′N, 114°01′E, hereafter Lambir) and is coordinated by the Sarawak Forest Department, Osaka City University and CTFS-AA. Both plots are in lowland mixed dipterocarp forest with an aseasonal climate of high and relatively evenly distributed rainfall.

The plots differ slightly in size with Lambir at 52 ha (1,040×500 m) and Pasoh 50 ha (1,000×500 m). Otherwise, methods of plot establishment were identical for the two plots and followed a standardized protocol (Manokaran et al. *1990*; Condit *1998*). All stems $\geq$1 cm dbh were tagged, mapped, identified to species and measured for diameter at breast height (dbh). In 1986, the Pasoh plot included 814 species and 335,348 stems (Kochummen et al. *1990*; Davies et al. *2003*), and in 1996 Lambir included 1,171 species and 339,266 stems (Lee et al. *2002*). Both plots include habitat-related spatial variation in species composition; however, they differ greatly in the extent of within-plot environmental heterogeneity (Lee et al. *2002*; Davies et al. *2003*). The Lambir plot spans two soil types of differing fertility, and includes over 140 m of altitudinal variation (Fig. 1). In contrast, the soils and topography in the Pasoh plot are relatively uniform, and altitude spans only 24 m (Manokaran and LaFrankie *1990*).

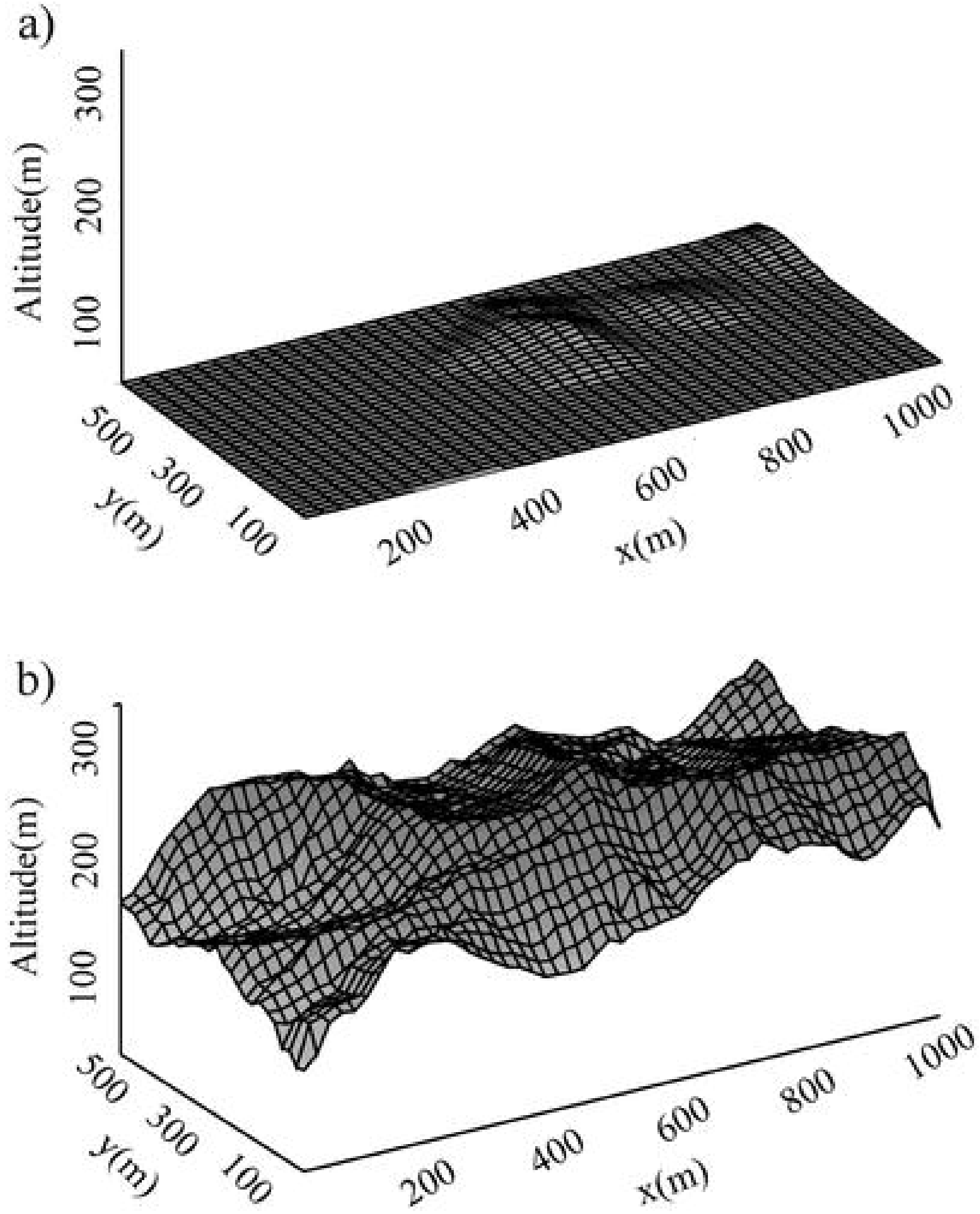


Fig. 1 Topographic map of **a** Pasoh, **b** Lambir

Niche measurement

Species’ niche structure was measured along a continuous altitudinal axis. Altitudinal data were used since they are a good proxy for plant water availability (Daws et al. *2002*). In both plots, low altitude sites are generally associated with high water availability and high altitude sites with lower water availability. In addition, at Lambir altitudinal variation is good proxy for environmental heterogeneity related to variation in soil nutrients (e.g. P, Mg, Ca, pH) (Davies et al. *2004*). Results of Mantel Test and Canonical Correspondence Analysis (CCA) (Legendre and Legendre *1998*) of floristic, habitat, altitudinal data support this conclusion. Detailed soil nutrient data were not available for the Pasoh plot, precluding analyses based on soil nutrients at both sites. Finally, using a continuous measured variable avoided the use of arbitrary habitat classes.

At plot establishment, altitude was measured to the nearest 0.1 m at 20 m intervals. This coarse scale altitude data was kriged using universal kriging on a 1 m^2 grid to produce an extremely accurate (<1% standard error) fine scale topographic map (Cressie *1991*, Fig. 1). Kriging is a technique of spatial statistical analysis which relates to the hypothesis that variance of spatial data is uniform over the sample region. Accuracy was judged by fitting the kriging model with 90% of the observed data and using the fit model to predict the values for the remaining 10% of data.

Both discrete (Levins *1968*; Feinsinger et al. *1981*) and continuous measures (MacArthur and Levins *1967*; Manly and Patterson *1984*) of niche breadth and overlap exist. Unfortunately, indices of niche breadth and overlap based on the distribution of species among discrete resources states inevitably lead to arbitrary decisions concerning the size and number of resource states (Levins *1968*; Feinsinger et al. *1981*). Indices of niche breadth and overlap that use continuous data require the assumption that the data were drawn from a certain probability distribution whether it be for example normal (MacArthur and Levins *1967*) or Weibull (Manly and Patterson *1984*). Given the continuous nature of altitude data and no a priori information on expected distribution of resource states, continuous measurements of species' niche breadth and overlap were developed.

The continuous measurement of niche breadth and overlap applied here is denoted as K-S and defined as follows. Given two species A and B and the altitudes occupied by each individual, the altitudes for each species were sorted into ascending order. We then calculated the cumulative sample distributions $P_A(x)$ and $P_B(x)$, the proportion of stems of species A and species B whose altitude is less than or equal to x. Niche overlap was calculated as twice the area between the curve formed by the pairs of points (P_A, P_B) and either the P_A or P_B axis, whichever was smaller, resulting in a measure ranging between 0 and 1 (Fig. 2). If two species did not overlap in altitudinal range then the curve would lie along either the P_A axis and the line P_A=1 or along the P_B axis and the line P_B =1 and the niche overlap would be zero. If two species have identical altitudinal ranges, P_A and P_B lie along the 45° line and the area between the curve and either axis is one-half which leads to a calculated niche overlap of one. Niche breadth for individual species was calculated using a similar procedure. In this case, each species' distribution of altitudes was tested against a random sample of 1,000 points in the plot. In addition, for comparison niche breadth was calculated using the normalized version of Levin's B with altitudinal bin widths of 5 m.

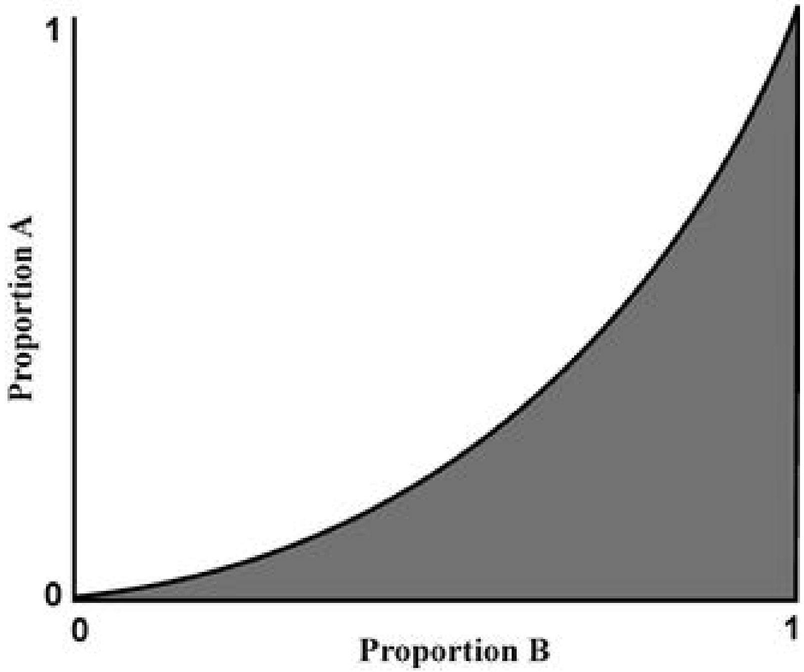


Fig. 2 K-S Method of niche measurement. Using the K-S method niche overlap is defined as twice the area of the grey region. See text for a full explanation of the method

---

In this way, the niche breadth (overlap) measurement reflected the degree of available habitat space utilized (shared) by a species (pair of species) (Feinsinger *1981*). Measuring niche breadth in this way differs from more traditional measures such as Levin's B. Levin's B measures both the proportion of each resource state used as well as the total number of resource states used (Feinsinger *1981*). In contrast, a niche breadth measure like ours indicates the proportion of available habitat space utilized by a species. This subtle distinction allows for the direct comparison of niche breadths from Pasoh and Lambir using the K-S method even though they span vastly different altitude ranges. Such a comparison is invalid using a measure such as Levin's B.

The K-S measurements of niche breadth were validated by comparisons with calculated Proportional Similarity (PS) measures of niche breadth (Feinsinger *1981*). The K-S measure of niche breadth was significantly correlated (r^2 ~0.85) with PS for a range of altitudinal bin widths (5–20 m). For niche overlap, K-S measurements were compared to the Pianka (*1973*) and Czechanowski (Legendre and Legendre *1998*) indices. Again for a range of bin widths, K-S niche overlap measurements were significantly correlated with these traditional measures (r^2 ~0.90).

All analyses were restricted to species with >50 individuals to prevent spurious results due to small sample sizes. Since preliminary analysis indicated no changes in niche breadth or species' spatial aggregation with ontogeny, individuals of all sizes classes were grouped together for subsequent analysis.

Dispersal-assembly model

To test whether empirical niche measurements were consistent with dispersal-assembly theories, a spatially-explicit null model was necessary. This model had two key requirements. First, it needed to maintain small-scale species' spatial aggregation which is most likely related to dispersal patterns (Plotkin et al. 2000). Second, in order to detect biologically based differences in niche overlap, it had to preserve species' niche breadths (Gotelli and Graves 1996). This was mandatory because an intrinsic correlation exists between species' niche breadth and overlap; species with broad niches generally have higher overlaps and vice versa.

The details of the model are described below but before doing so we put our model in context with regard to the neutral theory (Hubbell 2001). The neutral theory is commonly understood to be a dynamic model that explains community structure and diversity under the assumption that all species have identical mortality, identical fecundity, and identical probability that their propagules take over a vacant site (Chave et al. 2002). In addition, the neutral theory embraces a concept of dispersal limitation (Hubbell 2001). The model we employed, while in the spirit of the neutral theory, contrasts with it in a number of ways. First of all our model was statistical as opposed to dynamic. Using stochastic point process theory, we replicated the spatial patterning of tree species in such a way that maintained local aggregation that is primarily driven by dispersal limitation while eliminating deterministic species-species and species-habitat associations. In this, we created a static null model that was as consistent as possible with the key assumptions of the neutral theory.

A combination of two stochastic point process models of species' spatial patterning was used to meet these requirements: the torus random model (Diggle 1983) and Poisson cluster model (Plotkin et al. 2000). In the torus random model, species' spatial patterning is repeatedly torroidally shifted to remove species' habitat associations while maintaining small scale (dispersal-based) species' spatial patterning. In the Poisson cluster model, a two-parameter stochastic spatial model is fit for each species, which again reproduces the fine scale (dispersal-based) species' spatial patterning while removing species' habitat association.

The ability of these models to maintain niche breadths was judged by comparing niche breadth values from 1,000 realizations of the best fit Poisson-cluster and torus-random models to the observed species' niche breadths. The ability of the models to maintain species' spatial patterning was judged by comparing Ripley's K (Cressie 1991) values from 1,000 realizations of the best fit Poisson cluster model and torus random model to the observed species' Ripley's K values.

Species for which either the torus-random or Poisson-cluster model maintained both niche breadth and Ripley's K were included in the dispersal-assembly model. For species fit by both models the Poisson cluster model was used. A single realization of the dispersal-assembly community involved one realization for each species, utilizing either the torus or Poisson method, depending on the species. Empirical data were compared to 1,000 null dispersal-assembly communities. In addition, to make the results comparable to those of Silvertown et al. (2001), niche overlap values using species where the

Poisson cluster or torus random model maintained niche breadth but not Ripley's K were examined. This enabled investigation of the effect of species spatial aggregation on niche structure. Preliminary analyses using additional models (such as random placement) indicate that our model was sensitive to large-scale changes in community structure.

Results

Null model fits and niche measurements

Niche breadth and the Ripley's K statistic of spatial aggregation were fit by either the Poisson-cluster or torus-random models in 484 species in Lambir and 250 species in Pasoh, 64% and 47% of species with >50 individuals in each plot respectively (Table 1). In both Lambir and Pasoh, fit species represented a diversity of orders, families and genera (Table 2).

Table 1 Results of a Monte Carlo goodness of fit test to determine the ability of the Poisson cluster model and torus randomization method to replicate spatial aggregation and niche breadth. One thousand boot straps were performed and the threshold *P*-value was 0.05; 753 species in Lambir were analyzed while 527 were analyzed at Pasoh. *Aggregation and breadth* refers to the number and percentage of species whose breadth and aggregation were maintained by either the Poisson cluster or torus random models for each forest

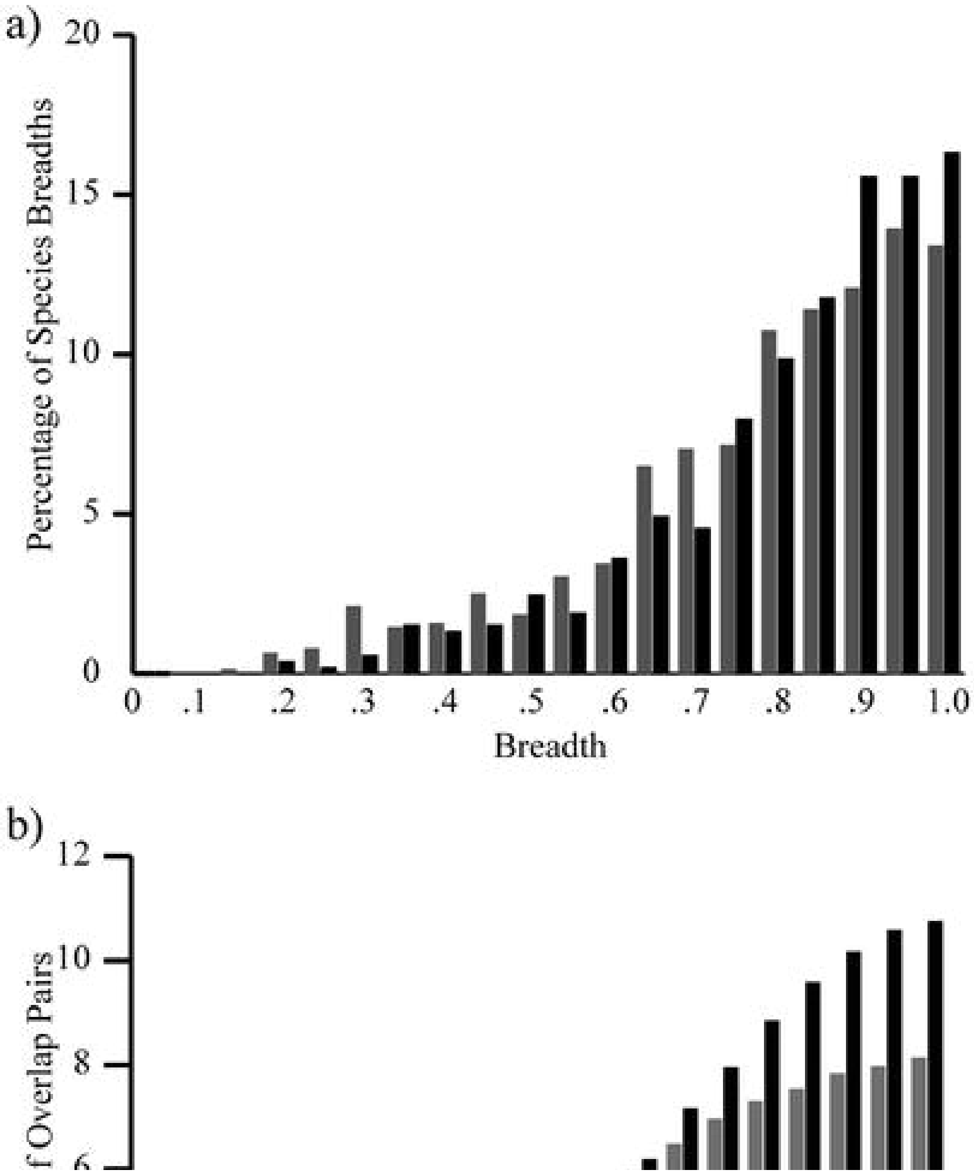
	Lambir species		**Pasoh species**	
	Fit by models		**Fit by models**	
	Poisson	**Torus**	**Poisson**	**Torus**
Aggregation	650 (86%)	393 (52%)	140 (27%)	310 (59%)
Breadth	484 (64%)	501 (67%)	313 (59%)	345 (65%)
Aggregation and breadth		484 (64%)		250 (47%)

Table 2 Comparison of species fit by Poisson cluster model and torus randomization method to all species with abundance greater than 50 individuals

	Lambir	**Pasoh**

	All species	Fit species	All species	Fit species
Order	27	25	26	19
Family	71	62	70	45
Genera	222	175	226	133

In both forests there was significant variation in species' niche breadth and species-species niche overlap (Fig. 3). In the relatively homogeneous Pasoh plot, mean niche breadth of all species was 0.79 ±0.03 using the K-S method and 3.0±0.74 using Levin's B (Table 3). Mean niche overlap for all species pairs was 0.70±0.05 (Table 4). In the heterogeneous Lambir plot, mean niche breadth of all species was 0.76±0.04 using the K-S method and 1.61±0.91 using Levin's B (Table 3). Mean niche overlap for all species pairs was 0.62±0.07 (Table 4).



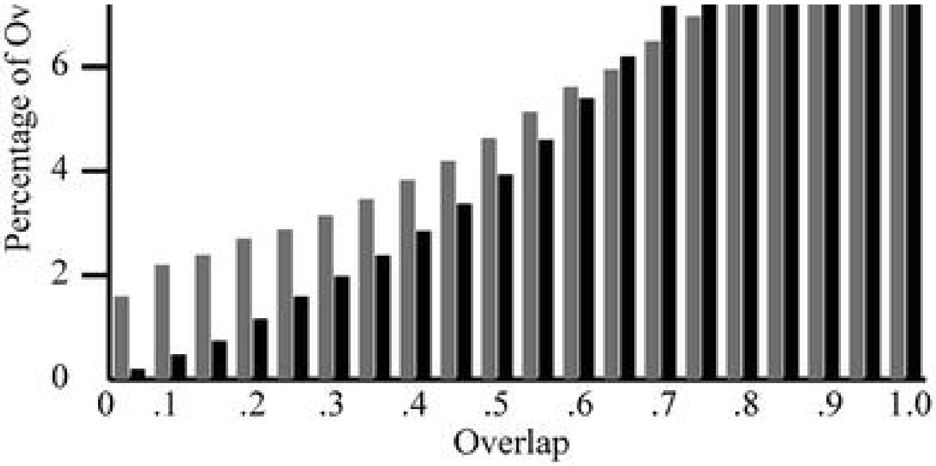


Fig. 3 Observed niche measurements in the two forests. **a** Histogram of niche breadths. **b** Histogram of niche overlaps. *Grey* indicates Lambir and *black* indicates Pasoh

---

Table 3 Summary of niche breadth measurements. Mean values and variances for all species, species where the null model maintains niche breadth as well as niche breadth and aggregation are given. The normalized version of Levin’s B was calculated with a bin width of 5 m. Different letters indicate significant differences in distributions of values within sites (K-S two sample test, P <0.05). In site comparisons * implies that a significant difference in the distribution of values existed between the two sites (K-S two sample test, P <0.05). *NS* not significant, *N/A* not applicable

	Lambir			**Pasoh**			**Actual site values compared**		
	KS-Breadth	**Levin’s B**	**Ripley’s K (10^6)**	**KS-Breadth**	**Levin’s B**	**Ripley’s K (10^6)**	**KS-Breadth**	**Levin’s B**	**Ripley’s K**
All	0.76 ±0.04 ^{a}	1.61 ±0.91 ^{a}	4.61 ^{b}	0.79 ±0.03 ^{c}	3.0 ±0.74 ^{a}	2.55 ^{b}	*	N/A	*
Not fit	0.60 ±0.06 ^{b}	1.68 ±0.83 ^{a}	15.2 ^{a}	0.62 ±0.03 ^{d}	2.9 ±0.86 ^{b}	4.88 ^{a}	NS	N/A	*
Breadth	0.77 ±0.03 ^{a}	1.59 ±0.81 ^{a}	4.33 ^{b}	0.84 ±0.02 ^{b}	3.1 ±0.62 ^{a}	2.12 ^{bc}	*	N/A	*

Breadth and aggregation	0.77 ±0.02 ^{a}	1.57 ±0.77 ^{a}	3.67 ^{b}	0.87 ±0.01 ^{a}	3.2 ±0.53 ^{a}	0.89 ^{c}	*	N/A	*

Table 4 Summary of niche overlap measurements. Mean values and variances for all species, species where the null model maintains niche breadth as well as niche breadth and aggregation are given. For the null models mean overlap values are given with the number in parenthesis indicating the rank (smallest-largest) of the observed data out of 1,000 realizations of the appropriate null model. Different letters indicate significant differences in distributions of values within sites (K-S two sample test, $P<0.05$). In site comparisons * implies that a significant difference in the distribution of values existed between the two sites (K-S two sample test, $P<0.05$). *N/A* not applicable

	Lambir		**Pasoh**		**Actual site values compared**
	Actual	**Null model**	**Actual**	**Null model**	
All	0.62±0.0 ^{a}	N/A	0.70±0.0 ^{c}	N/A	*
Not fit	0.44±0.1 ^{b}	N/A	0.55±0.0 ^{d}	N/A	*
Breadth	0.63±0.0 ^{a}	0.82 (1)	0.77±0.0 ^{b}	0.78 (228)	*
Breadth and aggregation	0.64±0.0 ^{a}	0.82 (1)	0.82±0.0 ^{a}	0.84 (1)	*

Species for which null models could not accurately estimate niche breadth and spatial aggregation had significantly lower mean niche breadth using the K-S method than the fitted species (Table 3). Many of these species had highly localized distributions which may have resulted from either strongly limited dispersal or from very strong associations with a habitat of limited spatial extent.

At Pasoh, due to the significantly lower niche breadths in species not fit by the null models, mean niche overlap for all species pairs was lower than mean niche overlap for the fitted species only (Table 4). In addition, mean niche breadth differed significantly between all species, species fitted for both niche breadth and spatial aggregation, and niche breadth only. Consequently, at Pasoh mean niche overlap differed significantly in null models that maintained just breadth or both breadth and spatial aggregation. At Lambir there were no differences in the distribution of niche breadths and overlaps between all species and fit species (Tables 3, 4).

Effects of heterogeneity

Two hypotheses were tested concerning the effects of habitat heterogeneity on niche breadth and overlap. The first was that high habitat heterogeneity should lead to lower species' niche breadths. Given our definition of niche breadth, there was support for this hypothesis. While species in both forests occupied a similar fraction of available habitat space, here defined along an altitudinal gradient, mean niche breadth for all species was slightly smaller in Lambir as compared to Pasoh (Table 3). In addition, among species fitted by the null models there was a significant difference in the mean and distribution of niche breadths (Table 3).

The second hypothesis tested in this study was that dispersal-assembly models could explain the distribution of niche overlaps in homogeneous but not in heterogeneous environments. The results did not support this hypothesis. In both plots mean observed species' niche overlaps were significantly less than those calculated using a null model that maintained niche breadth and spatial aggregation (Table 3).

Distributions of niche overlap values differed significantly between the two forests for all species, and for the reduced set of species that were fit by the null models (Table 4). The ability of the null models to explain the observed distribution of species-species niche overlaps was much better at Pasoh than at Lambir. At Pasoh there was no significant difference in mean niche overlap between the null model that maintained just species' niche breadth and observed data (Table 3). However, there was a significant difference in mean niche overlap between the full null dispersal-assembly model and observed data though the difference was quite small. In contrast at Lambir, neither null model fit the observed data. Observed mean niche overlap was significantly less than in the null models (Table 3).

Discussion

The analyses of niche structure in two tropical forests presented here indicate that aspects of both niche- and dispersal-assembly theories explain observed community structure. In the Pasoh forest, the null model that just maintains species' niche breadth retrieved observed species' niche overlaps. In addition, at Pasoh there may be little functional significance to the difference between niche overlap values from the full null model and actual data. However, in line with recent studies in meadow (Silvertown et al. *2001*) and arctic tundra communities (McKane et al. *2002*), there was evidence of habitat-driven mechanisms of species coexistence in the heterogeneous Lambir forest.

The result that niche breadths in Pasoh are higher than in Lambir is somewhat dependent on our definition of niche breath. As noted in the methods section, traditional niche indices measure the number as well as proportion of habitat states utilized. In contrast, our method calculates the relative proportion of available resource states utilized. Thus, as is the case with Lambir and Pasoh, a species with the same niche breadth as measured by our method would actually be found in a wider absolute range of altitudes and in some sense it is true that species' niche breadth may be broader at Lambir. However, it remains true using our definition that species are found in a wider range of available altitudes at Pasoh as compared to Lambir.

Habitat heterogeneity had different effects on niche breadth and overlap. There is a subtle difference between species' niche breadth and species' habitat association. The measurement of niche breadth used in this study indicates the amount of available resource space a species utilizes but not the exact resource level utilized. For example, a species may have a niche breadth of 0.20 and thus utilize 20% of available niche space but the measure used in this study would not indicate whether a species is found at high or low altitude. In contrast, species' habitat association indicates that a species is found in specific environmental conditions.

While species' niche breadth measurements do not account for where a species is found along an environmental axis, niche overlap depends on the specific distribution of the pair of species. Niche overlap values reflect where a species is found in niche space in relation to another species and thus niche overlap measurements are concerned with habitat specialization. The results indicate that greater habitat heterogeneity leads to greater habitat specialization. The Lambir plot overlays two soil types and contains a large number of species specialized to one or the other soil type.

An example using five species of *Dipterocarpus* in the Lambir plot illustrates the above two points (Fig. 4).The distributions of the five species were fit by the full null dispersal-assembly model. The observed mean species' niche overlap among these congeneric species was 0.41 while the mean null model overlap was 0.66 indicating that significant niche separation exists between these species. Graphically, this is illustrated by the large difference in observed mean altitude between species. This is an indication of strong habitat associations. In contrast, the differences in mean altitude between species in realizations of the dispersal assembly model are small. Fig. 4 also illustrates the point that while the dispersal assembly model maintains niche breadth, it may change a species' habitat position.

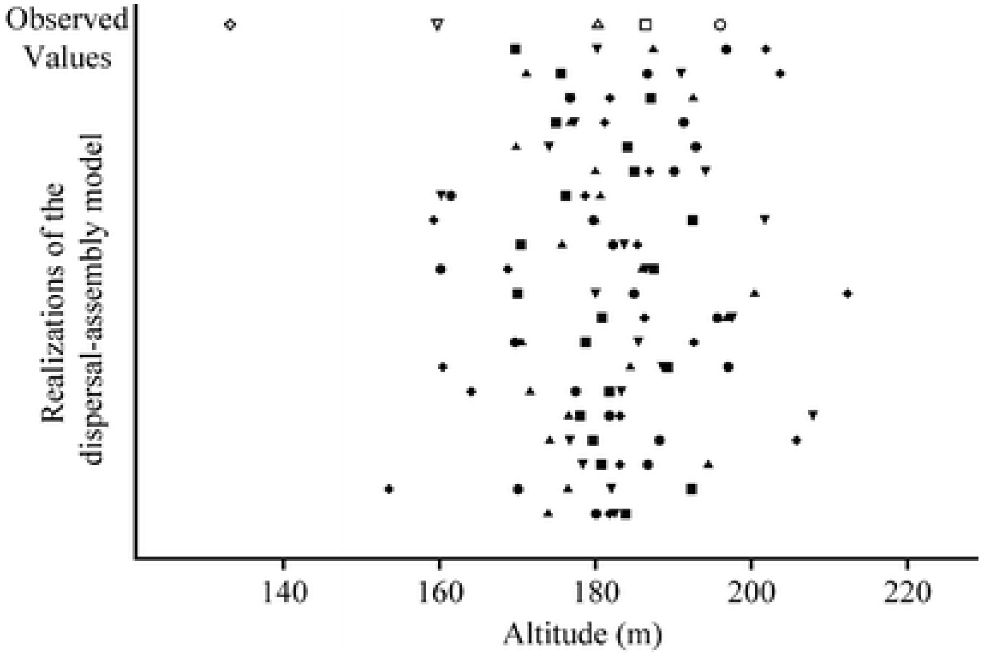


Fig. 4 Habitat position for five species in the genus *Dipterocarpus* at Lambir. Symbols indicate mean altitude for

each species. Actual data, indicated by *open symbols*, and 20 realizations of the dispersal-assembly model, indicated by *solid symbols*, are shown. ■,□ *D. acutangulus*; ●,○ *D. palembanicus* subspecies *borneensis*; ▲, △ *D. confertus*; ◆,◇ *D. kunstleri*; ▼,▽ *D. palembanicus* subspecies *palembanicus*

As alluded to in the introduction, while looking at species’ niche structure requires detailed species-specific spatial and environmental data, it provides better insight into community structure than other measures of community structure such as species-area curves and species-abundance distributions. Niche measurements implicitly give information about species’ environmental associations as well as species’ position in a community relative to other species. The results indicate that the arrangement of species with respect to each other is a key descriptor of community composition and assembly and that dispersal-assembly based null models do not adequately reproduce these features. Niche breadth and overlap should be additional measures used to judge the validity of theories of species diversity.

The null model use here is an improvement over the one used by Silvertown et al. (2001). As noted by them, their null model fails to take into account spatial aggregation due to limited dispersal of individual species. The null model used in this study overcomes this problem and has proven robust at replicating other aspects of community structure such as species-area curves (Plotkin et al. 2000). However, there is one caveat that should be attached to the null model. It was not possible to parameterize the null model for all species. The effects of this were particularly pronounced in the Pasoh plot. At Pasoh the mean and distribution of observed niche overlap and breadth values for species fit by the model were less than that for all species in the community. This does not create a problem for the interpretation of the results. All this difference in niche measurement values serves to do is increase the estimation of the relative strength of dispersal driven effects. Thus, it is likely that our analyses underestimate the effects of biologically driven niche partitioning. Finally, the differences in the ability of our null model to fit species at Pasoh and Lambir are most likely related to the degree of species aggregation. Species at Lambir are more aggregated than at Pasoh. The more aggregated a species is, the better the fit of the Poisson cluster or torus random model.

A number of future research areas should be pursued. One should be the development of better null models of community structure. The null-dispersal model used was the combination of two point process models that maintain species’ spatial patterning, and as a coincidental effect, maintain species’ niche breadth. The next step would be a null-dispersal model with the explicit aim of maintaining species’ aggregation as well as niche breadth. Further research should include the collection of additional environmental data so that species’ niche breadths and overlaps may be compared along multiple niche axes allowing for a better understanding of the relative importance of niche- versus dispersal-assembly theories in explaining community structure and diversity.

Acknowledgements M.D.P. was supported by an NSF Bioinformatics Post-Doctoral Fellowship, DBI-0204070 and 1-year post-doctoral research fellowship provided by the Center for International Development, John F. Kennedy School of Government, Harvard University. The research was supported by NSF grant DEB-0075334. We would like to thank Peter Ashton who provided comments on early drafts of the paper.

References

Bell G (2001) Ecology—neutral macroecology. Science 293:2413–2418.

Chave J, Muller-Landau HC, Levin SA (2002) Comparing classical community models: Theoretical consequences for patterns of diversity. Am Nat 159:1–23

Clark DB, Clark DA, Read JM (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. J Ecol 86:101–112

Condit R (1998) Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer, Berlin

Cressie N (1991) Statistics for spatial data. Wiley, New York

Davies SJ, Surpardi MNN, LaFrankie JV, Ashton PS (2003) The trees of Pasoh Forest: Stand structure and floristic composition of the 50-hectare forest research plot. In: Okuda T, Manokaran N, Thomas SC, Ashton PS (eds) Pasoh: ecology and natural history of a Southeast Asian lowland tropical rain forest. Springer, Berlin Heidelberg New York, pp 35–50

Davies SJ, Tan S, LaFrankie JV, Potts MD (2004) Soil-related floristic variation in the hyperdiverse dipterocarp forest in Lambir Hills, Sarawak. In: Roubik D (ed) Ecology of the Lambir Forest, Sarawak, Malaysia (in press)

Daws MI, Mullins CE, Burslem DFRP, Paton SR, Dalling JW (2002) Topographic position affects the water regime in a semideciduous tropical forest in Panama. Plant Soil 238:79–90

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Syst 18:431–451

Diggle P (1983) Statistical analysis of spatial point patterns. Academic Press, London

Feinsinger P, Spears EE, Poole RW (1981) A simple measure of niche breadth. Ecology 62:27–32

Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian, Washington

Harms KE, Condit R, Hubbell SP, Foster RB (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. J Ecol 89:947–959

Hubbell SP (1997) A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs 16:S9–S21

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, N.J.

Hubbell SP, Foster RB (1986) Biology, chance and history and the structure of tropical rain forest tree communities. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York, pp 314–329

Kochummen KM, LaFrankie JV, Manokaran N (1990) Floristic composition of Pasoh Forest reserve, a lowland rain forest in peninsular Malaysia. J Trop For Sci 3:1–13

Kohyama T (1994) Size-structure-based models of forest dynamics to interpret population-level and community-level mechanisms. J Plant Res 107:107–116

Lee HS, Davies SJ, LaFrankie JV, Tan S, Yamakura T, Itoh A, Ashton PS (2002) Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. J Trop For Sci 14:379–400

Legendre P, Legendre L (1998) Numerical ecology, 2nd English edn. Elsevier, Amsterdam

Levins R (1968) Evolution in changing environments; some theoretical explorations. Princeton University Press, Princeton, N.J.

Lieberman M, Lieberman D, Hartshorn GS, Peralta R (1985) Small-scale altitudinal variation in low-land wet tropical forest vegetation. J Ecol 73:505–516

MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. Am Nat 101:377–385

Manly BFJ, Patterson GB (1984) The use of Weibull curves to measure niche overlap, N Z J Zool 11:337–342

Manokaran N, LaFrankie JV (1990) Stand structure of Pasoh Forest Reserve, a lowland rain forest in peninsular Malaysia. J Trop For Sci 3:14–24

Manokaran N, LaFrankie JV, Kochummen KM, Quah ES, Klahn JE, Ashton PS, Hubbell SP (1999) The Pasoh 50-ha forest dynamics plot: 1999 CD-ROM Version. Forest Research Institute Malaysia, Kepong

McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin AE, Kielland K, Kwiatkowski BL, Laundre JA, Murray G (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415:68–71

Pianka ER (1973) The structure of lizard communities. Annu Rev Ecol Syst 4:53–74

Plotkin JB, Potts MD, Leslie N, Manokaran N, LaFrankie J, Ashton PS (2000) Species-area curves, spatial aggregation, and habitat specialization in tropical forests. J Theor Biol 207:81–99

Silvertown J, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. Nature:400:61–63

Silvertown J, Dodd M, Gowing D (2001) Phylogeny and the niche structure of meadow plant communities. J Ecol 89:428–435

Terborgh J, Foster RB, Nunez PV (1996) Tropical tree communities: A test of the non-equilibrium hypothesis. Ecology 77:561–567

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, N.J.

Whitfield J (2002) Ecology: neutrality versus the niche. Nature 417:480–481