Biodiversity and environmental change in the rainforests of Borneo
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Recent theoretical work has suggested that assemblage structure in rainforest biotas is not the result of environmental determinism but rather has arisen through stochastic processes and dispersal limitation. Using data collected in Borneo from more than 1000 species belonging to butterflies, odonates, lianas and trees we examined the relationship between distance, a set of environmental variables, and community structure. We found that environmental variables significantly explained variation in all four groups, but geographic distance only proved significant in lianas. These results emphasise the importance of the environment in determining the flora and fauna present within a habitat.

We also assessed whether patterns of spatial diversity were consistent among the four groups. In correspondence with previous studies of tropical biomes we found no relationship between patterns of alpha diversity among taxa. Patterns of beta diversity, however, proved to be significantly congruent. We suggest that studying patterns of beta diversity of groups of species can provide important insights into ecological processes and may be used to predict patterns of other species with which they share a habitat. In this respect butterflies that have a well-resolved taxonomy, reasonably known life-history, and a documented rapid response to environmental changes, may be an ideal focal subject for environmental and conservation studies.
Introduction

Recently, there has been considerable debate on the relative importance of deterministic versus stochastic processes in explaining patterns of beta diversity (Bell, 2001; Condit et al., 2002; Duivenvoorden, 2002; Wright, 2002; Whitfield, 2002). Whereas niche based theories have a long history in ecological research (Grinnell, 1917; Levin, 1970; MacArthur, 1970; Diamond, 1975) and are implicit in the work of Darwin, neutral theories that focus on the random nature of communities are of more recent origin (Caswell, 1976; Harte et al., 1999; Hubbell, 2001). An important stimulus in this debate is the recent work of Hubbell (2001) in which he describes a new ‘unified theory of biodiversity and biogeography’. Under Hubbell’s neutral theory all organisms within a trophic level are considered to function as ecologically indistinguishable units. Species in any given habitat at any point in time are assumed to be an amalgamation of individuals thrown together from a much larger and biogeographically constrained metacommunity.

One of the key factors in neutral theory is dispersal limitation. At very low dispersal rates, species in communities can become locally monodominant, leading to low alpha (local) but high beta diversity in the metacommunity. Under high rates of dispersal the reverse is expected. In a recent study that compared predictions of the neutral theory with observations of lowland tree communities in central and South America, Condit et al. (2002) found that patterns of beta diversity reflected those predicted by the neutral theory at intermediate spatial scales, but broke down at small and large scales. At the smaller spatial scales they noted that similarity declined rapidly with distances up to 3 to 5 km in all three areas they surveyed. They concluded that species are more aggregated than predicted by theory at small spatial scales and at large spatial scales low species turnover rates may be bounded by as yet unexplained processes.

Their study was, however, criticised by Ruokalainen and Tuomisto (2002). First of all Ruokalainen and Tuomisto claimed that Condit et al. (2002) had sampled relatively few plots over large spatial scales; 34 plots in Central America up to 50 Km apart, and 16 and 14 plots in two areas of South America at even greater spatial scales. This means that their rapid decline in similarity at small spatial scales was based on relatively poor sampling. Moreover the Central American study consisted of plots in old growth and new growth habitat without explicitly addressing this in the analyses, while the South American studies only consisted of plots in old growth habitat.

In the present study we assessed patterns of beta diversity within four important species groups (trees, butterflies, odonates, and lianas), in a tropical rainforest environment in Borneo. Borneo has long been renowned for its remarkable diversity (Wallace, 1869) and is located in one of the worlds most threatened hotspots (Myers et al., 2000).

Logging (Spitzer et al., 1997; Cannon et al., 1998; Vasconcelos et al., 2000), tree community composition (Laman, 1996; Summerville and Crist, 2002), and especially topography (Ohmann and Spies, 1998; Svenning, 1999; Condit et al., 2000) have all been identified as important determinants of species distribution. The environmental dataset therefore consisted of topography (relative elevation), the habitat-matrix (primary versus logged habitat), and for butterflies, odonates, and lianas tree community composition.

The use of four distinct species groups allows us, furthermore, to generalise the findings in relation to beta diversity to spatial and environmental processes. Hubbell (2001) predicted that his neutral theory is more likely to hold for plants and microbes than for animals because plant and microbe species tend to overlap in the way that they use resources. If this holds true then we would therefore expect a much higher proportion of variance in community similarity of both animal groups to be explained by environmental variables as opposed to both plant groups where distance may be a better predictor of community change.
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We furthermore assess whether the species groups are congruent in their patterns of alpha and beta diversity in order to assess if individual species groups can serve as surrogates for other species groups? Both birds and butterflies, for example, displayed similar responses to urbanisation at moderate (1 to 10 kms) spatial scales so that both could be used as a surrogate for the biodiversity of the other taxa (Blair, 1999). Lawton et al. (1998) and Howard et al. (1998), however, found little congruence in the species richness of a large number of species groups including woody plants, large moths, butterflies, birds, and small mammals in tropical Africa. Lawton et al. (1998) therefore concluded that no single group of organisms could serve as a good indicator for the changes in the species richness of other groups. This may in fact generally be true when dealing with small-scale species richness. Species richness or alpha diversity, for example, of trees on small plots can vary enormously even among primary forests. This can be due to among other factors, forest stature, tree density, soil type, and bias in selecting plots to avoid certain landscape elements such as gaps (Primack and Hall, 1992). Very few studies have, however, addressed whether different communities are congruent in their beta diversity. Beta diversity is essentially the turnover of species (along a gradient). Alpha diversity is assumed to be the result of niche differentiation whereas beta diversity is the result of habitat diversification (Gray, 2000). Bird alpha diversity, for example, which is related to vegetation structure is similar in the temperate zone and the tropics, but beta diversity is much higher in the tropics. Understanding why habitat diversification and beta diversity is much more pronounced in the tropics is potentially far more interesting that the study of alpha diversity (Gray, 2000).

The two main hypotheses we address with this study are:

1) If dispersal and stochastic processes are more important in determining beta diversity over intermediate spatial scales (here between 0.1 and 6 Km) then geographic distance will be a better predictor of community similarity than environment.

2) Because beta diversity is related to habitat diversification we expect species groups to have congruent beta diversities in so far as their habitat needs overlap. We expect the degree of congruence in alpha diversity to be less pronounced because of the reliance of alpha diversity on community-specific niche-packing and random processes.

Materials and Methods

A. Study area and habitat types

All research took place in Indonesian Borneo from May - July 2000. All plots were located in the province of East Kalimantan, Indonesian Borneo. Rainfall in the area varies but is usually between 2000 to 2500 mm per year with no pronounced dry season, although the period between June and October is somewhat drier (Slik et al., 2002). In two areas of known disturbance history (one primary and one logged), random plots were selected in advance using grid cells on maps. The primary area is located in the large (ca. 30 000 ha) Gunung Meratus Protected Forest. The logged area is located in the adjacent ITCI (International Timber Concessions Indonesia) concession, and was logged in 1993/94. Both areas and plots are depicted in Fig. 1. Logging in the area was selective, with a cutting cycle of 35 years, extracting mainly dipterocarp tree species (Slik et al., 2002). Commonly ten trees were felled per ha, although this was less where stocking density was low or when the terrain made
extraction difficult due to slope or adverse edaphic conditions. This level of extraction is moderate for Southeast Asian standards (Danielsen and Heegaard, 1995).

In the research area rocks from the Middle-late Miocene and Early Miocene dominate the geology, largely consisting of tertiary sedimentary rocks. Alternating layers of sandstone, claystone, mudstone, and siltstone dominate the lithology, but there are only slight differences in soil characteristics. Deep clay-rich soils dominate the area, predominantly ultisols, but also some inceptisols. Only soils over Miocene sandstone had different soil characteristics, but these spodosols were very rare (less than 3% of area). Most differences in soil chemistry were limited to the top-soil and were due to slight mineralogical differences in parent material and vegetation. Overall logged forest had a slightly more fertile A horizon than primary forest. The topography is very heterogeneous; steeply dissected hills and hillocks (150 – 500 m a.s.l) with short, steep slopes and narrow crests and valley floors dominated the area (Van Bremen et al., 1990).

B. Plot design and sampling

Sampling took place in 0.9 ha plots (a 300 x 30 metre strip that was demarcated with ironwood poles) assigned at random to a 450 ha area of each habitat. Each plot was located in the field with a compass and clinometer, and then georeferenced with a handheld GPS device (Garmin 12XL). Per habitat (primary and logged forest), 15 plots were sampled for a total of 30 plots of which the most distant were less than 6 Km apart. We therefore have a reasonably intense sampling network of plots that allows us to address patterns of community similarity at smaller spatial scales. Butterflies and odonates were sampled across the entire plot, while lianas and trees were sampled in 200-m² (10 x 20 m) plots nested within the 0.9 ha plot. An example of the layout of plots in each habitat is shown in Fig. 1.

Fig. 1. Map of research area showing a) location in Borneo, and b) layout of plots in primary and logged areas.

Butterflies and odonates were sampled when encountered within the boundaries of each plot. A plot was traversed repeatedly on foot from one end of the plot to the other at a steady
pace, which was only underbroken to collect specimens. This procedure was repeated until at least 200 butterflies and 20 odonates were caught per plot. The mean number of butterflies caught per plot was 200, and the mean number of odonates caught per plot was 52. We avoided small samples, which may yield unreliable similarity indices when comparing plots (Wolda, 1981).

It is very difficult, if not impossible to identify most Bornean butterflies and odonates on the wing (Walpole and Sheldon, 1999). We therefore caught individuals with nets, and subsequently identified them in the field. These individuals were marked with an edding 3000 permanent marker to avoid counting the same individual more than once. All field identifications were made by DFRC or trained students. Because of the minimum sample size, sometimes-adverse weather conditions, and local variations in abundance, the number of days spent at each plot varied (mean and standard deviation of 6.4 ± 0.7 days). Sampling took place between 9:00 and 16:00 hours, except during rain, using standard nets and with two people catching per plot. Samples were taken simultaneously in primary and logged habitats by different groups of trained technicians and students. The date of capture and location were noted for each individual. All butterflies were identified to species following Maruyama and Otsuka (1991), Otsuka (1988), and Seki et al. (1991). In a few cases it was not possible to identify beyond a species-pair or species-group (e.g., the butterflies *Allotinus leogoron* and *A. melos*). All such individuals were then considered to belong to the same species (*A. leogoron* in this case) because diagnostic characteristics could not be determined in the field (e.g., male genital characters) or females could not be further identified unambiguously. All individuals encountered in the superfamilies Papilionoidea and Hesperioidea were collected. Specimens from all butterfly and odonate species were preserved (using silica gel) and later rechecked in the Netherlands. Odonate works consulted include Liefinck (1954) and Wilson (1995). Voucher specimens of all species have been deposited in the Zoological Museum of the University of Amsterdam.

All woody vascular plants higher than 1.3 m were assessed in 200-m² subplots nested within the 0.9 ha plot. Diameter at breast height (dbh.) was assessed and height estimated. Lianas and trees were distinguished and all individual woody plants were furthermore collected and/or identified to species or morpho-species. All botanical collections have been identified to the lowest possible taxonomical level by herbarium staff at the Herbarium Wanariset, Samboja, at the Leiden branch of the Nationaal Herbarium Nederland, Leiden Branch, or by taxonomic specialists elsewhere.

Finally relative elevation was estimated from a digital elevation map of the area. We therefore have important environmental variables including elevation and disturbance history (primary and logged habitat), that allows us to partition community similarity into components explained by purely spatial and components explained by environmental variation. Since dispersal is a purely spatial process this allows us to assess dispersal limitation within the scales of this study.

**C. Analyses**

1. **Community similarity:** Community similarity between plots was based on the Bray-Curtis similarity index (Bray and Curtis, 1957) obtained with the package PRIMER (Clarke and Gorley, 2001). The Bray-Curtis similarity index is frequently used in ecological work (Clarke and Gorley, 2001, Ellingsen, 2002). We used matrix regression based on permutation tests using the program PERMUTE! 3.4.9 (Cagrain, 2001) to assess the relationship between response matrices of community similarity (for butterflies, odonates, lianas, and trees) and a
set of predictor matrices. First, we assessed multivariate relationships between \((\log_{e}+1\text{ transformed})\) response similarity matrices and predictor matrices of

1) Difference in elevation (Euclidean distance in elevation between pairs of plots)
2) The habitat-matrix (a binary data matrix where values in the predictor matrix were given a 0 if pairwise-comparisons of plots were between plots in the same habitat-matrix (i.e., both in logged or both in primary forest), and a 1 if pairwise-comparisons were between plots in different habitat-matrices (i.e., between a plot in the logged habitat-matrix and a plot in the primary habitat-matrix)
3) Tree community similarity \((\log_{e}+1\text{ transformed})\) (for butterflies, odonates, and lianas only)
4) Distance \((\log\text{ transformed})\).

In the program PERMUTE! we used the matrix permutation option, 999 permutations, forward selection, and a Bonferroni-corrected p-to-enter level of 0.10 (the default). For a full description of the use of matrix permutation tests in regression analyses see http://www.fas.umontreal.ca/biol/casgrain/en/labo/permute/index.html and Spencer et al. (2002) for the analogous use of mantel tests to assess relationships among distance matrices. An advantage of these tests is that no assumptions need be made about the distribution of data.

The multiple regression analysis resulted in partial regression coefficients and partial correlation coefficients that measured the effect of the various predictor matrices on the response matrix after controlling for all other independent predictor matrices (Spencer et al., 2002). At each step of the forward selection procedure, the predictor matrix is entered that produces the equation whose \(r^2\) coefficient has the lowest probability. This must also be smaller though than or equal to the Bonferroni-corrected p-to-enter value. This continues until no more predictor matrices meet these criteria.

**ii. Species richness:** Rarefied species richness was assessed with the DIVERSE option within PRIMER (Clarke and Gorley, 2001). We tested for congruence in patterns of species richness between taxa using Pearson's product-moment correlation after checking for normality with a Kolmogorov-Smirnov test (Statistica for Windows, 1996).

**Results**

For butterflies, elevation \((\text{partial } b = -0.599, p < 0.001, \text{partial } r^2 = 0.352)\) and the habitat-matrix \((\text{partial } b = -0.457, p < 0.001, \text{partial } r^2 = 0.206)\) explained 55.8% of variation in community similarity. Distance and tree community structure were not significant in the multivariate model. For odonates, elevation \((\text{partial } b = -0.493, p < 0.001, \text{partial } r^2 = 0.243)\) and tree community structure \((\text{partial } b = -0.284, p < 0.001, \text{partial } r^2 = 0.074)\) explained 31.7% of variation in community similarity. Distance and the habitat-matrix were not significant in the multivariate model. For lianas, tree community structure \((\text{partial } b = 0.261, p < 0.001, \text{partial } r^2 = 0.068)\) and distance \((\text{partial } b = -0.137, p = 0.012, \text{partial } r^2 = 0.018)\) explained 8.6% of variation in community similarity. Elevation and the habitat-matrix were not significant in the multivariate model.
Fig. 2. Relationship between community similarity and distance for a) butterflies, b) odonates, c) lianas, and d) trees. Relationship between community similarity and difference in elevation between plots for e) butterflies, f) odonates, g) trees and h) lianas. PP (a filled circle •) indicates a comparison between two primary plots. PL (a cross +) indicates a comparison between one primary and one logged plot. LL (an open circle ○) indicates a comparison between two logged plots.
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Finally, for trees, elevation (partial $b = -0.283$, $p < 0.001$, partial $r^2 = 0.080$) and the habitat-matrix (partial $b = -0.144$, $p = 0.006$, partial $r^2 = 0.020$) explained 10.0% of variation in community similarity. Distance was not significant in the multivariate model.

The relationships between community similarity and distance and community similarity and elevation are shown in Fig. 2 for all groups. There was no significant decline in similarity with distance in butterflies, odonates, and trees.

Similarity did, however, decline significantly with distance in lianas, but there was a pronounced difference between primary and logged habitats. Community similarity was furthermore considerably higher over distance in primary than logged forest in butterflies. Overall variance in similarity with distance increased strongly in logged forests in butterflies, odonates, and trees and in primary forests in lianas.

As with distance there was a very different response to elevation in primary and logged habitats in butterflies and odonates; in both taxa there was almost no response to differences in elevation in primary habitat and a decline in similarity with increasing difference in elevation between plots in logged habitat. In trees the decline in community similarity with difference in elevation between plots was similar in primary and logged habitats. In lianas there was no significant relationship between community similarity and difference in elevation between plots.

Table 1. Correlations of alpha diversity (species richness) and beta diversity (community similarity) between species groups. None of the pairwise comparisons of alpha diversity were significant. All of the pairwise comparisons of beta diversity were significant except those between odonates and lianas.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Alpha Diversity</th>
<th>Beta Diversity</th>
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<td>$r$</td>
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<tr>
<td>Butterflies</td>
<td>Odonates</td>
<td>0.021</td>
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<tr>
<td>Butterflies</td>
<td>Lianas</td>
<td>-0.015</td>
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<td>Butterflies</td>
<td>Trees</td>
<td>0.000</td>
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<tr>
<td>Odonates</td>
<td>Lianas</td>
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<tr>
<td>Odonates</td>
<td>Trees</td>
<td>-0.052</td>
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<tr>
<td>Lianas</td>
<td>Trees</td>
<td>0.068</td>
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</tbody>
</table>

There was no significant congruence in patterns of alpha diversity among taxa. There was, however, significant congruence in spatial patterns of beta diversity among all species group comparisons except odonates and lianas (Table 1).

Discussion

Environmental variables explained significant amounts of variation in all groups suggesting that community structure and thus beta diversity is to a large extent deterministically governed. Distance, however, did not play a significant role in rates of community similarity in all species groups except lianas, but even here the importance of distance on community similarity was minor. Variance, however, in community similarity did
increased with distance, especially in logged forest. This may help to explain the ‘sharp decline’ with distance found by Condit et al. (2002). In the four groups used here, however, there was no equivalent decline in community similarity with intra-habitat (primary or logged) distances up to 2 Km, and inter-habitat distances up to 6 Km.

Interestingly, however, the decline in liana community similarity was much more pronounced in primary forest, suggesting that lianas may be more dispersal limited in primary than logged forest. Explanations for this difference may be related to the presence of gaps and edges, which are more abundant in logged forest (Schnitzer and Bongers, 2002). Many studies (Gardette, 1998; Laurance et al., 2001; Schnitzer and Bonger, 2002) have indicated that logging-induced disturbance may facilitate dispersal of lianas via gaps and edges.

Overall elevation had a larger effect on community similarity than the habitat-matrix. This agrees with previous studies, which highlighted the importance of topography in influencing species distributions at both small (Svenning, 1999) and large (Rahbek and Graves, 2001; Webb and Peart, 2000) spatial scales. There are a variety of reasons why topography plays such an important role in determining species assemblages. The soil of ridge and upper slope habitats has, for example, different mineral concentrations (Burghouts et al., 1998). Forest growth is reduced on ridges, which are likely to be poor in nutrients (Corner, 1978). Upper slope habitats are also drier and more drought prone, and unique plant communities are known to form on ridges (Newberry et al., 1996).

Like Lawton et al. (1998) and Howard et al. (1998), we found no congruence in alpha diversity among species groups. We did, however, find significant congruence in beta diversity in all group comparisons with the exception of lianas and odonates. Butterfly and tree community structure was significantly related to community structure in all other groups suggesting that these two groups may be important surrogates in predicting patterns of diversity in other taxa. Our results are therefore analogous to those of Howard et al. (1998) who despite finding no significant correlation in alpha diversity among taxa found that certain taxa, especially butterflies and birds, could be used to identify patterns of complementarity in other taxa. Our data suggest that using patterns of beta diversity may prove to have important benefits for environmental and conservation-based censusing. Butterflies may be particularly useful due to their well-resolved taxonomy, ease of sampling, and preserving, reasonably well-known life histories, and rapid response to disturbance (Singer and Gilbert, 1978). This last aspect is particularly important for indicator studies since many long lived organisms such as trees and many vertebrates can persist for decades after they have been virtually doomed to extinction, the so-called ‘living dead’ (Janzen, 1986).

Among the things Hubbell (2001) predicted was that communities exhibit considerable variation under disturbance. The relationship between variation in community structure and disturbance may therefore suggest that disturbance is a spatially related process. Hubbell’s suggestion that plants are more likely to be governed by stochastic processes may also hold. In both our animal groups environmental variation explained from 32 to 56% of variation in community similarity and there was no evidence of dispersal limitation at the spatial scales assessed during this study. The environmental variables, however, explained less than 11% of variation in both plant groups. This suggests that non-distance related stochastic processes may be more important in structuring plant communities. Examples of non-distance related stochastic events abound in tropical rainforests. Chance events, for example, play an important role in influencing recruitment and survival. Falling debris, for example, in Panama killed 33% of liana saplings over a two-year period and falling debris in Costa Rica killed 19% of artificial seedlings over a one-year period (Wright; 2002 and refs therein). However, it is also possible that other unmeasured environmental variables, such as soil type or edaphic conditions, may explain residual variance in community similarity of both plant groups.
Other studies, however, have shown that such environmental factors are only of modest importance and not nearly as important as topography (Ohmann and Spies, 1998; Svenning, 1999). In the research area there was furthermore very little variation in soil characteristics (Van Bremen et al., 1990).

Despite the proven importance of environmental variables such as topography previous studies have in fact suggested that plant communities are largely governed by chance events. In a tropical rainforest study in Panama Harms et al. (2001) found that although the environment (topographic and edaphic features) did contribute to significant differentiation among species, very little local variation in diversity could be attributed to environmental variation. Even gap dynamics may not be as important in structuring communities as has often been suggested. Although it has been established that tree species are clearly differentiated for regeneration in gaps or closed canopy forest, the stochastic nature of gaps, however, leads to gap communities that are filled mostly by chance occupants rather than by species best adapted to gap environments (Brokaw and Busing, 2000). The species composition of gaps was unpredictable even for pioneer species, and strong recruitment limitation appeared to decouple the gap disturbance regime from control of biodiversity. Generally, it is the largest plant that happens to be in a gap at a given time that will win. Recruitment limitation is considered to be the factor that decouples the control of species richness and relative species abundance from resource-based niches in ecological communities thereby explaining the coexistence of large numbers of species with similar resource requirements. Recruitment limitation can slow down the elimination of inferior competitors (Hubbell, 2001).

Interestingly, and contrary to our expectations we found that distance had no impact on tree community structure. Although many tree species may be excellent dispersers via wind dispersal or mobile vertebrate seed dispersers we had expected there to be a signal from the gravity-dispersed dipterocarps that are assumed to be very poor dispersers (Turner et al., 1997). Although seeds are consumed en masse by invertebrates and vertebrates alike, this is mainly considered to have a negative effect. The vertebrates that eat dipterocarp seeds are considered to be seed predators and not seed dispersers (Curran and Webb, 2000). Because of their dominance in Bornean forests, if all dipterocarp species are truly as severely dispersal limited as is assumed, then this should have been revealed by a marked decline in community similarity with distance. That this was not the case indicates that dipterocarp species may be able to disperse via as yet unknown mechanisms. Normally seed predation and factors such as negative density dependence via increased intraspecific competition and pest facilitation may constrain dispersal to very limited spatial scales. Huge quantities of seeds, however, are produced during masting events. Most of these die or are consumed by seed predators such as nomadic pigs or parakeets (Curran and Webb, 2000). Due to the nomadic nature of the main seed predators, pigs, it is, however, possible that seeds may rarely survive and get transported to distant habitats; under certain conditions so-called seed predators may function as seed dispersers. Such very rare long distance dispersal events combined with very limited dispersal at small to intermediate spatial scales may explain the lack of a significant effect of distance, and the particularly low mean similarity among plots of trees compared to the other groups (Fig. 2). Our study also included a wide range of size classes so that juvenile trees numerically dominated all plot samples. High mortality and low growth rates characterise most juvenile rainforest trees due to high rates of disturbance and low-light conditions in the forest understory (Davies, 2001). Further theoretical implications of negative density dependence and related issues such as the Janzen-Connell hypothesis are dealt with in detail in Wright (2002).

In summary our results seem to favour mechanisms of non-distance related stochastic processes and deterministic processes as the main structuring agents in tropical rainforest.
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communities. This suggests that dispersal is pronounced in rainforests via as yet unknown mechanisms. Future research should try to ascertain the main dispersal mechanisms of rainforest communities and further the goal of deterministic and non-distance related stochastic processes in regulating community similarity. Clearly, though, the tropical rainforest is a rich field for future research.

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