

Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest

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Summary

1. One of the primary goals in community ecology is to determine the relative importance of processes and mechanisms that control biodiversity. Here, we examined habitat-driven species assemblages and species distribution patterns as well as their temporal variations for three life stages of two censuses of a 25-ha mixed dipterocarp forest at Sinharaja (Sri Lanka).

2. Our general objective was to find out whether the species assemblages and associated habitat types changed with life stage, spatial scale and species attributes. We also analyse whether the habitat types were related to certain indicator species. Habitat types were determined with multivariate regression tree analyses driven by topographic variables.

3. We found species assemblages associated with five distinct habitat types that appeared consistently for all life stages of the two censuses. These habitats were related to ridge-valley gradients and a pronounced contrast in south-west versus north-east aspect. Habitat-driven structuring was weak at the recruit stage but strong in the juvenile and adult stages. The species assemblage variance explained by topographic variables for different life stages ranged between 10% for recruits and 23% for juveniles.

4. The species assemblages determined for different spatial scales (10, 20, 50 m) showed similar habitat partitioning, but the variance explained by the topographic variables increased in all life stages with spatial scale. This could be due to the homogenizing effect of topographic variables at the larger scales and unaccounted environmental variation at the smaller scales. The number of indicator species identified in the two censuses was higher in the juvenile stage than in the adult stage, and nearly all indicator species in the adult stage were also indicator species in the juvenile stage.

5. *Synthesis.* Our study showed that approximately 75% of the variance in local species composition is unexplained. This may be due to spatially structured processes such as dispersal limitation, unaccounted biotic and abiotic environmental variables, and stochastic effects, but only 25% were due to topographic habitat association. Although the pronounced ridge-valley gradient and contrast of south-west versus north-east aspect created consistent habitats, our results suggest that local species assemblages at Sinharaja forest are jointly shaped by neutral and niche processes.

Key-words: determinants of plant community diversity and structure, dispersal limitation, habitat association, indicator species, multivariate regression tree, neutral theory, Sinharaja forest, spatial scale, topography

Introduction

Explaining the high diversity of tree species in tropical forests is a persistent challenge in community ecology and a subject of lively and enduring discussion (Pitman *et al.* 1999; Chesson 2000). The classical exclusion principle by Gause (1934) states

that two species competing for the same resources cannot stably coexist. However, the number of competing species often exceeds the number of limiting resources (Hutchinson 1961; Connell 1978). Several hypotheses have been developed to resolve this enigma (Grubb 1977; Connell 1978; Hubbell 2001; Wright 2002). The best known are classical niche theory (Tilman 1982) and the unified neutral theory of biodiversity (Hubbell 2001). According to the neutral theory, species are functionally equivalent and diversity is mainly controlled by sto-

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chastic processes such as drift and dispersal limitation (Hubbell 2001; McGill 2003). Functional equivalence of plant species would mean that segregation along environmental niche axes are not the primary drivers of species assembly. In contrast, classical niche theory states that competing plant species can avoid competitive exclusion by relying on different, spatially segregated, resources (i.e. habitat partitioning; Harms *et al.* 2001; Sugihara *et al.* 2003; Cheng *et al.* 2012). Niche theory predicts that similar species assemblages should emerge on sites having similar environmental characteristics (Leibold & Norberg 2004; Tilman 2004) and that niches are uniform and constant throughout all life stages (e.g. MacArthur & Levins 1967).

Many studies found evidence for topographic niche partitioning (e.g. Whittaker 1956; Harms *et al.* 2001; Valencia *et al.* 2004; Gunatilleke *et al.* 2006). For plants and especially trees, topography is a good predictor of habitat because it correlates with variables that are more directly related to plant resources. For example, topographic features such as slope and aspect often correlate with distribution of nutrients (Ahmad 2001; John *et al.* 2007), and topography may determine soil moisture (Ashton 1992; Daws *et al.* 2002; Gibbons & Newbery 2002; Engelbrecht *et al.* 2007; Sukri *et al.* 2011). Topography is also a determinant of the amount of direct and diffuse radiation (Larsen & Speckman 2004), which may provide a habitat axis for species differing in their light requirements: for example, due to a trade-off between growth rate under high light and survival in the shade (Denslow 1980; Sterck, Poorter & Schieving 2006; John *et al.* 2007).

There is ample evidence for habitat associations of individual species along ridge-valley gradients (Svenning 1999; Harms *et al.* 2001; Valencia *et al.* 2004; Gunatilleke *et al.* 2006); however, separate topographic niches for hundreds of species which coexist within small areas in tropical forests are difficult to imagine (Valencia *et al.* 2004). For example, up to 300 tree species per hectare have been found in tropical Amazonia (Gentry 1988). One hypothesis is that niche requirements may change with life stage (Webb & Peart 2000; Comita, Condit & Hubbell 2007). Insufficient niche separation at the adult stage may be compensated by habitat partitioning at earlier life stages, where environmental conditions are often more heterogeneous than those experienced by an adult plant (Webb & Peart 2000). Changing habitat requirements with tree size may also be related with ontogenetic shifts in resource requirements such as light (Poorter *et al.* 2005; Comita, Condit & Hubbell 2007) or in physiological and morphological traits related to light capture (Kitajima & Fenner 2000). For example, empirical results from Barro Colorado Island (BCI) in Panama, a lowland moist tropical forest with relatively weak topographic structuring, showed that habitat associations of the majority of species were not consistent across life stages (Comita, Condit & Hubbell 2007; Kanagaraj *et al.* 2011). Similar results were found for a subtropical broad-leaved forest of China with strong topographic structure (Lai *et al.* 2009).

A fundamental task in understanding the factors that determine the distribution of species in forests is therefore to find out whether the forest comprises of areas with distinct species assemblages that can be distinguished based on their topo-

graphic properties (Legendre *et al.* 2009; Kanagaraj *et al.* 2011), and whether the habitat types related to these assemblages are invariant with life stages (as assumed by classical niche theory). For example, Kanagaraj *et al.* (2011) found that the BCI forest was structured into five habitat types. However, the associated species assemblages were relatively weak (i.e. species were not confined to discrete habitat types but rather varied in abundance among habitat types), and species assemblages were not invariant with life stage and showed some temporal variability. In forests with stronger topographic structuring, we may expect a stronger habitat impact on the emerging species assemblages and fewer changes with life stage. Comparing two forests with contrasting topographic structure may therefore shed light on the relative importance of topographic habitats and their consistency among life stages and allowing hypotheses on the underlying processes to be posed.

An approach to better understand and interpret the emerging habitat types is to evaluate how strongly different habitat types are related to certain indicator species and how much variability in species composition is explained by the emerging habitat types. Because spatially structured environmental variables are associated with niche processes (Laliberté *et al.* 2009), a large percentage of species variance explained by the habitats would be in support of niche theory. The unexplained variance could be due to pure spatial variation, internal processes of population dynamics such as dispersal limitation, stochastic processes more associated with neutral theory and unaccounted biotic and abiotic environmental variables that emphasize the importance of niches. Additionally, the scale-dependent nature of most processes and mechanisms hypothesized to contribute to species coexistence (Crawley & Hurrall 2001; Wright 2002) calls for examining species variation due to environmental heterogeneity at different scales (Legendre *et al.* 2009). While species assemblages at the community scale should primarily be driven by habitat filtering, competition among similar species and stochastic effects should become more important at local neighbourhood scales (Webb *et al.* 2002). Finally, species with different attributes may be subject to weaker competition than species that are more similar. For example, growth form differentiation is a way to avoid direct competition, and species of different growth forms may benefit from the presence of each other (e.g. Kohyama & Takada 2009).

The general objective of this study is to analyse species assemblages in a tropical forest at Sinharaja (Sri Lanka) that shows strong topographic structuring to find out whether the species assemblages and associated habitat types change with life stage, spatial scale and species attributes. More specifically we ask (i) whether this forest shows habitat-driven species assemblages and whether they are invariant with life stage, (ii) how much variability in local species composition is explained by the different habitat types and whether the habitat types are related to certain indicator species, and (iii) whether spatial scale and species properties (i.e. canopy, sub-canopy and understorey trees) influence species assemblages. We expected that the Sinharaja forest would show a distinct topographic habitat structure (Gunatilleke *et al.* 2006), and, because of the strong topography, distinct species

assemblages should emerge already at the early life stage and the associated habitats should remain consistent during all life stages. However, this does not mean that individual species may not change their requirements with life stage; even if the habitats of species assemblages are stable, individual species that contribute to the assemblages may change with life stage. Compared to the BCI analysis of Kanagaraj *et al.* (2011), we expect that substantially more variability in local species composition will be explained by habitat. In addition, we expect that more of the variability will be explained if we increase the spatial scale of the analysis (Legendre *et al.* 2009).

Materials and methods

STUDY SITE

The 25-ha (500 m × 500 m) Sinharaja forest dynamic plot (FDP) was established in 1993 at the centre of the ever wet south-western region of Sri Lanka (6°21'–26' N, 80°21'–34' E). The forest type in this plot represents a *Mesua-Doona* community, where all the stems ≥ 1 cm diameter at breast height (d.b.h.) have been identified to species, measured and mapped (Gunatilleke *et al.* 2004a, 2006). Due to the strong environmental heterogeneity, the plot provides optimal opportunities to study species compositions and their topographic habitat partitioning, including analyses of their different life stages. The elevation of the permanent plot ranges from 424 to 575 m a.s.l. A valley lies between two slopes, a steep higher slope facing south-west and a less steep slope facing north-east. Two perennial streams and several seasonal streamlets run across these slopes (see Fig. S1 in Supporting Information). More details on the study plot and its floristic structure can be found in Gunatilleke & Gunatilleke (1981) and Gunatilleke *et al.* (2004a,b, 2006).

Soils in the high-elevation and hilltop areas of the Sinharaja forest plot have lower nutrient levels and are drier, shallower and more prone to desiccation compared with the lower elevation (valley) areas (Ashton & Berlyn 1992; Ashton, Gunatilleke & Gunatilleke 1995; Gunatilleke *et al.* 2006). Trees in the higher elevation slopes and ridges grow slower and are shorter than those in the valleys, and their roots ramify deeper to search water and nutrients (Ashton, Gunatilleke & Gunatilleke 1995; Gunatilleke *et al.* 2004a, 2006). As a consequence, higher elevation areas show smaller and fewer canopy gaps and lower light levels reach the ground (Gunatilleke *et al.* 2006). Several dominant canopy species (e.g. *Mesua nagassarium*, *Shorea affinis*, *Shorea disticha*) reach high densities and are mostly limited to the high-elevation and hilltop areas.

TREE DATA

We used tree data from two censuses. The first were measured during 1994–96 and the second during 1999–2003, where 207 and 219 co-occurring species and 205 332 and 211 090 individuals (d.b.h. ≥ 1 cm) were mapped, respectively. These included canopy species, sub-canopy species, understorey tree species, treelets/shrub species and liana species. We categorized all individuals of the two censuses into adults (d.b.h. ≥ 10 cm), juveniles (d.b.h. < 10 cm) and recruits (plants that appeared the first time in census 2). Adults and juveniles in the first census were represented by 16 907 (172 species) and 188 425 (206 species) individuals, and in the second census by 17 184 (177 species) and 193 906 (218 species) individuals, respectively. The number of new recruits in the second census was 11 123 (169 species).

TOPOGRAPHIC VARIABLES

In the main analysis, we divided the plot into 625 (20 m × 20 m) subplots, and for each subplot, we estimated six topographic variables: elevation, slope, aspect, terrain convexity, topographic wetness index (TWI) and altitude above channel (ACH) (Fig. 1). The topographic variables were derived using the Spatial Analyst Tools in ArcGIS 9.3 and SAGA GIS (for TWI and ACH). Elevation (m) is defined as the average elevation of the four corners of the 20-m square plot. Slope (°) is calculated by dividing each quadrat into four triangular planes such that each triangle is formed by joining three corners of the quadrat and taking the average angular deviation of these planes. Aspect is defined as compass direction to which the slope faces. Terrain convexity is the difference between mean elevation of the focal quadrat and the average elevation of eight neighbouring quadrats. The TWI is calculated as the ratio of the area upslope from any given point on the landscape to the local slope at that point and calculated using Tarboton's Deterministic Infinity Method (Tarboton 1997; Sørensen, Zinko & Seibert 2006; Kanagaraj *et al.* 2011). The ACH is the vertical distance from the channel network. Because we lack direct hydrological data, we included the two indices: TWI and ACH, which are commonly used to quantify topographical control on hydrological processes (Kanagaraj *et al.* 2011). This may allow us to capture important aspects of wetness. To determine the scaling properties of the topographic habitat-driven species assemblages, we calculated these six topographic variables also for 10 m × 10 m and 50 m × 50 m subplots that give 2500 small and 100 large subplots, respectively.

STATISTICAL METHODOLOGY

Multivariate regression tree

We used multivariate regression tree (MRT) techniques (De'ath 2002; Larsen & Speckman 2004) to group areas with similar species composition (i.e. species assemblages) according to environmental variables. Because aspect is a circular variable, we used in the MRT a transformation of aspect by sine and cosine (Legendre *et al.* 2009). MRT is basically a method of constrained clustering that determines clusters (in our case groups of quadrats) that are most similar in a certain measure of, for example, species dissimilarity (in our case the Bray–Curtis dissimilarity), with each cluster defined by threshold values of environmental variables (De'ath 2002). Each cluster defines a species assemblage, and the threshold values of environmental variables define an associated habitat type.

More specifically, the MRT is a recursive algorithm where the root node consists of all the quadrats. In our main analysis, quadrats are defined as 20-m square subplots in the 25-ha FDP; therefore, the root node consists of 625 quadrats (we also repeated the analysis for 10- and 50-m square subplots that yield 2500 and 100 quadrats, respectively). At each recursive level, an attempt is made to divide the quadrats in the parent node (N) into two child nodes, a 'left' node N_{left} and a 'right' node N_{right} , that minimize the species dissimilarity within the two child nodes (Larsen & Speckman 2004). Our topographic variables are all continuous, and hence all splits are of the form $N_{left} = \{i \in N: x_{ij} \leq t\}$, $N_{right} = \{i \in N: x_{ij} > t\}$ for threshold value t where the x_{ij} are the i th topographic variable in quadrat j . The algorithm performs putative splits for each threshold t and topographic variable x_i to find the combination that minimizes the Bray–Curtis dissimilarity index among all pairs of cells within the two child nodes (De'ath 2002; Legendre *et al.* 2009). The Bray–Curtis dissimilarity index between two quadrats j and k is defined as

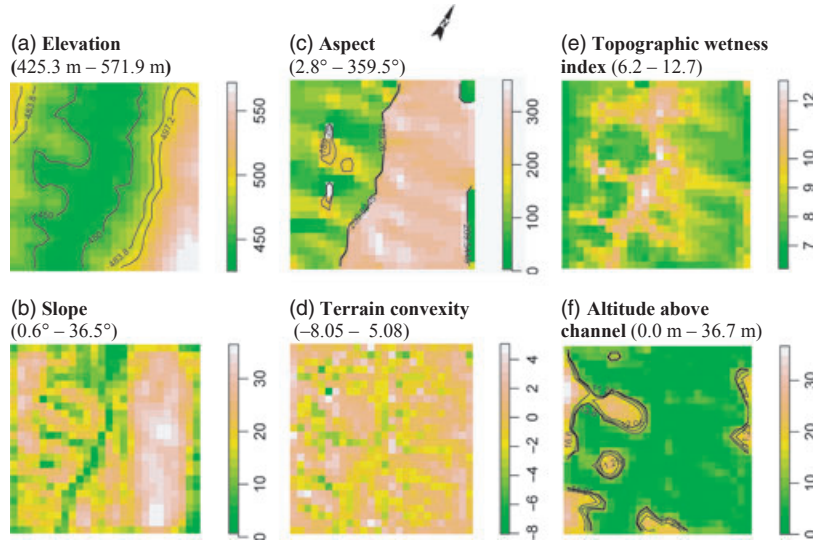


Fig. 1. The six topographic habitat variables elevation (range: 425.3–571.9 m), slope (range: 0.64–36.50°), aspect (range: 2.79°–359.53°), altitude above channel (ACH) (range: 0.0–36.7 m), topographic wetness index TWI (range: 6.2–12.7), and terrain convexity (range: –8.05–5.08) at the spatial resolution of 20 m × 20 m cell size. Contours in (a), (c), and (f) represent the threshold values [for elevation (E) = 483.8, 450 and 497.2 m, for aspect (A) = 209.54 and 189.26°, and for ACH = 16.6, 12.05 and 13.8] of multivariate regression tree (MRT) for adults, juvenile and recruit trees.

$\sum_i (y_{ij} - y_{ik}) / \sum_i (y_{ij} + y_{ik})$ where y_{ij} is the abundance of the i th species in quadrat j . The recursive partition occurs until a certain condition is met (Larsen & Speckman 2004). As this resulted in an exceptionally large tree that over-fits the data, we pruned the tree by removing successive pairs of child nodes that increase the deviance by a minimum. The best tree was selected as the tree with a minimum cross-validated relative error (CVRE) (Borcard, Gillet & Legendre 2011). The CVRE varies from 0 to 1 for the best to the worst predictor. MRT analysis was performed using the 'mvpart' package (De'ath 2006) built in R software (R Development Core Team. 2007).

Indicator species analysis

Because we defined habitats in the Sinharaja FDP based on species assemblages, it is interesting to explore which species are the most important ones (i.e. the indicator species) in defining the assemblages and which species constitute mostly 'noise'. Indicator species analysis (Dufrene & Legendre 1997) identifies the species that are for a given MRT analysis statistically significant indicators of the different habitat types (Legendre *et al.* 2009). The indicator value is calculated as the product of specificity and fidelity, and it varies between 0 and 1 (Roberts 2006). Specificity is defined as the mean abundance of the species in the target site group divided by the sum of the mean abundance values over all groups, and fidelity is the relative frequency of occurrence of the species inside the target site group (Dufrene & Legendre 1997). A species is assigned the maximum value of 1 if that species appears at all the sites of the particular group and does not appear in any other group. The minimum value of zero means that the species does not at all appear in the group. We defined a species as an indicator species if the indicator value is between 0.25 and 1.0. Strong indicator species have values between 0.5 and 1.0, and moderate indicator species have values between 0.25 and 0.50. Indicator values were computed using the 'labdsv' package (Roberts 2006) built in R software (R Development Core Team. 2007). We conducted indicator species analysis for each life stage and census.

Abundance and species richness

Abundance and species richness were defined as the total number of individuals per hectare and the number of species per hectare. They were calculated for each topographic habitat.

Unconstrained cluster analysis

Multivariate regression tree is a form of constrained clustering (De'ath 2002). In the MRT analysis, we used seven topographic variables as constraining variables to determine habitats with similar species composition. It is useful to compare the result of a MRT analysis with that of an unconstrained cluster analysis (De'ath 2002). If unconstrained cluster analysis explains more variance than MRT, the additional variance occurs due to important unobservable variables. Conversely, if MRT accounts for all important variables, it should explain approximately the same variance as unconstrained cluster analysis and the habitat classification of the two approaches should coincide. The K -means unconstrained cluster algorithm was used in this analysis (Legendre & Legendre 1998).

Topographic species assemblages at different scales

To determine the scaling effect on topographic habitat–species assemblages, we used the same MRT techniques, but the topographic variables and the species abundance were additionally measured at the 10- and 50-m quadrat sizes.

Species assemblages for all canopy, sub-canopy and understorey trees and individual strata

In the main analyses of different life stages (i.e. adults, juveniles, and recruits), a threshold of d.b.h. ≥ 10 cm was used to define the adult trees. However, treelets, shrubs and liana species frequently enter the adult stage at smaller sizes and are often very abundant. This may bias

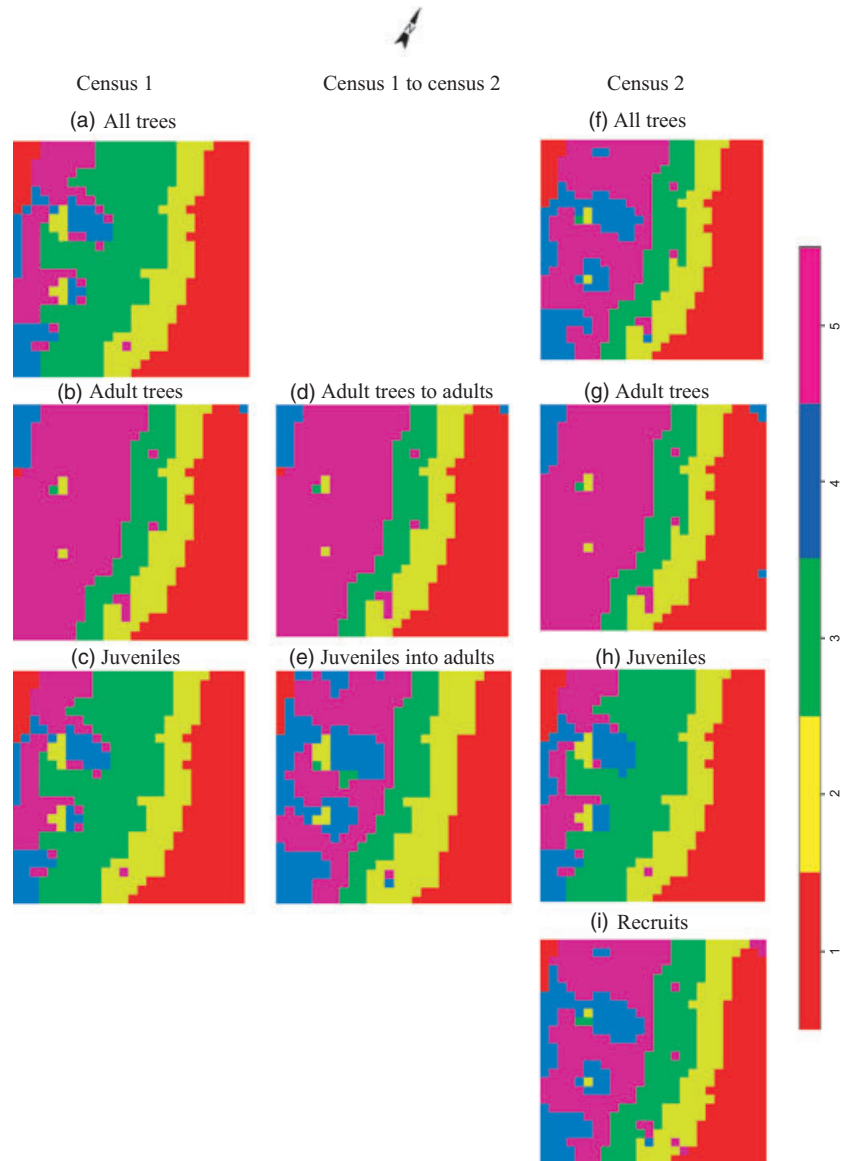


Fig. 2. Results of the multivariate regression tree analysis for the different life stages in the Sinharaja forest dynamic plot (FDP) in the two censuses (1994–96 and 1999–2003), based on the 20 m × 20 m quadrat size. The five topographic habitats are (1) high elevation (> 483 m a.s.l.; red), (2) SW mid elevation (yellow), (3) SW part of the valley (green), (4) NE low elevation with high altitude above channel (ACH) (blue), and (5) NE low elevation with low ACH (magenta). We conducted additional analyses for all adults surviving from the first to the second census (adult to adult, panel d) and for all juveniles which made the transition to adults (juvenile to adult, panel e).

our analysis. We therefore repeated our main analysis without the individuals belonging to the treelet/shrub and liana categories. Moreover, to explore whether canopy, sub-canopy and understorey species behave differently, we conducted separate analyses for each of these three categories.

Results

MULTIVARIATE REGRESSION TREE

The Sinharaja plot can be divided into five habitats (Fig. 2): (1) high-elevation (> 483 m a.s.l.), (2) SW mid-elevation, (3) SW part of the valley, (4) NE low elevation (< 483 m a.s.l.) with high ACH (NE hilltops) and (5) NE low elevation with low ACH of the plot (NE depressions). For both censuses, the CVRE errors of the MRTs were smallest at the juvenile stage, moderate at the adult stage and largest for the new recruits (Table 1, column: CVRE). Interestingly, the spatial

allocation of the different habitats was similar for all life stages. However, we noticed a homogenization in the transition from juveniles (Fig. 2c,h) to adults (Fig. 2b,d,g), where the NE hilltop habitat (type 4) almost disappeared in the adult stage. In contrast to recruits and adults, juveniles showed an expanded SW valley habitat (type 3) and a reduced NE depression habitat (type 5). We further observed that habitat change due to temporal variation was negligible (Fig. 2). To assess whether dynamic processes of growth and mortality also conform to these habitat types, we analysed the assemblages of adult trees separately that survived from the first to the second census (Fig. 2d; 15 356 individuals) and that of juveniles of the first census that became adults in the second census (Fig. 2e; 1387 individuals). Again, the same five habitat types emerged; however, the recent adults still conserved the NE hilltop habitat but already showed the expanded SW valley and the reduced NE depression habitat.

Table 1. Results of multivariate regression tree analysis and identified indicator tree species for all individual plants and those in the categories of adults, juveniles and recruits in the Simharaja 25-ha Forest Dynamics Plot, Sri Lanka

Life form	Year	Total no. stems	Total no. of stems in habitat	Total no. of species	No. of spp. habitat	CVRE	Habitat index	Breakpoints for group	No. of sites	Stems per ha	Species per ha	No. indi. species
All trees	2000	211 090	81 853	204	0.519	1	$E \geq 483.8$	202	10 130	25.25	15	
			27 797	185		2	$E < 483.8, A < (-0.4931), E \geq 451.6$	95	7315	48.68	4	
			22 586	188		3	$E < 483.8, A < (-0.4931), E < 451.6$	93	6071	50.54	1	
			29 320	177		4	$E < 483.8, A \geq (-0.4931), ACH \geq 12.05$	84	8726	52.68	7	
			49 534	206		5	$E < 483.8, A \geq (-0.4931), ACH < 12.05$	202	6130	25.50	20	
All trees	1996	205 332	77 036	195	0.507	1	$E \geq 483.8$	202	9534	24.13	14	
			31 411	181		2	$E < 483.8, E \geq 450, A < (-0.161)$	109	7204	41.51	5	
			55 728	197		3	$E < 483.8, E < 450$	224	6219	21.99	17	
			17 649	163		4	$E < 483.8, E \geq 450, A \geq (-0.161), ACH \geq 16.6$	52	8485	78.37	7	
			23 508	176		5	$E < 483.8, E \geq 450, A \geq (-0.161), ACH < 16.6$	89	6603	49.44	5	
Adults	2000	17 184	4605	115	0.668	1	$E \geq 483.8, A < 0.5927$	181	636	15.88	5	
			2550	104		2	$E < 483.8, A < (-0.4931), E \geq 451.6$	95	671	27.37	1	
			2454	126		3	$E < 483.8, A < (-0.4931), E < 451.6$	93	660	33.87	0	
			567	81		4	$E \geq 483.8, A \geq 0.5927$	21	675	96.43	1	
			7008	144		5	$E < 483.8, A \geq (-0.4931)$	286	613	12.59	0	
Adults	1996	16 907	4636	114	0.667	1	$E \geq 483.8, A < 0.7332$	185	626	15.41	5	
			2579	109		2	$E < 483.8, A < (-0.4931), E \geq 451.4$	96	672	28.39	1	
			2488	121		3	$E < 483.8, A < (-0.4931), E < 451.4$	92	676	32.88	0	
			444	62		4	$E \geq 483.8, A \geq 0.7332$	17	653	91.18	2	
			6760	143		5	$E < 483.8, A \geq (-0.4931)$	286	591	12.50	0	
Juveniles	2000	193 906	76 681	196	0.526	1	$E \geq 483.8$	202	9490	24.26	13	
			29 133	185		2	$E < 483.8, E \geq 450, A < (-0.161)$	109	6682	42.43	4	
			49 003	202		3	$E < 483.8, E < 450$	224	5469	22.54	4	
			20 816	169		4	$E < 483.8, E \geq 450, A \geq (-0.161), ACH \geq 13.8$	64	8131	66.02	4	
			18 273	177		5	$E < 483.8, E \geq 450, A \geq (-0.161), ACH < 13.8$	77	5933	57.47	14	
Juveniles	1996	188 425	71 956	189	0.511	1	$E \geq 483.8$	202	8905	23.39	14	
			28 462	178		2	$E < 483.8, E \geq 450, A < (-0.161)$	109	6528	40.83	4	
			50 234	193		3	$E < 483.8, E \geq 450, A \geq (-0.161), ACH \geq 16.6$	224	5606	21.54	13	
			16 334	162		4	$E < 483.8, E \geq 450, A \geq (-0.161), ACH < 16.6$	52	7853	77.88	5	
			21 439	171		5	$E < 483.8, E < 450$	89	6022	48.03	4	
Recruits	2000	11 123	3543	105	0.828	1	$E \geq 497.2$	153	579	17.16	6	
			1891	84		2	$E < 497.2, A < (-0.4931), E \geq 460.6$	100	473	21.00	0	
			1731	92		3	$E < 497.2, A < (-0.4931), E < 460.6$	123	352	18.70	0	
			1228	99		4	$E < 497.2, A \geq (-0.4931), ACH \geq 11.25$	97	316	25.52	0	
			2730	148		5	$E < 497.2, A \geq (-0.4931), ACH < 11.25$	203	336	18.23	1	

No. of spp. habitat, number of species in a habitat; CVRE, cross validated relative error; E , elevation; A , sin (aspect); TWI, topographic wetness index; C , convexity; S , slope; ACH, altitude above channel; no. of sites: number of 20 m × 20 m cells; no. indi. species, number of indicator species.

Table 2. Percentage of species variation explained from two components for juveniles, adults, recruits and all trees at three different spatial scales (10, 20 and 50 m)

Variance explained in census 2 by	Juveniles			Adults			Recruits			All trees		
	10 m	20 m	50 m	10 m	20 m	50 m	10 m	20 m	50 m	10 m	20 m	50 m
MRT	15.26	21.95	32.08	6.75	16.33	30.41	2.96	10.38	34.81	16.03	22.73	33.38
Unexplained by MRT	84.74	78.05	67.92	93.25	83.67	69.59	97.04	89.62	65.19	83.97	77.27	66.62

MRT, multivariate regression tree.

The habitat types were mainly determined by the three topographic variables: elevation, aspect and ACH (Table 1, column: Breakpoints for groups). For all life stages, elevation was the basic split (Table 1, column: Breakpoints for groups) for habitat separation and it explained 10–13% of total species variance, and the species variation explained by the MRT was maximal at the juvenile stage. Aspect and ACH were the second and fourth splits of habitat separation in every life stage in both censuses. Most of the area in Sinharaja FDP for adult trees was covered by NE depressions habitat (42%) and high-elevation habitat (28%). Interestingly, for juvenile trees, most of the area was covered by SW valley habitat (33%) and high-elevation habitat (30%).

The total species variance of the second census explained by the MRT at the adult, juvenile and recruitment stages were approximately 16%, 23% and 10%, respectively (Table 2 and see Tables S2.5, S2.6, S2.7). Eighty-three per cent of total species variance of the juvenile stage was explained by the species *Agrostistachys hookeri*, *Humboldtia laurifolia*, *Agrostistachys intramarginalis*, *M. nagassarium*, *Mesua ferrea*, *Shorea worthingtonii* and *S. disticha* (see Tables S2.3, 2.6). In the adult stage, 64% of the total species variance was explained by *M. nagassarium*, *Garcinia hermonii*, *Cullenia ceylanica*, *Shorea trapezifolia*, *A. hookeri*, *S. disticha* and *S. worthingtonii* (see Tables S2.3, 2.5).

INDICATOR SPECIES ANALYSIS

The different life stages showed different numbers of indicator species. In the first and second census, the number of indicator species for adults was found to be seven and eight and for juveniles 39 and 40 species, respectively; for recruits in the second census, the corresponding result was seven indicator species (see Fig. S6). Interestingly, only juveniles showed strong indicator species in both censuses (four species; see Tables S3.2, 3.4), and all of them were associated with the high-elevation habitat (see Tables S3.2, 3.4; Fig. 3). Notably, almost all the indicator species for juveniles from the first census were also indicator species in the second census, and no indicator species switched habitats. The indicator species of adults coincided between censuses and did not switch habitats.

Among recruits, almost all the indicator species were associated with the high-elevation habitat (see Table S3.5). Further, we found that strong or moderate indicator species within juveniles changed to either non-indicator species or moderate indicator species as adults.

VARIATIONS IN ABUNDANCE AND SPECIES RICHNESS AMONG HABITATS

The different habitats showed up to twofold differences in juvenile and recruit densities. The two habitat types with highest abundances were the high-elevation habitat 1 and habitat 4 (NE hilltops) with approximately 9000 and 8000 juveniles ha^{-1} , respectively. Remarkably, the adult density did not vary much among habitat types and was approximately 650 individuals ha^{-1} (Table 1).

UNCONSTRAINED CLUSTER ANALYSIS

Unconstrained *K*-means cluster analysis explained approximately 41%, 56% and 62% of the species variances of adult trees, juvenile trees and recruits, respectively (Table 2). Also *K*-means cluster analysis (see Fig. S7) with five groups (i.e. five habitats) always yielded a substantially reduced relative error compared to MRT. In general, unconstrained clustering detected the high-elevation habitat and the hilltops, but not the topographic gradient revealed by the MRT analyses.

TOPOGRAPHIC SPECIES ASSEMBLAGES AT DIFFERENT SCALES

Variation in all trees explained by the environmental component increased with scale (10 m: 16%, 20 m: 23%, and 50 m: 33%; Table 2). The unexplained species variation decreased from fine to broad scales (10 m: 84%, 20 m: 77% and 50 m: 67%). The emerging topographic habitats were similar across all scales investigated (Fig. 2, see Figs S9 and S11).

SPECIES ASSEMBLAGES WITHOUT LIANA AND TREELETS, AND OF INDIVIDUAL STRATA

Excluding liana and treelets had no influence on the topographic habitats (cf. Fig. 2 and see Fig. S2). Also, the results of separate analyses for canopy trees (see Fig. S3), sub-canopy trees (see Fig. S4) and understorey trees (see Fig. S5) were similar to the spatial arrangement of the habitats emerging for all life forms.

Discussion

Use of MRT analysis showed that the Sinharaja FDP is topographically strongly structured into five habitats related

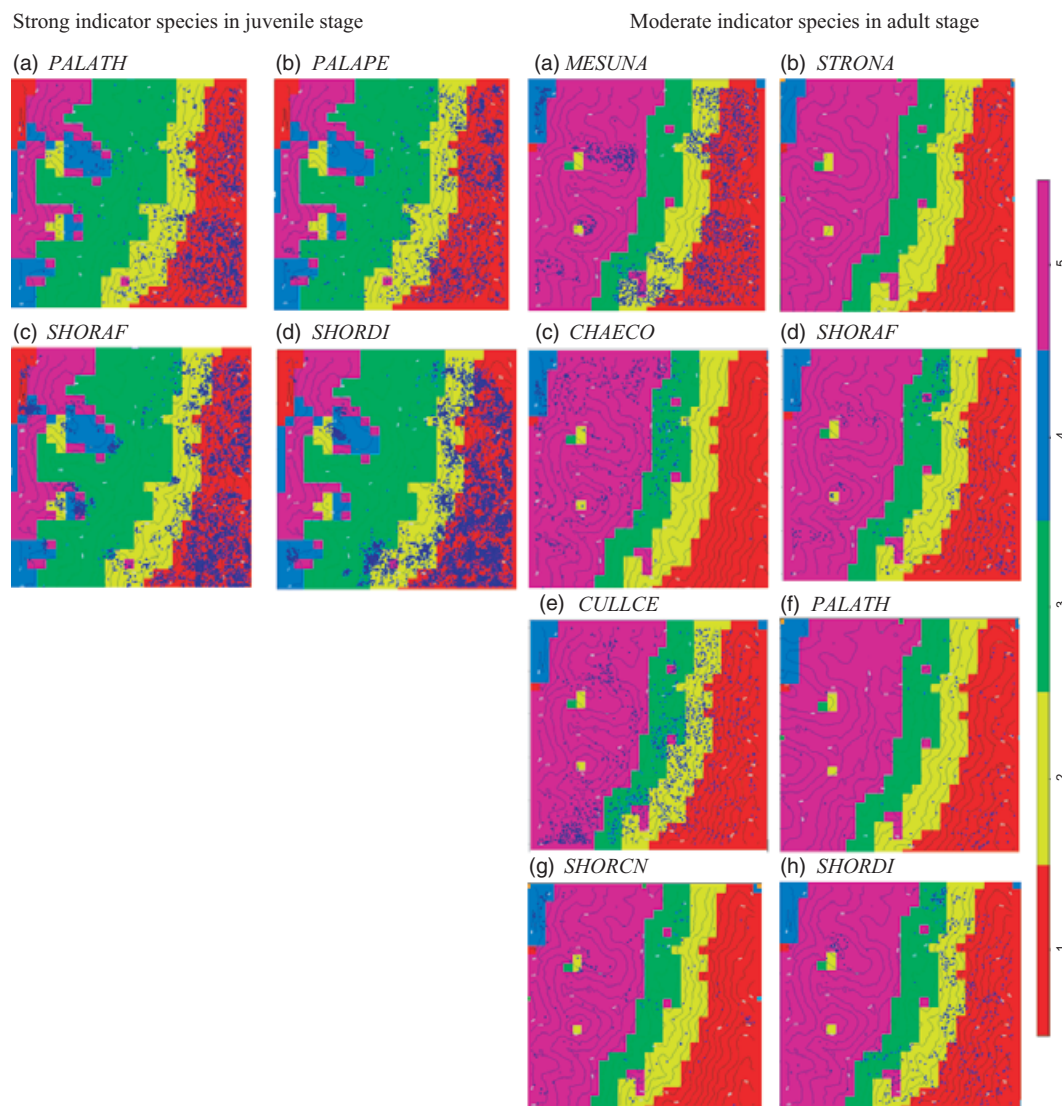


Fig. 3. Habitat fidelity of indicator species. Four strong indicator species (with indicator values > 0.5) are shown for the juvenile stage (left to right): *Palaquium thwaitesii* (PALATH), *Palaquium petiolare* (PALAPE), *Shorea affinis* (SHORAF), and *Shorea disticha* (SHORDI). Eight moderate indicator species (with indicator values ranging between 0.25 and 0.5) are shown for the adult stage (left to right): *Mesua nagassarum* (MESUNA), *Strombosia nana* (STRONA), *Chaetocarpus coriaceus* (CHAECO), *S. affinis* (SHORAF), *Cullenia ceylanica* (CULLCE), *Palaquium thwaitesii* (PALATH), *Shorea congestiflora* (SHORCN), and *S. disticha* (SHORDI). The five topographic habitats are (1) high elevation (> 483 m a.s.l.; red), (2) SW mid elevation (yellow), (3) SW part of the valley (green), (4) NE low elevation with high altitude above channel (ACH) (blue) and (5) NE low elevation with low ACH (magenta).

to ridge-valley gradients and a pronounced contrast in its south-west versus north-east aspect. We found that the topographic habitat types did not change with life stage, growth form or spatial scale. Although we expected that topographic habitat types would not vary with life stages, the strength of this outcome was unexpected given the recent evidence for shifts in habitat association with life stages (e.g. Webb & Peart 2000; Comita, Condit & Hubbell 2007; Lai *et al.* 2009; Kanagaraj *et al.* 2011). Recruits at Sinharaja showed a much higher habitat structuring compared to those at BCI. This may indicate that habitat filtering at Sinharaja was stronger at early life stages, that Sinharaja showed stronger

dispersal limitation (which forces the majority of recruits to establish in the same habitats as adults) or that recruitment was more stochastic at BCI. However, although the variance in local species composition explained by MRT was clearly larger than at BCI, it did not exceed 25% and was dependent on life stage and spatial scale. Although we observed distinct species assemblages, only few species were confined to individual habitats but rather showed different densities among habitats. This indicates that stochastic effects or other spatially structured processes such as dispersal limitation may also play a prominent role in structuring the Sinharaja forest.

TOPOGRAPHIC HABITAT TYPES AT SINHARAJA

We found three topographic elements that were responsible for the habitat structuring at the Sinharaja plot: high versus lower elevation, SW versus NE aspect, and NE local hilltops in the lower elevation area. First, elevation separated a high-elevation habitat (i.e. habitat 1) from the rest. The consistent emergence of the high-elevation habitat with a threshold of 483 m in all analyses (Table 1) can be explained by distinct changes in microenvironmental conditions and forest structure along the elevational gradient of the plot (see section 'Study site') which create at the higher elevation areas habitat conditions very different from the rest of the plot, as indicated by the four strong indicator species in the juvenile stage and the five indicator species in the adult stage. Habitat conditions at the high-elevation habitat are apparently well suited for slow growing canopy tree species such as *M. nagassarium* or *S. disticha* which reach high juvenile and adult densities in this habitat. The high-elevation habitat shows higher tree densities (slightly higher canopy tree densities and remarkably greater juvenile densities) and basal area per unit area, compared to low-elevation habitats. Slope instability and greater uprooting on such inclination in valley sites may partly cause this decrease in abundances along the slope (Ashton, Gunatilleke & Gunatilleke 1995; Gale 2000; Sukri *et al.* 2011).

The second structuring topographic element was aspect. The study plot is basically divided into two areas: one with SW orientation and one with NE orientation (Fig. 1c and see Fig. S1). We were somewhat surprised by the strong impact of aspect on species assemblages. The SW versus NE orientation may create differences in availability of irradiance at ground level among these two areas and different microclimates, but further research is required to confirm this hypothesis. Given the distinct changes in microenvironmental conditions and forest structure along the elevational gradient, it is not surprising that the SW slopes subdivide into three habitats, the high-elevation habitat (1), the SW mid-elevation habitat (2) and the SW part of the valley (3). The lower density of juveniles at lower elevations may be related to increased wetness in the valley areas (Fig. 1e). It may also be partly due to intense competition from the dense growth of herbaceous and semi-woody species (such as *Strobilanthes* and *Coleus* spp.) in the larger gaps and along the perennial streams within the plot which fall below the census diameter limit. Damage by water flow during intense rainfall or the high chance of bacterial or fungal attacks in wetter micro-sites can have a negative effect on survival of juveniles and cause lower densities in the valley (Daws *et al.* 2005; Comita, Condit & Hubbell 2007). Frequent disturbances from falling trees in valleys may also contribute to the observed lower juvenile densities in the valley habitat (Ashton, Gunatilleke & Gunatilleke 1995).

The greater light heterogeneity at the low-elevation habitat (3), caused by more frequent disturbances such as falling trees, facilitates a wide range of species with different light requirements (Ashton 1992; Gunatilleke *et al.* 2006), and this results in higher total species richness in this low-elevation habitat despite its smaller area. The emergence of the SW mid-eleva-

tion habitat may be related to small landslides following consecutive days of intense rainfall. Such disturbed habitats facilitate fast-growing species, with a high shoot/root ratio. These species grow taller than species found at the high-elevation and ridge top habitats (Ashton, Gunatilleke & Gunatilleke 1995). Finally, the part of the plot with NE orientation is separated into two habitats: the NE low elevation with high ACH of the plot (NE hilltops; habitat 4) and the NE low elevations with low ACH (NE depressions; habitat 5) which are best separated by the variable 'ACH'. The NE hilltops show a similar juvenile density to that at SW high-elevation habitat, but host more than triple the species richness (NE hilltops: 78 species ha⁻¹, SW high elevation: 23 species ha⁻¹).

Our habitat classification differs from that of an earlier study by Gunatilleke *et al.* (2006), which was not based on statistical analysis, but a plausible *a priori* classification into eight habitats defined by thresholds in elevation, slope and convexity. While we confirmed the overarching importance of elevation, our analysis did not support the importance of convexity and slope, but points rather to the importance of aspect, that is, a SW-NE contrast.

We noticed that most of the species were not limited to a single habitat but rather changed in abundance. As a consequence, only few species reached high indicator values and the CVRE were relatively high in all life stages (0.5–0.83), but still substantially lower than those found at BCI (Kanagaraj *et al.* 2011). Most indicator species were related to the high-elevation habitat. For example, *M. nagassarium*, the most abundant canopy species had the highest indicator value associated with the high-elevation habitat at the adult stage (0.40). This species has the ability to grow under low soil water (Ashton, Gunatilleke & Gunatilleke 1995). The species, *S. worthingtonii*, a shade and drought tolerant species (Ashton & Berlyn 1992), was the second strongest indicator species (0.29) in the adult stage and was also associated with high-elevation habitats.

Multivariate regression tree analysis justified five different habitats in our study. This is similar to the number of habitats identified for the 24-ha Gutianshan FDP in China (Legendre *et al.* 2009) and the 25-ha plot of Yasuni in Amazonia, Ecuador (Valencia *et al.* 2004). The habitats at Sinharaja were situated along ridge-valley gradients (catenas). This is not surprising because catenas are fundamental in plant ecology (e.g., Gartlan *et al.* 1986; Tuomisto *et al.* 1995; Svenning 1999; Webb & Peart 2000; Valencia *et al.* 2004). However, topography may not provide substantially more than five habitats, and these by far do not account for the coexistence of hundreds of species within small areas of tropical forests. For example, in the hyperdiverse Amazonian rain forests, Valencia *et al.* (2004) could justify only three habitat types, although they initially assumed five.

HABITATS DO NOT CHANGE WITH TREE SIZE, TIME OR GROWTH FORM

One striking result of our analysis is that the emerging habitat types were virtually the same for all life stages (recruits, juve-

niles, and adult trees) and for separate analyses of canopy, sub-canopy and understorey trees. This result is in sharp contrast to an analogous analysis for the BCI forest (Kanagaraj *et al.* 2011), which showed weaker structuring into topographic habitats, strong differences among life stages, a homogenization in species assembly from juveniles to adults and overall more 'noise' in species assemblages. All these results support the view that topographic habitats were more important for the emergence of species assemblages at Sinharaja, but that habitat independence was more important at BCI. The pronounced difference in topographic structures between the two plots (e.g. elevation difference at BCI = 40 m vs. 151 m at Sinharaja) may explain these findings, but studies in other tropical forests with pronounced topographic structure are needed to confirm this hypothesis.

Interestingly, the noise in the regression tree analysis for recruits was quite low at Sinharaja (CVRE = 0.83) compared to a CVRE of 0.97 at BCI although overall recruit densities were similar (444 ha⁻¹ at Sinharaja and 400–740 ha⁻¹ at BCI, depending on the census). This result points to stronger habitat filtering of the earliest life stage at Sinharaja compared to BCI. The strong decrease in the noise in the regression tree analysis from recruits (CVRE = 0.83) to juveniles (CVRE = 0.51) indicates habitat filtering at the juvenile stage, but the larger values for adults (CVRE = 0.67), and loss of substantial number of indicator species, suggest that juveniles in optimal habitat experienced negative density-dependent mortality not related with habitat which weakened their habitat association. Stochastic effects may additionally contribute to the smaller CVRE error of juveniles compared with adults. The mean number of individuals in 20 m × 20 m quadrats was more than 10 times larger for juveniles which should yield a larger impact of chance events for adults. This effect may be stipulated by stochastic outcomes of local neighbourhood exclusion of competing species.

Although the CVRE error for adult species assemblages was larger than that of juveniles, the habitats remained relatively stable (cf. Fig. 2b,c,g,h); only the NE hilltop habitat shrunk and the SW valley habitat somewhat expanded. The constancy in habitats may be partly explained by the dispersal limitation of most of the dominant species in Sinharaja forest plot where seeds fall near parent trees (e.g. *M. ferrea*, *M. nagassarium*, *S. affinis*, *Shorea congestiflora*, *Shorea cordifolia*, *S. disticha*, *Shorea megistophylla*, *S. trapezifolia*, *S. worthingtonii*, *A. hookeri*, *A. intramarginalis*). This may cause the mass of juveniles to be distributed within the same habitat as adults (Ribbens, Silander & Pacala 1994; Hubbell *et al.* 1999; Webb & Peart 2000). However, this does not exclude the possibility that individual species may show ontogenetic shifts in resource requirements, for example as a result of changes in physiological requirements or selective pressures (Werner & Gilliam 1984; Clark & Clark 1992; Lai *et al.* 2009). This may partly explain the change of strong indicator species into moderate or non-indicators from juveniles to adult stage. Nevertheless, a notable result is that despite some variability at the species level, habitats at the community level were stable.

Our analysis showed that dynamic transitions between life stages from one census to the next (i.e. transition of juveniles to adults, and recruitment) and survival of adults followed the same habitat structure as the static snap shots. Nevertheless, data on longer time periods are required to make firm conclusions about temporal shifts in habitat assemblages. Due to the low mortality and growth of trees in Sinharaja FDP, species assemblages may not change dramatically between two censuses (Condit *et al.* 2006).

COMMUNITY ASSEMBLY MECHANISMS

The MRT analysis based on topographic variables explained 22% of the variance in species composition for juveniles and approximately 16% each for adults and recruits and most indicator species did not reach high indicator values (i.e. few species occur predominantly in a single habitat). This indicates that although there was a strong signal of topographic structuring, it explained only one-fourth of the variance in species composition within 20 m × 20 m quadrats. This may be an underestimation because our topographic variables may not have been measured at a fine enough scale to fully capture the underlying variation in biotic conditions, edaphic and/or light resources. For example, studies from Borneo lowland tropical rainforests have shown that edaphic variables can be very influential in structuring plant communities (Potts *et al.* 2002; Phillips *et al.* 2003; Paoli, Curran & Zak 2006; John *et al.* 2007; Sukri *et al.* 2011). Thus, inclusion of soil moisture, soil nutrients or light environment (Sollins 1998; Daws *et al.* 2002; Phillips *et al.* 2003; John *et al.* 2007) may capture more of the species variation.

It is difficult to assess how much of the environmental drivers were missed out by the six topographic variables used in our analysis. However, unconstrained cluster analysis that did not consider any topographic variable explicitly detected also three of the five habitats revealed by the MRT (i.e. the high-elevation habitat, the NE depressions and the NE hilltops), but not the fine structuring with elevation (i.e. SW mid elevation and SW valley). This suggests that our variables are reasonably good proxies for the underlying environmental variability.

We suspect that a large proportion of the unexplained variance should be due to processes such as dispersal limitation that create spatial structures independent of (or superimposed on) habitat or stochasticity. The latter is supported by the finding that the percentage of variation explained by topography increased with increasing scale (unexplained variation, 10 m: 84%, 20 m: 77% and 50 m: 67%) and that even with *K*-mean clustering, a considerable proportion of variance remained unexplained. One 10 m × 10 m quadrat contained on average 87 trees, but a 50 m × 50 m quadrat 542 trees. Larger quadrats therefore gloss over stochasticity in species composition and abundance at small quadrat sizes and explain therefore more variability. However, this works only up to a scale where the quadrat becomes too large to represent only one habitat type.

Conclusions

Our analysis provides indications on the relative importance of topographic habitat factors in structuring local species composition in a tropical forest. We found that 25% of the species variance was due to topographic habitat association. This outcome is somewhat surprising because the distinct topographic structuring of the plot let us expect a stronger impact of habitat-associated effects in shaping local species assemblages in this tropical forest. While unaccounted environmental variables could contribute to the unexplained species variance, our results suggest that stochastic effects and spatially structured processes such as dispersal limitation may also have a substantial contribution and that local species assemblages at Sinharaja forest may be jointly shaped by both neutral and niche processes. Little is known on the relative importance of topographic habitat factors in structuring local species composition in a tropical forest. Our results therefore provide important information on this issue, but raised also a number of open questions that call for similar studies in other tropical forest sites.

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References

Ahmad, W.J.W. (2001) *Habitat specialisation of tree species in a Malaysian tropical rain forest*. Dissertation. University of Aberdeen, Aberdeen, UK.

Ashton, P.M.S. (1992) Some measurements of the micro-climate within a Sri Lankan tropical rain forest. *Agricultural and Forest Meteorology*, **59**, 217–235.

Ashton, P.M.S. & Berlyn, G.P. (1992) Leaf adaptations of some *Shorea* species to sun and shade. *New Phytologist*, **121**, 587–596.

Ashton, P.M.S., Gunatilleke, I.A.U.N. & Gunatilleke, C.V.S. (1995) Seedling survival and growth of four *Shorea* species in a Sri Lankan rain forest. *Journal of Tropical Ecology*, **11**, 263–279.

Borcard, D., Gillet, F. & Legendre, P. (2011) *Numerical Ecology with R*. Use R! series. Springer, NY.

Cheng, J., Mi, X., Nadrowski, K., Ren, H., Zhang, J. & Ma, K. (2012) Separating the effect of mechanisms shaping species-abundance distributions at multiple scales in a subtropical forest. *Oikos*, **121**, 236–244.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.

Clark, D.A. & Clark, D.B. (1992) Life-history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*, **62**, 315–344.

Comita, L.S., Condit, R. & Hubbell, S.P. (2007) Developmental changes in habitat associations of tropical trees. *Journal of Ecology*, **95**, 482–492.

Condit, R., Ashton, P., Bunyavechewin, S., Dattaraja, H.S., Davies, S., Esufali, S. *et al.* (2006) The importance of demographic niches to tree diversity. *Science*, **313**, 98–101.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Crawley, M.J. & Harral, J.E. (2001) Scale dependence in plant biodiversity. *Science*, **291**, 864–868.

Daws, M.I., Mullins, C., Burslem, D., Paton, R. & Dalling, J. (2002) Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil*, **238**, 79–90.

Daws, M.I., Pearson, T.R.H., Burslem, D., Mullins, C.E. & Dalling, J.W. (2005) Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panama. *Plant Ecology*, **179**, 93–105.

De'ath, G. (2002) Multivariate regression trees: a new technique for modeling species–environment relationships. *Ecology*, **83**, 1105–1117.

De'ath, G. (2006) mvpart: multivariate partitioning. R package version 1.2.4. <http://cran.r-project.org/>.

Denslow, J.S. (1980) Gap partitioning among tropical rainforest trees. *Biotropica*, **12**(Supplement), 47–55.

Dufrène, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.

Gale, N. (2000) The aftermath of tree death: coarse woody debris and the topography in four tropical rain forests. *Canadian Journal of Forest Research*, **30**, 1489–1493.

Gartlan, J.S., Newbery, D.M., Thomas, D.W. & Waterman, P.G. (1986) The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve Cameroon. *Vegetatio*, **65**, 131–148.

Gause, G.F. (1934) *The Struggle for Existence*. Williams and Wilkins, Baltimore, MD.

Gentry, A.H. (1988) Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the USA*, **85**, 156–159.

Gibbons, J.M. & Newbery, D.M. (2002) Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. *Plant Ecology*, **164**, 1–18.

Grubb, P.J. (1977) Maintenance of species-richness in plant communities – importance of regeneration niche. *Biology Reviews of the Cambridge Philosophical Society*, **52**, 107–145.

Gunatilleke, C.V.S. & Gunatilleke, I.A.U.N. (1981) The floristic composition of Sinharaja – a rain forest in Sri Lanka with special reference to endemics. *Malaysian Forester*, **44**, 386–396.

Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Ashton, P.S., Ethugala, A.U.K., Weerasekara, N.S. & Esufali, S. (2004a) Sinharaja forest dynamics plot, Sri Lanka. *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network* (eds E.C. Losos & E.G. Leigh), pp. 599–608. The University of Chicago Press, Chicago, IL.

Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Ethugala, A.U.K. & Esufali, E. (2004b) *Ecology of Sinharaja Rain Forest and the Forest Dynamics Plot in Sri Lanka's Natural World Heritage Site*. WHT Publications (Pvt) Ltd, Colombo, Sri Lanka.

Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Esufali, S., Harms, K.E., Ashton, P.M.S., Burslem, D.F.R.P. & Ashton, P.S. (2006) Species–habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology*, **22**, 371–384.

Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, **89**, 947–959.

Hubbell, S.P. (2001) *Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & de Lao, S.L. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.

Hutchinson, G.E. (1961) The paradox of the plankton. *American Naturalist*, **95**, 137–145.

John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M. & Foster, R.B. (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the USA*, **104**, 864–869.

Kanagaraj, R., Wiegand, T., Comita, L.S. & Huth, A. (2011) Tropical tree species assemblages in topographical habitats change in time and with life stage. *Journal of Ecology*, **99**, 1441–1452.

Kitajima, K. & Fenner, M. (2000) Seedling regeneration ecology. *Seeds: Ecology of Regeneration in Plant Communities*, 2nd edn (ed. M. Fenner), pp. 331–360. CAB International, Wallingford, UK.

Kohyama, T. & Takada, T. (2009) The stratification theory for plant coexistence promoted by one-sided competition. *Journal of Ecology*, **97**, 463–471.

- Lai, J.S., Mi, X.C., Ren, H.B. & Ma, K.P. (2009) Species-habitat associations change in a subtropical forest of China. *Journal of Vegetation Science*, **20**, 415–423.
- Laliberté, E., Paquette, A., Legendre, P. & Bouchard, A. (2009) Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. *Oecologia*, **159**, 377–388.
- Larsen, D.R. & Speckman, P.L. (2004) Multivariate regression trees for analysis of abundance data. *Biometrics*, **60**, 543–549.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. Second English edition. Elsevier, Amsterdam, the Netherlands.
- Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I. & He, F. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, **90**, 663–674.
- Leibold, M.A. & Norberg, J. (2004) Biodiversity in metacommunities: plankton as complex adaptive systems? *Limnology and Oceanography*, **49**, 1278–1289.
- MacArthur, R.H. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, **101**, 377–385.
- McGill, B.J. (2003) A test of the unified neutral theory of biodiversity. *Nature*, **422**, 881–885.
- Paoli, G.D., Curran, L.M. & Zak, D.R. (2006) Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology*, **94**, 157–170.
- Phillips, O.L., Vargas, P.N., Monteagudo, A.L., Cruz, A.P., Zans, M.C., Sánchez, W.G., Yli-halla, M. & Rose, S. (2003) Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology*, **91**, 757–775.
- Pitman, N.C.A., Terborgh, J., Silman, M.R. & Nuñez, P.V. (1999) Tree species distributions in an upper Amazonian forest. *Ecology*, **80**, 2651–2661.
- Poorter, L., Bongers, F., Sterck, F.J. & Woll, H. (2005) Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology*, **93**, 256–267.
- Potts, M.D., Ashton, P.S., Kaufman, L.S. & Plotkin, J.B. (2002) Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology*, **83**, 2782–2797.
- R Development Core Team. (2007) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Ribbens, E., Silander Jr, J.A. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Roberts, D.W. (2006) *labdsv: Laboratory for Dynamic Synthetic Vegetation Phenomenology*. R package version 1.2-2. <http://ecology.msu.montana.edu/labdsv/R>.
- Sollins, P. (1998) Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology*, **79**, 23–30.
- Sørensen, R., Zinko, U. & Seibert, J. (2006) On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth System Sciences*, **10**, 101–112.
- Sterck, F.J., Poorter, L. & Schieving, F. (2006) Leaf traits determine the growth-survival trade-off across rain forest tree species. *American Naturalist*, **167**, 758–765.
- Sugihara, G., Bersier, L.F., Southwood, R.E., Pimm, S.L. & May, R.M. (2003) Predicted correspondence between species abundances and dendrograms of niche similarities. *Proceedings of the National Academy of Sciences of the USA*, **100**, 5246–5251.
- Sukri, R.S., Wahab, R.A., Salim, K.A. & Burslem, D.F.R.P. (2011) Habitat associations and community structure of dipterocarps in response to environment and soil conditions in Brunei Darussalam, Northwest Borneo. *Biotropica*, **44**, 595–605.
- Svenning, J.C. (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology*, **87**, 55–65.
- Tarboton, D.G. (1997) A new method for determination of flow directions and upslope areas in grid digital elevation models. *Water Resource Research*, **33**, 309–319.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the USA*, **101**, 10854–10861.
- Tuomisto, H., Ruokolainen, K., Kalliola, R., Linna, A., Danjoy, W. & Rodríguez, Z. (1995) Dissecting Amazonian biodiversity. *Science*, **269**, 63–66.
- Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J.C., Hernández, C., Romoleroux, K., Losos, E., Magård, E. & Balslev, H. (2004) Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology*, **92**, 214–229.
- Webb, C.O. & Peart, D.R. (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, **88**, 464–478.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, **15**, 393–425.
- Whittaker, R.H. (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs*, **26**, 1–80.
- Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of Sinharaja forest dynamic plot.

Figure S2–S5. Structure of species assemblages of different growth forms (canopy, sub-canopy and understorey) for different life stages at 20 m spatial scale.

Figure S6. Number of indicator species for five topographic habitats in census 1 and 2 in different life stages.

Figure S7. Complete linkage and *K*-mean cluster analysis for different life stages of two censuses.

Figure S8. Multivariate regression tree analysis of different life stages for census 1 and 2 at 20 m spatial scale.

Figure S9. Structure of species assemblages for different life stages at 10 m spatial scale.

Figure S10. Structure of species assemblages and species richness for different life stages at 20 m spatial scale.

Figure S11. Structure of species assemblages for different life stages at 50 m spatial scale.

Table S1. Results of multivariate regression tree analysis and identified indicator species for the all canopy plants in different life stages.

Table S2. Variation of species composition explained by multivariate regression tree for different life stages in census 1 and 2.

Table S3. Indicator species analysis.