

# Effect of spatial processes and topography on structuring species assemblages in a Sri Lankan dipterocarp forest

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**Abstract.** Niche and neutral theories emphasize different processes that contribute to the maintenance of species diversity and should leave different spatial structures in species assemblages. In this study we used variation partitioning in combination with distance-based Moran's eigenvector maps and habitat variables to determine the relative importance of the effects of pure habitat, pure spatial, and spatially structured habitat processes on the spatial distribution of tree species composition and richness in a 25-ha tropical rain forest of Sinharaja/Sri Lanka. We analyzed the contribution of those components at three spatial scales (10 m, 20 m, and 50 m) for all trees and the three life stages: recruits, juveniles, and adults. At the 10-m scale, 80% of the variation in species composition remained unexplained for recruits and adults, but only 55% for juveniles. With increasingly broader scales these figures were strongly reduced, mainly by an increasing contribution of the spatially structured habitat component, which explained 4–30%, 20–47%, and 8–35% of variation in species composition for recruits, juveniles, and adults, respectively. The pure spatial component was most important at the 20-m scale and reached 20%, 32%, and 23% for recruits, juveniles, and adults, respectively. The spatially structured habitat component described variability at broader scales than the pure spatial component. Our results suggest that stochastic processes and spatially structuring processes of community dynamics, such as dispersal limitation and habitat association, contributed jointly to explain species composition and richness at the Sinharaja forest, but their relative importance changed with scale and life stage. Species assembly at the local scale was more strongly impacted by stochasticity, whereas the signal of habitat was stronger at the 50-m scale where plant-scale stochasticity is averaged out. Recent research points to an emerging consensus on the relative contribution of stochasticity, habitat, and spatial processes in governing community assembly, but how these components change with life stage, and how this is influenced by sample size, remains to be explored.

**Key words:** distance-based Moran's eigenvector maps; neutral theory; niche theory; Sinharaja forest, Sri Lanka; spatial scale; species composition and richness; variation partitioning.

## INTRODUCTION

Ecologists have attempted to explain species diversity and its distribution patterns across scales for over half a century (Hutchinson 1961, Chesson 2000, Chave 2004), but processes that maintain species diversity are still not fully understood. Niche and neutral theories emphasize different processes that maintain species diversity. Niche theory suggests that changes in species compositions are closely related to changes in local environmental conditions (Tilman 1982). Therefore, sites with similar local environmental conditions should harbor similar species assemblages (Tilman 1982, Li et al. 2011). In contrast, neutral theory (Hubbell 2001) assumes that all species are functionally equivalent and that species diversity is maintained through random birth and death,

dispersal, speciation, and stochastic extinction (Hubbell 2001). Thus, neutral theory explicitly ignores the possible effects of local environmental conditions on the differences in species composition between two sites (McGill et al. 2006). Under neutral theory, spatial structure in species composition is independent of habitat and mainly driven by dispersal limitation (Etienne and Alonso 2007).

Niche theory predicts that nearby sites maintain more similar species compositions than sites farther away because most of the habitats are spatially autocorrelated, i.e., the local environmental condition of a certain site is similar to that of neighboring sites (Nekola and White 1999). Neutral theory also predicts distance decay of species similarities. However, here the mechanism that creates spatial autocorrelation structures in local species composition is dispersal limitation independent of local environmental conditions: the larger the distance, the larger the species dissimilarity (Nekola

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and White 1999, Gilbert and Lechowicz 2004). Thus it is unclear if distance decay of species similarity observed at a given community is driven by niche theory, dispersal, or both.

Variation partitioning (Borcard et al. 1992, Borcard and Legendre 1994, He et al. 1996) allows for an assessment of the relative contribution of environmental factors and spatially structured processes on variation in species richness and community composition. Distance-based Moran's eigenvector maps (Legendre and Legendre 2012) provide variables that quantify spatial structure, and habitat variables represent the potential influence of the environment (Legendre et al. 2009). This method allows partitioning of the variation of species richness and species composition data into the four complementary components: (a) "pure habitat" (non-spatial habitat factors), (b) "spatially structured habitat" (induced by spatially structured habitat variables), (c) "pure space" (spatial autocorrelation independent of habitat variables), and (d) "undetermined" (Legendre et al. 2009). The proportion of variation explained by the pure habitat and the spatially structured habitat components (a + b) can be related to niche processes (Laliberté et al. 2009). However, the pure space component, (c), can be attributed to a mixture of factors including the contributions of unobserved and spatially structured environmental variables and spatially structuring processes of community dynamics (Borcard and Legendre 2002, Borcard et al. 2004, Legendre et al. 2009). The latter includes dispersal limitation, which, however, would only be purely neutral if all species showed similar patterns in effective dispersal distances, and other biological processes that can generate spatial structures independent of habitat (e.g., competition, facilitation, and Janzen-Connell effects [Legendre et al. 2009]). The undetermined species variation, (d), can be caused by drift and stochasticity in death, birth, and dispersal or by undetermined nonspatially structured biological or environmental factors (Legendre et al. 2009, Dumbrell et al. 2010).

Both niche and neutral theory lead to distance decay of species similarities, but because their relative importance in structuring communities varies with spatial scale (Gilbert and Lechowicz 2004, Girdler and Barrie 2008, Legendre et al. 2009) we may assess their relative importance by conducting scale-dependent analyses. This, however, requires additional information, because the separation of scales is dependent on the scale of environmental variation and also dependent on dispersal mechanisms of different species. For example, habitat filtering has only a weak potential to induce spatial structures in species composition at finer scales (say 10–20 m), where habitat conditions are more homogeneous and effects of stochasticity are expected to be strong (Shiple et al. 2012), but will become important at larger scales (say 50 m). In contrast, dispersal limitation has a strong potential to structure communities at fine scales, especially in communities where seeds are dispersed

close to their parents (Gilbert and Lechowicz 2004, Girdler and Barrie 2008). At intermediate scales, both processes interact. Habitat filtering tends to favor better-adapted species, but because of dispersal limitation the best competitor may not reach all suitable sites. This delays competitive exclusion and favors coexistence (Tilman 1994, Hurtt and Pacala 1995).

The relative importance of processes that structure local species composition and richness is also likely to change with life stage. For example, the spatial distributions of seedlings should be strongly determined by chance events, seed deposition mechanisms (i.e., scatter vs. clump dispersal [Howe 1989]), regeneration niches (Grubb 1977, Tilman 1982), and by the distance to seed-producing trees, but less by environmental gradients (Clark et al. 1998). While seedlings are generally found to be highly clustered (Howe 1989, Hubbell et al. 1999), density-dependent mortality and increasing importance of habitat filtering (Comita et al. 2007, Lai et al. 2009) could substantially alter the local species composition and richness in their transition to juveniles. Thus, we may expect that a higher proportion of variation in species richness and composition remains undetermined for seedlings, but that the habitat variables become more important for juveniles. Partitioning of spatial patterns into the four complementary components introduced above may therefore allow us to assess how the relative importance of different mechanisms changes with life stage.

The general objective of this paper is to assess the relative importance of the habitat components (a + b), (i.e., pure habitat and spatially structured habitat) and the pure space component (c), (i.e., spatial autocorrelation independent of habitat variables) and the undetermined component (d), in structuring species composition and richness in the Sinharaja mixed dipterocarp forest (Sri Lanka). We analyzed the size and the space axes in concert, conducting analyses at different spatial scales (10 m, 20 m, and 50 m) and for different life stages: recruits, juveniles, and adults. Assessment of the different contributions of habitat, spatially structured processes, and stochasticity among spatial scales and life stages will increase our understanding of the mechanisms that drive species assembly in tropical forests with pronounced topographical variation.

## MATERIALS AND METHODS

### *Study site*

The 25-ha (500 × 500 m) Sinharaja forest dynamic plot (FDP) was established in 1993 at the center of the constantly wet southwestern region of Sri Lanka (6°21'–6°26' N, 80°21'–80°34' E). The mixed dipterocarp forest has been recognized by the Center for Tropical Forest Science for its *Mesua-Doona* community, and strong topographic heterogeneity. The Sinharaja plot is located in the northwestern sector of the Sinharaja World Heritage Site, which was not subjected to human

disturbance in the recent past. The plot is surrounded by regenerating forest that was selectively logged in the 1970s (Gunatilleke et al. 2004b). The elevation of the permanent forest plot ranges from 424 m to 575 m above sea level. A valley lies between two slopes, a higher steep slope facing southwest and a less steep slope facing northeast. A perennial stream and several seasonal streamlets run across these slopes (Appendix A: Fig. A1). The plot receives a mean annual rainfall of 5016 mm, with no clear dry season. Most of the tree species in the FDP are endemic to Sri Lanka (Gunatilleke et al. 2006). More details on the study plot and its floristic structure can be found in Gunatilleke and Gunatilleke (1981) and Gunatilleke et al. (2004a, b, 2006).

#### *Tree data*

All the stems  $\geq 1$  cm in diameter at breast height (dbh) in the plot have been identified to species, enumerated, measured, and mapped in 1994, and recensused in 1999. We used the tree data from the 1999 census, where 219 co-occurring species and 211 090 individual trees were mapped. We classified all trees into recruits, juveniles, and adults. Recruits were all trees that appeared the first time in the second census (i.e., they crossed the 1-cm dbh threshold during the last five years). To distinguish between juveniles and adults we ranked the remaining trees by their dbh and determined the 99th percentile (dbh99). Following Bagchi et al. (2011), juveniles were trees with  $\text{dbh} < \text{dbh}99^{1/2}$ , and adults, trees with  $\text{dbh} \geq \text{dbh}99^{2/3}$ . Trees at sizes of  $\text{dbh}99^{1/2} \leq \text{dbh} < \text{dbh}99^{2/3}$  were excluded to accentuate the difference between classes (Bagchi et al. 2011). With this classification we obtained 9927 recruits (159 species), 129 755 juveniles (193 species), and 27 587 adult trees (204 species).

We also repeated analyses with the classification of juveniles (dbh < 10 cm) and adults (dbh  $\geq$  10 cm), where we obtained 9927 recruits (159 species), 193 906 juveniles (218 species), and 17 184 adult trees (177 species). We explored the effect of sampling size for the data of all trees (second census) by randomly removing 10%, 20%, 30% ... and 90% of all trees (while maintaining the relative species abundances).

#### *Habitat variables*

We divided the Sinharaja plot into 100 (50  $\times$  50 m), 625 (20  $\times$  20 m), and 2500 (10  $\times$  10 m) subplots (hereafter called quadrats). We calculated values for the six habitat variables: elevation, slope, topographic wetness index (TWI), altitude above channels (ACH), terrain convexity, and aspect for each quadrat (Appendix A: Fig. A2, Appendix B: *Habitat variables*). Topography is often a good proxy for soil variation (Baldeck et al. 2013) and aspect describes differences in light availability (Punchi-Manage et al. 2013). We also included the two indices TWI and ACH, which are commonly used to quantify topographical control on hydrological processes due to lack of hydrological data (Kanagaraj et al. 2011, Punchi-Manage et al. 2013).

#### *General statistical methodology*

The basic response variables were a species composition table (quadrats in rows, species abundances in columns) and species richness (number of species per quadrat) of a given life stage. Prior to the analysis we used a transformation of the species composition table to fit the data into linear models (Appendix B: *Hellinger transformation* [Legendre and Gallagher 2001]). The response variables were calculated at fine, medium, and broad spatial scales (10 m, 20 m, and 50 m), for all trees and the three different life stages, recruits, juveniles, and adults.

Following the recommendation by Legendre et al. (2009), we used the third-degree polynomial function of five variables: elevation, slope, topographic wetness index, altitude above channel, and convexity (i.e., yielding 15 variables). Since aspect is a circular variable, we used the  $\cos(\text{aspect})$  and  $\sin(\text{aspect})$  (i.e., two variables) in order to make it linear (Appendix B: *Reconstruction of habitat variables*). We therefore obtained 17 reconstructed variables from the six original habitat variables. Third, we computed eigenfunctions of distance-based Moran's eigenvector maps (*dbMEM*), formally called "Principal coordinates of neighbor matrices" (Legendre and Legendre 2012), across the 2500 quadrats (10-m scale), 625 quadrats (20-m scale), and 100 quadrats (50-m scale) of the spatial grid (Appendix B: *Distance-based Moran's eigenvector maps*; see also Borcard and Legendre 2002, Borcard et al. 2004, Dray et al. 2006). We used eigenfunctions (only with positive eigenvalues) of *dbMEM* as explanatory variables to represent spatial structure (Borcard and Legendre 2002) and the 17 topographic habitat variables just described to represent the environment. We used the forward selection method to extract the significant eigenfunctions of *dbMEM* and habitat variables from above. This was done by permutation tests with 9999 randomizations (Dray et al. 2011) (Appendix B: *Forward selection of habitat and dbMEM variables and variation partitioning*).

Finally, we used the response variable together with the two sets of variables (i.e., *dbMEM* and topographic variables from the forward selection) in the variation partitioning to determine the individual and joint contribution of *dbMEM* and topographic variables to describe the species composition and richness (Borcard et al. 1992, Borcard and Legendre 1994, Peres-Neto et al. 2006).

Variation partitioning was used to assess the amount of variation in species composition and richness explained by the four different components: (a) pure habitat, (b) spatially structured habitat, (c) pure space, and (d) undetermined (Appendix A: Fig. A3). Our habitat variables show a considerable degree of spatial structure (Appendix A: Fig. A2). We therefore needed several steps to determine the unique contribution of (a), (b), and (c) (Legendre et al. 2005). We used both sets of predictors (habitat and spatial) together to assess (a + b

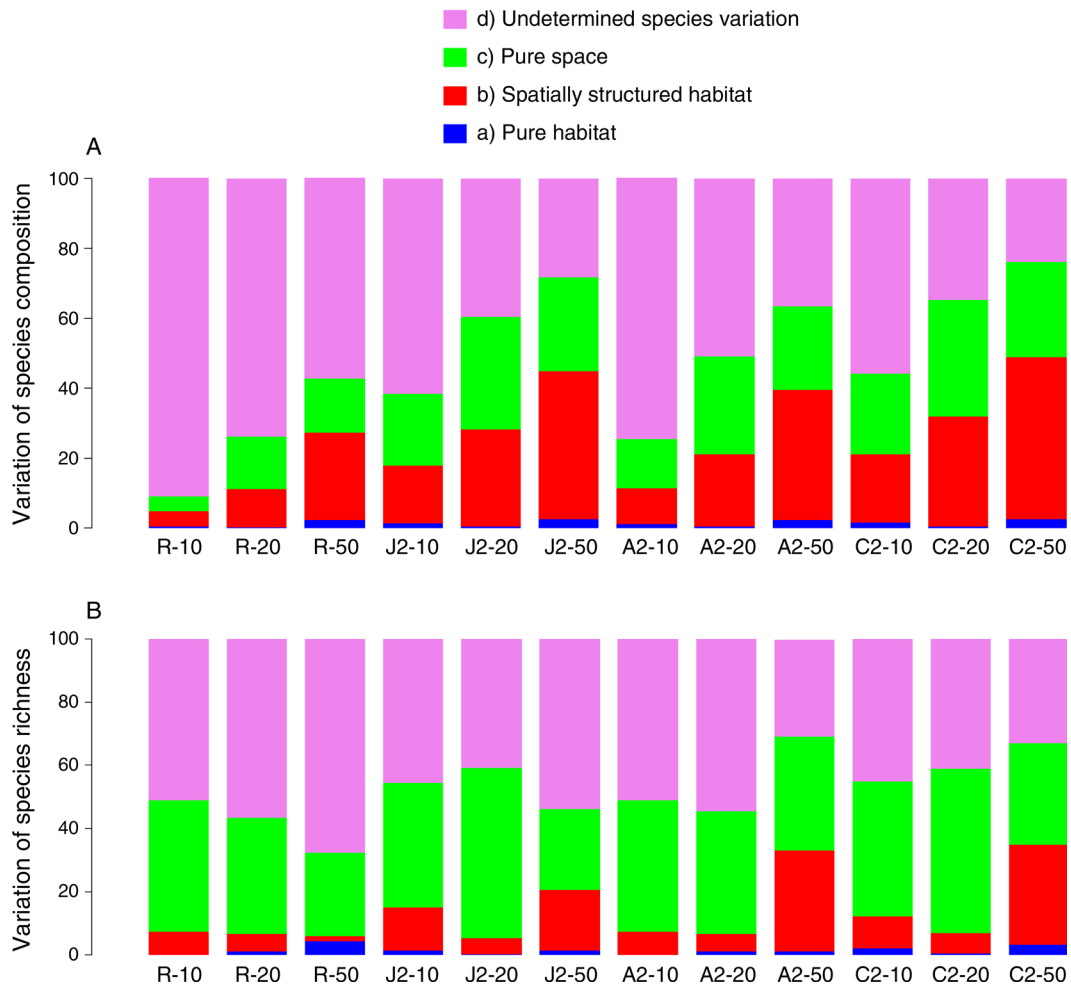


FIG. 1. The variation partitioning method was used to divide the variation of total species composition (panel A) and richness (panel B) into four components: (a) pure habitat; (b) spatially structured habitat; (c) pure space; and (d) undetermined species variation, which includes stochastic variations. The symbols R, J, A, C indicate recruits, juveniles, adults, and all trees, respectively, and the numbers 10, 20, and 50 indicate the quadrat size (in meters).

+ c), only the set of habitat variables to assess the proportion of variation accounted for by habitat (a + b), and only the spatial variables to assess the proportion of spatially structured variation (b + c) (Peres-Neto et al. 2006). The individual fractions of the partitioning can then be obtained by simple subtraction. To detect the environmental variables that best explained the habitat components, we derived canonical axes from redundancy analysis (Rao 1964).

## RESULTS

### *Variation partitioning of species composition*

The variation of species composition explained by habitat component (a + b) increased for all life stages systematically with the scale (10 m; 20 m; 50 m; Fig. 1A); however, the contribution of the pure habitat component was negligible (<3%; Fig. 1A). The pure space component (c) explained at the 20-m scale between 15% and 33% of the variation in species composition, but was

somewhat less important at the finer 10-m and the broader 50-m scales. We found a marked general pattern in the undetermined variation, which generally decreased with increasing scale. The fraction of undetermined variation was especially high for recruits and adults at the 10-m scale (>75%) and lowest for juveniles at the broadest 50-m scale (Fig. 1A). The pattern for all trees together was largely the same as for the juveniles that dominated the abundance.

Fig. 2A–F represents variation of species composition of all trees in  $20 \times 20$  m plots described by the six most important canonical axes obtained from redundancy analysis. The first, second, and third canonical axes of (a + b + c) describe 32.1%, 7.9%, and 4.2% of total species composition, respectively (Fig. 2A–C). The first canonical axis of the habitat component, (a + b), explained 24.3% of total species composition variation (Fig. 2D). The total variation of species composition explained by

the first two canonical axes of the pure space component, (c), were 10.2% and 4.7%, respectively (Fig. 2E, F).

The first canonical axis of (a + b + c) was strongly correlated with the elevation ( $R_{\text{adj}}^2 = 0.53$ ). The first canonical axis of (a + b) was strongly correlated with elevation ( $R_{\text{adj}}^2 = 0.74$ ), aspect ( $R_{\text{adj}}^2 = 0.56$ ), and moderately correlated with topographic wetness index ( $R_{\text{adj}}^2 = 0.31$ ) and slope (0.25) (Table 1). We repeated this analysis for species composition also for the separate life stages: recruits, juveniles, and adults in  $20 \times 20$  m plots (Table 1). In general, the strongest and most consistent correlations were found for all life stages taken together with elevation ( $R_{\text{adj}}^2 > 0.7$ ), aspect ( $R_{\text{adj}}^2 > 0.5$ ), and topographic wetness ( $R_{\text{adj}}^2 \approx 0.3$ ). Slope and convexity showed a weak correlation with all the life stages.

Results for the response variable species composition remained essentially the same when using the classification juveniles (dbh < 10 cm) and adults (dbh  $\geq$  10 cm) (cf. Fig. 1A and Appendix A: Fig. A6). When exploring the effect of sample size we found that the undetermined component (d) increased only when the number of trees dropped below 50% (i.e., <100 000 individuals) (Appendix A: Fig. A7). At 10% (i.e., 22 000 individuals), the undetermined component yielded 45% compared with 25% for all trees (Appendix A: Fig. A7).

#### *Variation partitioning of species richness*

The results of variation partitioning with the response variable species richness differed substantially from that with the response variable species composition (cf. Fig. 1A, B). The variation of species richness explained by the habitat components (a + b) was substantially lower than for species composition; it ranged between 5% for juveniles at the 20-m scale and 33% for adults at the 50-m scale, and showed no clear pattern with spatial scale (Fig. 1B). Species richness of all trees explained by the habitat components (a + b) at the 20-m scale made up only 7% of the variation in total species richness (panel D3 in Fig. 3).

The variation of species richness explained by the pure space component (c) was always larger (except juveniles at 50 m) than the corresponding variation of species composition (Fig. 1B). It ranged between 26% for juveniles at the 50-m scale and 54% for juveniles at the 20-m scale. Approximately 52% of the variation in species richness of all trees at 20-m scale was explained by pure space (c) (Figs. 1B and 3A). The undetermined variation in species richness was largest for recruits at the 50-m scale (68%), but smallest for adults ( $\approx$  31%). No clear scale pattern as for species composition was detected (Fig. 1B). For all trees together the undetermined variation in species richness yielded approximately 33–45%.

#### *Scales of dbMEM eigenfunctions*

The selected eigenfunctions of distance-based Moran's eigenvector maps (*dbMEM*) provide information on whether a given fraction corresponds mostly to

broad-scaled or fine-scaled spatial structure. The small square boxes (Appendix A: Fig. A4) represent the selected *dbMEM* eigenfunctions of species composition calculated for recruits, juveniles, adults, and all trees at three different spatial scales (10 m, 20 m, and 50 m) obtained after the forward selection. Eigenfunctions were arranged from broad to fine scales. Most of the selected *dbMEM* eigenfunctions were descriptors of medium and broad spatial scales (Appendix A: Fig. A4).

The first 25 *dbMEM* eigenfunctions (i.e., first block) explained  $\sim$ 81% (i.e., 0.253/0.314) of variation in species composition of all trees ( $R^2 \approx 0.81$ ) fitted to habitat component (a + b) at the 20-m scale (Appendix A: Fig. A5d). The second block of *dbMEM* eigenfunctions (26–50) described a further 4%, but the rest of the *dbMEM* blocks did not contribute. Since the first 50 eigenfunctions represent large-scale spatial variations, nearly 85% of the variation in species composition of all trees described by the habitat component was related to broad-scale spatial structures. Similar patterns were observed for variation of species composition for recruits, juveniles, and adult trees that were fitted to the habitat component at the 20-m scale (Appendix A: Fig. A5a–l). Thus habitat variables were strongly correlated with the *dbMEM* eigenfunctions at broad scales, and they were weakly correlated or uncorrelated with the medium- to fine-scale spatial structures.

The pure space component (c) was generally correlated to *dbMEM* eigenfunctions describing finer-scale spatial structure than that of the habitat component (a + b) (Appendix A: Fig. A5). The first block of eigenfunctions explained 55% of the variation in species composition of all trees fitted to the pure space component, but the second, third, and fourth block of *dbMEM* eigenfunctions still explained 15%, 12%, and 6%, respectively (Appendix A: Fig. A5d). Similar results were found for juveniles and adults (Appendix A: Fig. A5b, c). Recruits differed somewhat from this general pattern and showed only moderate correlation with the *dbMEM* eigenfunctions even at the fine scale (Appendix A: Fig. A5a).

#### DISCUSSION

In this study we partitioned the variation in species richness and composition observed for different life stages and quadrat sizes at the Sinharaja tropical forest into different components related to topographic habitat variables and pure spatial structure. Our analysis was based on two axes, life stage and spatial scale, and allowed us to reveal systematic differences in the different components that point to the relative importance of niche and neutral processes in structuring the Sinharaja forest community. Our results indicate that the variation of species composition explained by habitat components (pure and spatially structured) increased for all life stages substantially with broader spatial scale, and the undetermined variation decreased

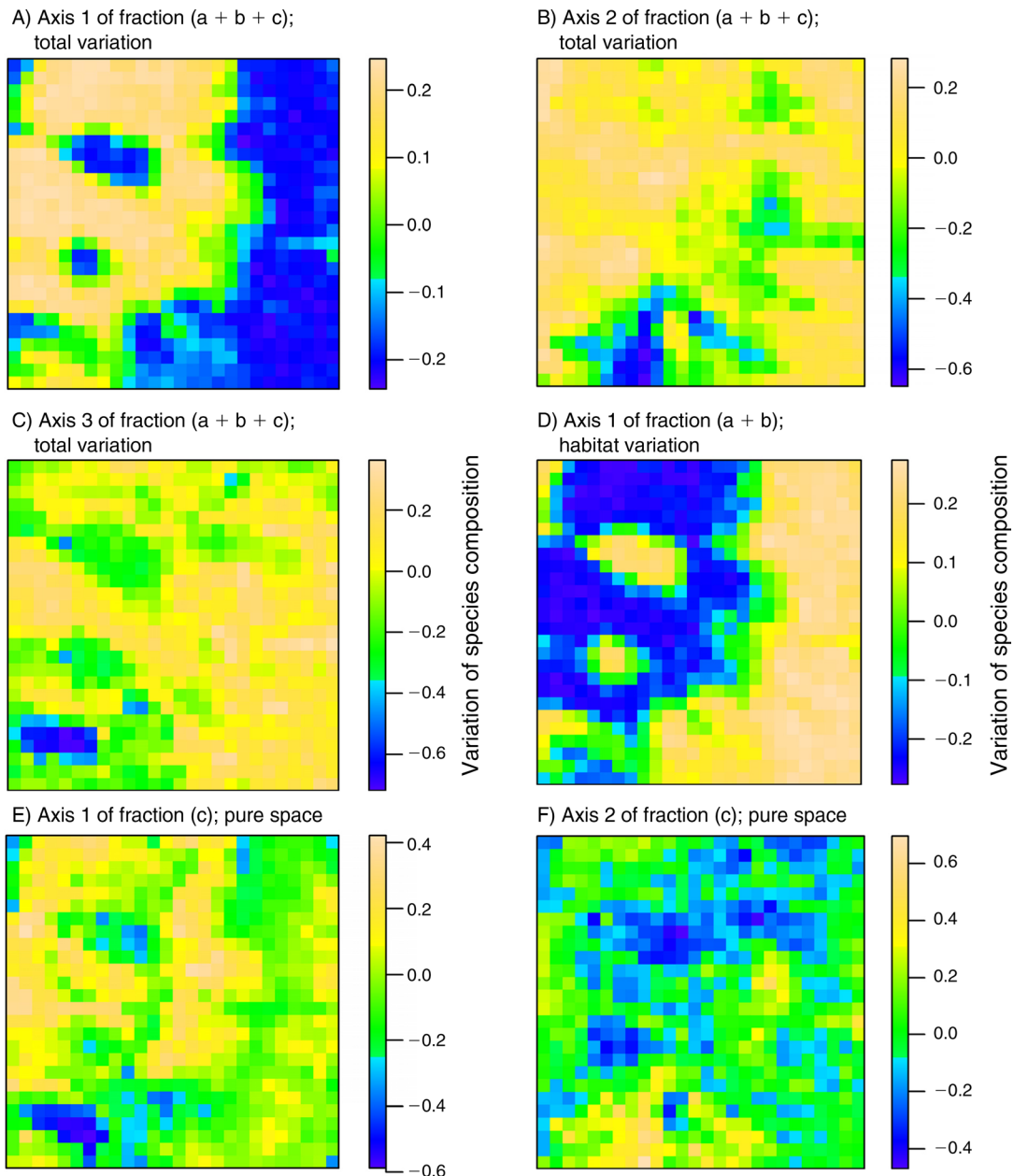


FIG. 2. The variation of species composition explained by the first six most significant canonical axes for  $20 \times 20$  m quadrat size. These six significant canonical axes are: (A) first, (B) second, and (C) third canonical axes of total species composition variation, (D) first canonical axes of habitat-related species composition, and (E) first, and (F) second canonical axes of pure space component. Color values range from highest (orange) to lowest (blue).

dramatically with broader scales. In the following we will discuss these results in detail.

#### *Effects of spatial scale*

A unique feature of the Sinharaja plot is that the proportion of undetermined variation in species composition was very high at fine spatial scales (up to 90% for recruits and 75% for adults) but decreased systematically with increasing spatial scale (up to a minimum of 28% for juveniles at the 50-m scale). This result is in

sharp contrast to findings by Legendre et al. (2009) for a broad-leaved forest in China, where the undetermined variation in species composition was fairly constant among spatial scales, ranging between 33% and 37%. The high proportion of undetermined variation in species composition indicates that species assembly at Sinharaja forest is highly stochastic at fine scales, but that this stochasticity tends to even out at the 50-m scale, where more consistent habitat-driven species assemblages emerged. Indeed, the decrease in the

TABLE 1. Total variation explained by first canonical axes of the habitat variables (a + b) and correlation coefficients between the first canonical axis of the habitat component (a + b) of species composition with habitat variables for the 20 × 20 m quadrat size.

Habitat variables	All life stages	Recruits	Juveniles	Adults
Total variation (%) explained by first canonical axes of the habitat variables	24.3	9.1	20.8	16.0
Correlation ( $R_{adj}^2$ ) with				
Elevation	0.74	0.81	0.75	0.75
Aspect	0.56	0.48	0.54	0.57
Topographic wetness index	0.31	0.32	0.32	0.30
Slope	0.25	0.27	0.26	0.25
Convexity	0.16	0.15	0.17	0.15

Notes: The correlation is measured with the  $R_{adj}^2$ .

undetermined component was mostly because of an increase in the spatially structured habitat component. The 10-m scale represents the “plant’s-eye individual scale,” and within the 10-m quadrats we can therefore expect that stochasticity in local exclusion produces basically stochastic samples of the species pool associated with a given habitat. However, the 50-m quadrats capture the average over 25 small 10-m quadrats, and should therefore yield a better representation of species assemblages associated with a given habitat. This interpretation is strengthened by our finding that the proportion of variation explained by the habitat components increased with spatial scale (e.g., for juveniles from 28% to 43%), and that the eigenfunctions of the distance-based Moran’s eigenvector maps selected for the habitat component described mostly broader-scale spatial variation.

Several studies found scale dependence in the relative importance of different factors in explaining the variation of species composition in plant communities (e.g., Legendre et al. 2009, Li et al. 2011, Hu et al. 2012, Shipley et al. 2012), and point to an emerging consensus of how scale impacts the relative importance of neutral and niche processes. Overall, they confirm that distance decay of species similarity observed in plant communities is driven by both niche and neutral processes, and that their relative importance varies with the spatial scale and also site characteristics. First, stochasticity, which is an important part of neutral theory, acts most strongly at small spatial scales (the present study, Li et al. 2011, Hu et al. 2012, Shipley et al. 2012; but not Legendre et al. 2009). For example, Shipley et al. (2012) tentatively ascribed unexplained variation at smaller scales to demographic stochasticity, because chance fluctuations in individual birth and death rates should increasingly dominate population dynamics at smaller population sizes. Second, the importance of niche processes increases with scale (our study, Legendre et al. 2009, Li et al. 2011, Hu et al. 2012, Shipley et al. 2012) because smaller scale stochasticity, dispersal effects, and environmental heterogeneity are smoothed over. Third, in all these studies the pure space component explained a substantial proportion of the

variation which was attributed mostly to neutral or “pseudo-neutral” spatial structuring processes of community dynamics such as dispersal limitation. However, the pure spatial component may also hide deterministic biological processes such as Janzen-Connell effects, facilitation, or unmeasured environmental variables. For example, Janzen-Connell effects and facilitation could play an important role in structuring the Xishuangbanna forest plot at small spatial scales (0–5 m) (Lan et al. 2012), and Hu et al. (2012) found in this forest a peak in the pure space component at intermediate spatial scales.

There were also results from particular studies that did not match the general tendencies outlined above. For example, the contribution of stochasticity was largely scale independent in the study of Legendre et al. (2009), or did not always decrease in Hu et al. (2012), or the contribution of the pure space component in Shipley et al. (2012) remained largely independent of scale. A particular challenge for future studies is the rarely asked question of how the different components change with life stage (our study and Hu et al. 2012). While the effects of stochasticity (e.g., in seed deposition) and dispersal limitation should be largest at earlier life stages, habitat-specific mortality at the transition from recruits to juveniles may result in stronger effects of niche processes at the juvenile stage. However, we found that the large effects of stochasticity (for recruits and adults) may be partly caused by an effect of small sample sizes (Appendix A: Fig. A7).

#### *Habitat effects*

Almost the entire variations in species composition and richness explained by habitat variables were spatially structured and mostly correlated with elevation and aspect. This is not surprising given the strong spatial ridge–valley elevation structure of the Sinharaja forest plot and the strong division between southwest- and northeast-facing slopes (Appendix A: Fig. A1). Punchi-Manage et al. (2013) showed that the Sinharaja plot is basically divided into five distinct habitats, which were driven mainly by the variables elevation and aspect. The underlying reason for this sorting may be attributed to marked changes in microclimatic conditions along the

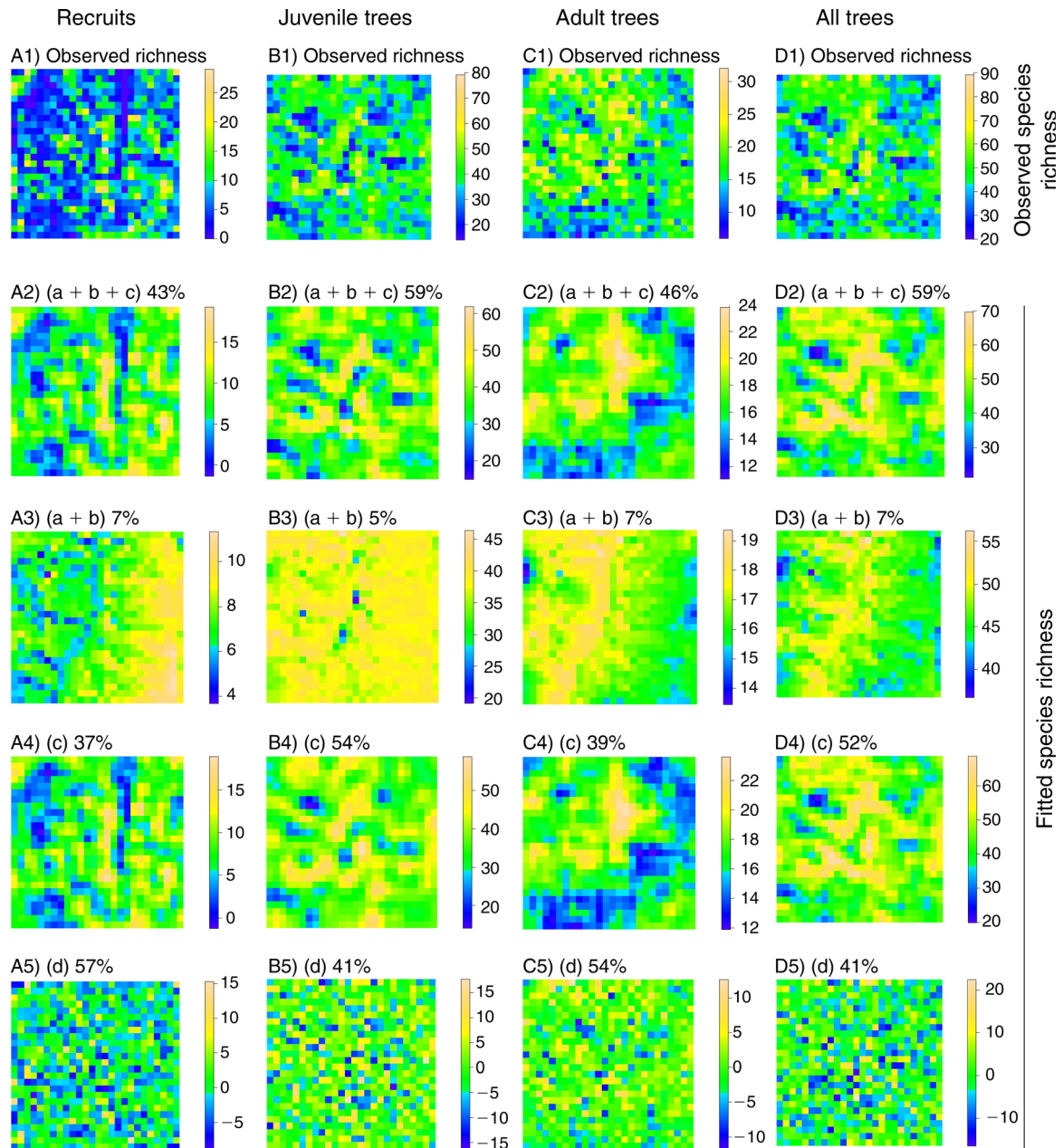


FIG. 3. Observed species richness (first row of panels [1]) for recruits, juveniles, adults, and all trees. The remaining panels (rows 2–5) show the percentage of variation of species richness described by (a + b + c) habitat and spatial components, (a + b) habitat component, (c) pure spatial component, and (d) undetermined component, for  $20 \times 20$  m spatial grid size. Color values range from highest (orange) to lowest (blue).

elevation gradient (Punchi-Manage et al. 2013). Strong water flows during intense rainfall disperse soil cover of upper ridges into valley and low-elevation areas. These spatially structured abiotic patterns can create strong species sorting along the elevation gradient (Girdler and Barrie 2008).

The habitat components explained for juvenile trees the largest proportion of variation in species composition (almost 45% at the 50-m scale), and for recruits the

smallest proportion (25% at the 50-m scale). This is in agreement with our expectation that the juvenile life stage may be more impacted by habitat filtering than recruits. While the spatial patterns of recruits may still be determined to a larger extent by chance events, dispersal, and local fine-scale conditions (regeneration niches), habitat filtering may become more important when these recruits grow to juvenile size and are subject to increasing density-dependent mortality (Comita et al.



2007, Lai et al. 2009). However, topographic habitat 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 relevant for recruits.

Species compositions of adult trees were more weakly associated with the measured habitat variables than were juveniles. One explanation for this would be that adults are more responsive to the unmeasured (non-spatially structured) site characteristics such as soil type or soil pH that caused a high proportion of undetermined variation (Paoli et al. 2006). Another, mutually nonexclusive explanation is that species may have lost during the transition from juveniles to adults the advantage of being in the habitat with which they had become associated (Kanagaraj et al. 2011). Habitat-specific mortality at the transition from recruits to juveniles may result in high densities of juveniles in their preferred habitat, but increasing thinning caused by negative density dependence at the transition to reproductive individuals may weaken the association of adults with habitat variables (e.g., Webb and Peart 2000). Ontogenetic shifts in resource requirements may also partly neutralize the species-specific effects of habitat structure that emerged during the juvenile stage (Comita et al. 2007). Additionally, disturbance events faced by adults but not (yet) by juvenile trees may contribute to the high proportion of undetermined variation in adults (Stohlgren et al. 1998). Indeed, slope instability and greater uprooting in valley sites represent frequent disturbances at the Sinharaja site (Ashton et al. 1995, see also Gale 2000, Sukri et al. 2011). The spatial distributions of adult trees provoked by excessive chance events (e.g., disturbances) rarely create spatial structures and leave a large undetermined (stochastic) component in the model.

#### *Spatial processes*

Limited dispersal is a major mechanism that can create species aggregation and spatial autocorrelation in species richness (Nathan and Muller-Landau 2000, Seidler and Plotkin 2006, Legendre et al. 2009). We found that pure spatial structure independent of topographic habitat variables, i.e., pure space component (c), contributed substantially to the variation in species richness and composition. The pure space component in species composition was highest at the 20-m spatial scale for juveniles ( $\approx 32\%$ ). One explanation for this finding is that most of the dominant species at the Sinharaja forest plot show strong seed dispersal limitations (e.g., seeds disperse ballistically in *Agrostistachys hookeri* and *A. intramarginalis*, by gravity in *Mesua ferrea* and *M. nagassarium*, and by gyration in all the *Shorea* species [*S. affinis*, *S. congestiflora*, *S. cordifolia*, *S. disticha*, *S. megistophylla*, *S. trapezifolia*, and *S. worthingtonii*]), with most seeds landing close to their parents. This creates a short-range seed dispersal kernel, which may be modified by host-specific patho-

gens that reduce the amount of seeds surviving in the immediate neighborhood of parent trees. These two opposing mechanisms should result in spatial structures that are best visible for juveniles at the 20-m spatial scale (note that recruits are less numerous and are subject to stronger stochasticity). At the fine (10-m) and medium spatial scales (20-m), we found that the pure space component explained a larger proportion of variation in species composition and richness than the habitat components. However, the pure space component may not only represent spatially structuring processes of community dynamics, but also unmeasured spatially structured habitat variables. Indeed, Baldeck et al. (2013) found that the unmeasured effect of soil that contributed to the pure space component yielded (for all trees in Sinharaja at the 20-m scale)  $\sim 7\%$ , and there may be additional unmeasured environmental variation that contributed to pure space component. It is therefore likely that we somewhat overestimated the pure space component and underestimated the habitat component.

#### *Differences between species richness and species composition*

Our study revealed substantial differences between the effects on species composition and species richness. First, no systematic trends with spatial scale were found for species richness. Second, the pure space component explained a much higher proportion of the variation in species richness than species composition, whereas the habitat components contributed much less. This was especially strong for juveniles, where the pure space component explained  $>50\%$  of the variation in species richness (Fig. 3). This indicates that dispersal limitation of juveniles becomes especially manifested when looking at local species richness patterns. Clearly, species richness transforms the abundance of each species into presence-absence data for each quadrat, and should therefore be less sensitive to processes such as gradients in habitat association that modulate abundance. Thus, more subtle abundance differences in juveniles may be more strongly influenced by habitat factors, whereas dispersal limitation strongly structures local species richness. Nevertheless, it is interesting that the study of Legendre et al. (2009) found little difference in the response of species richness and composition for the Gutianshan forest plot in China.

#### CONCLUSIONS

In this study we found that the relative importance of habitat and purely spatially structured processes varied with life stage and spatial scale in assembling the tree community at the Sinharaja tropical forest. At fine spatial scales we found, especially for recruits and adults, a large proportion of variation in species composition that remained undetermined ( $>80\%$ ), and an additional 10% was explained by spatially structured processes such as dispersal limitation. Thus, when looking at the local plant scale where direct plant-plant

interactions take place, species assembly of the Sinharaja forest is to a large extent driven by mechanisms that are related to neutral theory. However, at larger spatial scales, substantially more variation in species composition was explained by spatially structured habitat factors related to changes in environmental conditions along the valley–ridge gradient.

Little is known about the relative importance of topographic habitat factors, stochasticity, and spatial processes in structuring local species compositions in tropical forests. Here we found in a tropical forest with considerable topographic variation that stochasticity and dispersal limitation accounted for a similar amount of variation as habitat factors. Our results provide novel insights, but raised also a number of open questions that call for similar studies in other tropical forest sites. Of course, our method does not unambiguously separate neutral processes from niche effects, but it can be seen as a valuable tool to generate new hypotheses and to provide some insights about future research that could follow from this work. One obvious avenue would be to investigate the fine-grained abiotic variables or processes that we were unable to detect, or incorporate the dispersal traits (e.g., Li et al. 2011), in order to tease apart neutral and nonneutral processes. Our study also suggests that further research is needed to elucidate how the relative contribution of stochasticity, habitat, and spatial processes on community assembly changes with life stage, and how this is influenced by sample size.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Sinharaja forest dynamic plot, topographic habitat variables, variation partitioning, eigenfunctions of dbMEM, percentage of variation of species composition explained by blocks of eigenfunctions, variation partitioning for species composition, and effects of sample size ([Ecological Archives E095-033-A1](#)).

### Appendix B

Methodology of habitat variables, Hellinger transformation, reconstruction of habitat variables, distance-based Moran's eigenvector maps (dbMEM), forward selection of habitat and dbMEM variables, and variation partitioning ([Ecological Archives E095-033-A2](#)).