

Neighborhood diversity of large trees shows independent species patterns in a mixed dipterocarp forest in Sri Lanka

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Abstract. Interactions among neighboring individuals influence plant performance and should create spatial patterns in local community structure. In order to assess the role of large trees in generating spatial patterns in local species richness, we used the individual species–area relationship (ISAR) to evaluate the species richness of trees of different size classes (and dead trees) in circular neighborhoods with varying radius around large trees of different focal species. To reveal signals of species interactions, we compared the ISAR function of the individuals of focal species with that of randomly selected nearby locations. We expected that large trees should strongly affect the community structure of smaller trees in their neighborhood, but that these effects should fade away with increasing size class. Unexpectedly, we found that only few focal species showed signals of species interactions with trees of the different size classes and that this was less likely for less abundant focal species. However, the few and relatively weak departures from independence were consistent with expectations of the effect of competition for space and the dispersal syndrome on spatial patterns. A noisy signal of competition for space found for large trees built up gradually with increasing life stage; it was not yet present for large saplings but detectable for intermediates. Additionally, focal species with animal-dispersed seeds showed higher species richness in their neighborhood than those with gravity- and gyration-dispersed seeds. Our analysis across the entire ontogeny from recruits to large trees supports the hypothesis that stochastic effects dilute deterministic species interactions in highly diverse communities. Stochastic dilution is a consequence of the stochastic geometry of biodiversity in species-rich communities where the identities of the nearest neighbors of a given plant are largely unpredictable. While the outcome of local species interactions is governed for each plant by deterministic fitness and niche differences, the large variability of competitors causes also a large variability in the outcomes of interactions and does not allow for strong directed responses at the species level. Collectively, our results highlight the critical effect of the stochastic geometry of biodiversity in structuring local spatial patterns of tropical forest diversity.

Key words: independence null model; individual species–area relationship; neighborhood diversity; point pattern analysis; Sinharaja tropical forest; spatial scale; stochastic dilution.

INTRODUCTION

Identifying the processes that structure tropical rain forests and maintain their high species richness are persistent challenges in plant ecology (Hubbell 2001, Wright 2002). One approach to advance this question is to conduct detailed analyses of the observed spatial patterns (Hubbell et al. 2001). For example, the performance (i.e., recruitment, growth, and survival) of a focal individual is the outcome of interactions with neighboring plants within a limited neighborhood

(Lebrija-Trejos et al. 2014). Mechanisms underlying negative interactions of an individual with neighboring plants include shared pests (pathogens, herbivores) and competition for limiting resources (light, nutrients), whereas shared mutualists (mycorrhizae, seed dispersers), facilitation (nurse plants), and shared responses to abiotic conditions can cause positive interactions (Lebrija-Trejos et al. 2014). Indeed, many studies using neighborhood approaches found significant effects of the biotic neighborhood on the performance of species (e.g., Hubbell et al. 2001, Uriarte et al. 2004, 2005, 2010, Comita et al. 2010, Mangan et al. 2010). While seedling performance (i.e., growth and survival) appears to be most strongly regulated by conspecific neighbors (or closely related heterospecifics; e.g., Queenborough et al.

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2007, Comita et al. 2010, 2014, Mangan et al. 2010, Metz et al. 2010), results for larger size classes showed for many species no difference between con- and heterospecific effects or even positive effects of heterospecific crowding (e.g., Peters 2003, Uriarte et al. 2004, 2005).

Negative or positive species–species interactions should result in distinct spatial patterns in the placement of species (Lieberman and Lieberman 2007) and have the potential to generate spatial structure in local species richness. For example, if an intense negative interaction occurs between individuals of two species, f and j , one or both individuals will have a higher risk of mortality. As a consequence, individuals of species j are likely to be eliminated from the neighborhoods around survivors of the focal species f . Conversely, if species j interacts positively with the focal species f , for example by shared responses to abiotic conditions or because species j and f are dispersed together by the same frugivores, species j may, in the long run, become relatively more frequent in the neighborhoods of the focal species f . While many of these interactions are not very likely to be picked up in species-rich forests with species-by-species analyses (e.g., Lieberman and Lieberman 2007, Wiegand et al. 2007a, 2012, Perry et al. 2009, 2014), species-by-all-species analyses that integrate across all species j around a focal species f are likely to detect effects of interactions, such as competition for light or space, that collectively affect all nearby neighbors of the focal species f . Additionally, negative interactions of large trees, such as competition for space, can result in a lower density of heterospecific neighbors that will then most likely translate into reduced species richness in their neighborhood (Condit et al. 1996, Wolf et al. 2012). Thus, the net balance of negative and positive species interactions can result in reduced or elevated species richness in the neighborhoods of the large individuals of a focal species (compared to random neighborhoods), or the neighborhood species richness may not differ significantly from that of random neighborhoods.

In tropical forests, species richness typically shows large spatial variation at local scales (He et al. 1996, Wiegand et al. 2007b), and a large proportion of this variability is not explained by variables representing the environment or pure spatial structures (such as variation created by dispersal limitation; e.g., He et al. 1996, Legendre et al. 2009, Wolf et al. 2012, Punchi-Manage et al. 2014). The spatial variation in local species richness can be illustrated as landscapes of local species richness (Wiegand and Moloney 2014) based on counts of species richness within distance R of a large number of focal locations located on a regular grid. For large trees at the Sinharaja plot, at the $R = 10$ m neighborhood scale, the species richness ranged approximately from 2 to 13 species (6.6 ± 2.5 [mean \pm SD]), and at the 30-m scale from 12 to 42 species (25.7 ± 5.5), with notable spatial variation (Fig. 1). Given the strong potential of species interactions to generate spatial structure in local

species richness, we expect that some of this variability can be tracked back to species interactions, especially with large trees. In this case, we expect that the locations of the large trees of the focal species are mostly located within local minima or maxima of the landscape of local species richness. Focal species that are mostly located in local minima are termed repeller species, and species that are located in mostly local maxima are termed accumulator species. For example, *Mesua nagassarium* is for $R = 10$ m neighborhoods mostly found in local minima of the landscape of local species richness and therefore likely to be a repeller species (Fig. 1B).

A suitable summary statistic for quantifying this observation is the individual species–area relationship $ISAR_f(r)$ (Wiegand et al. 2007b, Queenborough et al. 2012, Rayburn and Wiegand 2012, Wiegand and Moloney 2014) that we use here to estimate the mean local species richness of a given life stage within distance r of large trees of a given focal species f . To find out if a focal species is mostly located at local minima or maxima of the landscape of local species richness, the ISAR function can be used to compare the observed local biotic neighborhood of the individuals of focal species with that of the null model of neighborhoods of randomly selected locations (Wiegand et al. 2007b).

We use census data from a species-rich tropical forest, the 25-ha, fully mapped, Sinharaja mixed dipterocarp forest plot in Sri Lanka, to assess if the net effects of species interactions translate into identifiable spatial patterns in local species richness of trees of different size classes around large trees of different focal species. To this end, we use techniques of spatial point pattern analysis based on the ISAR function (Wiegand et al. 2007b) to determine the species richness of large trees, intermediate trees, large saplings, small saplings, recruits, and dead trees in 1–50 m neighborhoods of the large individuals of different focal species. More specifically, we investigate whether the proportion and the strength of repeller and accumulator effects at different neighborhoods change with size class and whether the repeller and accumulator property of a focal species is correlated with characteristics of the spatial pattern of the focal species (e.g., abundance or mean distance to nearest neighbors) and its dispersal syndrome.

A previous ISAR analysis of the Sinharaja data by Wiegand et al. (2007b) that was limited to the community of intermediate and large trees (i.e., dbh ≥ 10 cm, where dbh is the diameter at breast height or 1.3 m aboveground) found only for 25% of the focal species significant departures from the null model. Thus, for the community of larger trees, most species did not show identifiable spatial pattern in their neighborhood species richness. The expanded size-class analysis presented here enables us to investigate how this lack of spatial patterns in the community of larger trees was reached. The range of possible outcomes of this analysis is bounded by two possible extreme cases: (1) accumulator or repeller

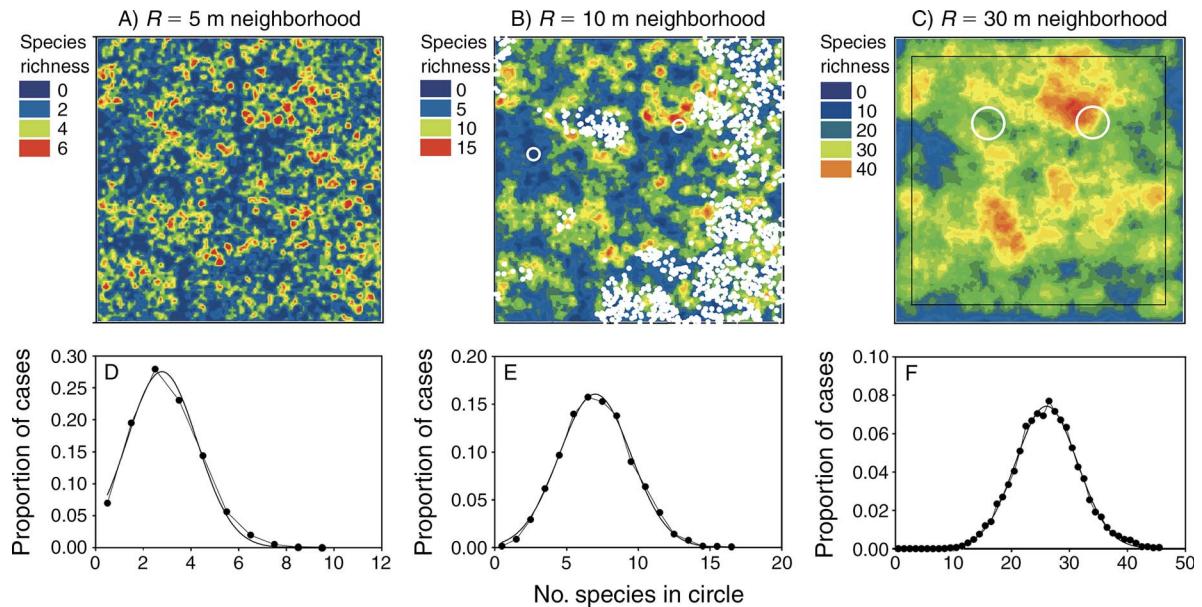


FIG. 1. Spatial variability of local species richness of large trees (dbh > 20 cm) at the Sinharaja tropical forest plot. Panels (A–C) show the spatial variation in local species richness at neighborhoods of $R = 5$ m, 10 m, and 30 m. Panels (D–F) show the corresponding empirical frequency distributions of the neighborhood species richness (dots) measured at the nodes of a 5×5 grid together with the fit with the normal distribution (lines). To give a scale, the white, open circles in (C) have a radius of 30 m and those in (B) of 10 m. White dots in panel (B) show the distribution pattern of the large trees of the species *Mesua nagassarium*, which is generally surrounded by low local species richness (see Appendix: Fig. A2c).

effects are frequent for smaller trees (as expected by neighborhood analysis), but fade away with increasing size class, or alternatively, (2) all size classes show few and weak effects (stochastic dilution).

The first possible outcome is expected based on strong evidence for neighborhood effects of large trees on small trees (e.g., Hubbell et al. 2001, Peters 2003, Uriarte 2004, 2005). Several mechanisms can generate elevated species richness of saplings in the neighborhood of large trees. For example, initially higher species richness of small trees around large trees can arise if the focal species has fruits eaten by seed-dispersing animals that also defecate or drop seeds of other species below or nearby the canopy of the focal species (Jayasekara et al. 2007, Stevenson 2011). Large heterospecific neighbors can also offer favorable microhabitats for seedling germination and seed recruitment (e.g., by building up a humid or shaded micro environment; McIntire and Fajardo 2013). Elimination of conspecifics by negative density- or distance-dependent mechanisms at the seed and seedling stages around large trees (e.g., Janzen Connell and herd protection effects; Janzen 1970, Connell 1971) should translate into relatively higher densities of heterospecific saplings around large trees. With increasing size, however, saplings are expected to suffer from stronger interspecific competition for light, space, and nutrients from large trees (Kohyama 1993). This should reduce the species richness around large trees with increasing tree size.

The second possible outcome of our analyses across different size classes is that species interactions may operate as observed by many neighborhood analyses, but stochastic dilution effects prevent emergence of consistent neighborhood patterns at the species level (McGill 2010, Wiegand et al. 2012). The underlying rationale of the stochastic dilution hypothesis is that, in species-rich tropical forest, each individual of a given focal species is surrounded by a largely different set of competitors (e.g., Goldberg and Werner 1983, Hubbell and Foster 1986, Hubbell 2006). While the outcome of local species interactions for individuals of a given species would be governed, as expected, by deterministic fitness and niche differences, the large variability of outcomes prevents directed responses at the species level. In this case, we expect that only a few focal species should show significant repeller or accumulator effects for any of the sizes classes analyzed here. We also expect that abundant focal species are more likely to show significant effects because their potential signals are less likely to disappear in the background noise of large neighborhood variability.

MATERIALS AND METHODS

Study site

Sinharaja, the largest tract of mixed dipterocarp and lower montane rain forests in Sri Lanka (area of 11 250 ha) constitutes part of the Western Ghats/Sri Lanka biodiversity hotspot. Most of the species in Sinharaja forest are endemic to Sri Lanka (Gunatilleke and

Gunatilleke 1981, Gunatilleke et al. 2004). To monitor the long term forest dynamics and understand the species diversity of tropical forests, the Center for Tropical Forest Science initiated in 1993 the 25-ha (500 × 500 m) Sinharaja long-term forest dynamics plot (FDP). The plot is located at the center of the ever-wet southwestern region of Sri Lanka (6°21–26' N, 80°21–34' E; see Fig. 1 in Gunatilleke et al. 2006). All free-standing stems ≥ 1 cm dbh in the plot have been tagged, measured, identified to species, and mapped in 1994 and recensused in 1999 and 2006. The altitude of the forest plot varies from 424 to 575 m above sea level. The plot receives an average annual rainfall of 5016 mm with no clear dry season. Mean annual temperature of the plot varies from 20.4–24.7°C. More details on the study plot can be found in Gunatilleke and Gunatilleke (1981) and Gunatilleke et al. (2004, 2006).

Tree data

Our analysis considers 181 248 and 173 406 live trees and 15 865 and 8832 dead trees belonging to 206 and 213 species in the second and third census, respectively. The trees were categorized by size into large trees (dbh ≥ 20 cm), intermediates (10 cm ≤ dbh < 20 cm), large saplings (5 cm ≤ dbh < 10 cm), small saplings (1 cm ≤ dbh < 5 cm), and dead trees (≥ 1 cm). Recruits are all trees with dbh ≥ 1 cm in the current census but dbh < 1 cm in the previous census (i.e., they just crossed the 1-cm size threshold). The number of individuals in the different size classes is given in the Appendix A: Table A1. Note that approximately 4% of all living trees have a dbh larger than 20 cm. We estimated the individual species–area relationship $ISAR_f(r)$ for focal species f comprising ≥ 50 large trees. This resulted in a total of 31 and 30 focal species from the second and third census, respectively.

Individual species–area relationship (ISAR) analysis

The standard individual species–area relationship $ISAR_f(r)$ for one community (i.e., all trees > 20 cm dbh) is defined as the mean number of species in circular areas with radius r around the location of the individuals of a given focal species f (Wiegand et al. 2007b) and can be estimated as

$$ISAR_f(r) = \sum_{o=1, o \neq f}^S D_{fo}(r) \quad (1)$$

where the cumulative nearest neighbor distribution function $D_{fo}(r)$ describes the proportion of individuals of the focal species f that have their nearest neighbor of another species o within distance r , and the total number of species is denoted by S . We extend the standard ISAR function to incorporate comparison between size classes. To this end, we use for the focal species f only individuals with dbh > 20 cm (i.e., large trees) and estimate the species richness of individuals of a given size class, such as small saplings (or dead trees), in the

neighborhood r of the focal individuals. We calculated $ISAR_f(r)$ for neighborhoods r from 1 to 50 m with an increment of 1 m. Note that the neighborhoods are estimated from the point location of the stems but not from the outside of the stem.

The independence null model

The key to detect the potential effects of species interactions with the ISAR is use of a null model of species independence (Lotwick and Silverman 1982, Dixon 2002, Wiegand and Moloney 2014). We used a null model that randomly relocates the individuals of the focal species f in a way that the new locations are independent of the distribution pattern of the species of all other species o . The implementation of the independence null model is in general a difficult problem (Wiegand and Moloney 2014). First, it needs to maintain the observed spatial autocorrelation structure of the pattern of the focal species and that of all other species (Lotwick and Silverman 1982, Dixon 2002). For homogeneous patterns, this problem has been approximately solved by the nonparametric torus-translation test (Lotwick and Silverman 1982, Harms et al. 2001) and finally solved by nonparametric techniques of pattern reconstruction (Tscheschel and Stoyan 2006, Wiegand et al. 2013). Pattern reconstruction uses optimization techniques to generate point patterns that very closely match several observed summary statistics simultaneously and therefore resemble the spatial structure of the observed pattern closely (Tscheschel and Stoyan 2006, Wiegand et al. 2013).

A second difficulty in implementing the independence null model arises if the observed patterns are heterogeneous. In this case, it is also necessary to consider spatial variation in the intensity function. More specifically, to study the pure effects of interspecific interactions, the null model must be conditioned on the observed variation in the intensity function $\lambda(x)$ of the focal species. This can be done by using a nonparametric kernel estimate of $\lambda(x)$ with bandwidth R (Stoyan and Stoyan 1994, Wiegand et al. 2007a, b). This approach counts basically all individuals within distance R of a target location x and divides by the area πR^2 to obtain $\lambda(x)$. This is then repeated for all locations x within the study plot (on a 1 × 1 m grid). This procedure averages over potential small-scale variation in tree placement caused by species interactions, but maintains larger scale variation in the intensity function as caused, for example, by habitat association and dispersal limitation. This enables us to detect signatures of small-scale species interactions at distances r shorter than the bandwidth R . Pattern reconstruction that additionally conditions on the observed intensity function (Jacquemyn et al. 2012, Wiegand et al. 2013, Wiegand and Moloney 2014) can thus be used as null model of independence for heterogeneous patterns. The resulting null model patterns show the same larger scale distribution pattern as that observed for the focal species (i.e., the same areas of

the plot have low or high densities of the focal species), and the typical small-scale structures reappear, but at somewhat displaced locations (see Wiegand et al. 2013 and Wiegand and Moloney 2014 for examples of heterogeneous pattern reconstruction). Note that we do not use a parametric approach to estimate the intensity function (e.g., Shen et al. 2009, Wang et al. 2011) because a parametric approach is only able to describe the effect of the available environmental variables on the intensity function. The intensity function may differ from the observed one if important variables are missed out or if the focal species does not occupy the entire suitable area in the plot, as expected under dispersal limitation.

In general, species interactions cause (relative to the expectation of independence) small displacements in the species distribution patterns within the distances over which species interactions may operate (in forests up to some 20 or 30 m; Hubbell et al. 2001, Uriarte et al. 2004, Stoll and Newbery 2005). We therefore used a bandwidth of $R = 50$ m for the estimation of the intensity functions of the focal species. This allows us to assess the effects of interspecific species interactions at distances below 50 m. If positive interactions of the focal species with its interspecific neighbors dominate, it will show a higher species richness in its neighborhood than expected by the null model. A species where the observed $\text{ISAR}_f(r)$ value is above the simulation envelopes is therefore called an accumulator (Wiegand et al. 2007b). Conversely, if negative interactions of the focal species with its interspecific neighbors dominate, it will show a lower species richness in its neighborhood than expected and is called a repeller. If the empirical $\text{ISAR}_f(r)$ falls within the simulation envelopes, we have several possibilities: (1) the focal species exerts no or only weak and insignificant interactions, (2) stronger positive and negative species interactions of the focal species with other species average each other out, or (3) the large variability of the biotic neighborhood of individuals of the focal species does not allow for a directed response on the species level (i.e., the stochastic dilution hypothesis). In these cases, the species has no effect on its neighborhood diversity. Note that this approach cannot separate the effects of interspecific interactions from those mediated, for example, by small-scale edaphic factors (or disturbances) that operate at small spatial scales similar to those of species interactions.

To estimate Monte Carlo simulation envelopes for the empirical ISARs, we generated 199 reconstructed patterns for each focal species and determined the fifth lowest and highest values of the $\text{ISAR}_f(r)$ from these null model simulations. Additionally, to obtain a standardized measure of the effect size for departures from the null model at specific neighborhoods r , we transformed the ISAR function based on the mean $M(r)$ and the standard deviation $\text{SD}(r)$ of the $\text{ISAR}_f(r)$ values taken over the 199 simulation of the null model as

$$\text{ES}(r) = [\text{ISAR}_f(r) - M(r)]/\text{SD}(r). \quad (2)$$

We use the distribution of the effect sizes $\text{ES}(r)$ across all focal species for a given neighborhood r to assess the strength of significant repeller and accumulator effects.

Species-specific analyses

The tendency of a focal species to act as repeller or accumulator species may depend on properties such as the abundance of the focal species (n), the dispersal syndrome of the focal species (gravity/gyration and animal dispersal), the mean nearest-neighbor distance from the individuals of the focal species to conspecific trees (NN_c), and the mean nearest-neighbor distance from the individuals of the focal species to heterospecific trees (NN_h ; see data in Appendix A: Tables A2, A3). These analyses were done for specific size classes, as specified in the Results.

To relate these properties of the focal species to ISAR properties, we used the response variable $D_{r_1-r_2} = \sum_{r=r_1}^{r_2} D_r$ that measures if the focal species acts over a given distance interval (r_1, \dots, r_2) mostly as a repeller, accumulator, or no-effect species. The D_r is a dummy variable that takes values of 0 (for no effect), 1 (for the accumulator effect), and -1 (for the repeller effect) at distance r . In addition, we determined the number of scales at which the focal species has an effect, $N_{r_1-r_2} = \sum_{r=r_1}^{r_2} N_r$. N_r takes values of either 0 (for the no effect) or 1 otherwise. We used the rank correlation coefficient to test for relationships between the response variables and the indices of spatial structure n , NN_c , and NN_h . A Kruskal-Wallis test was used to test the relationships between $D_{r_1-r_2}$ (and alternatively $N_{r_1-r_2}$) and the dispersal syndrome of the focal species. We used a paired two-sample signed rank test to assess the degree of uniqueness of the diversity pattern left by large trees of focal species at 1–25 m scale (see example for Appendix A: Table A4).

RESULTS

General results

Except for small saplings (the most abundant size class; Appendix A: Table A1), the ISAR functions increase almost linearly with neighborhood radius and show considerable variation among focal species (Appendix A: Fig. A1). This variation can be seen by comparing the ISAR results for some focal species. For example, the two animal-dispersed species, *Xylopia championii* and *Myristica dactyloides*, are accumulator species with higher than expected species richness of large trees in their neighborhood (Appendix A: Fig. A2a, b), whereas the species *Mesua nagassarium* is a repeller species with lower than expected species richness of large trees in its neighborhood (Appendix A: Fig. A2c). The fruits of *M. dactyloides* are eaten by bats, Myna (*Gracula ptilogenys*), and Hornbills (*Ocyrceros gingalensis*), which often defecate or drop seeds of other species around these trees. However, small saplings of *M. dactyloides* show no departures from the null model (Appendix A: Fig. A1h). In contrast, large trees of the species *M. nagassarium* have

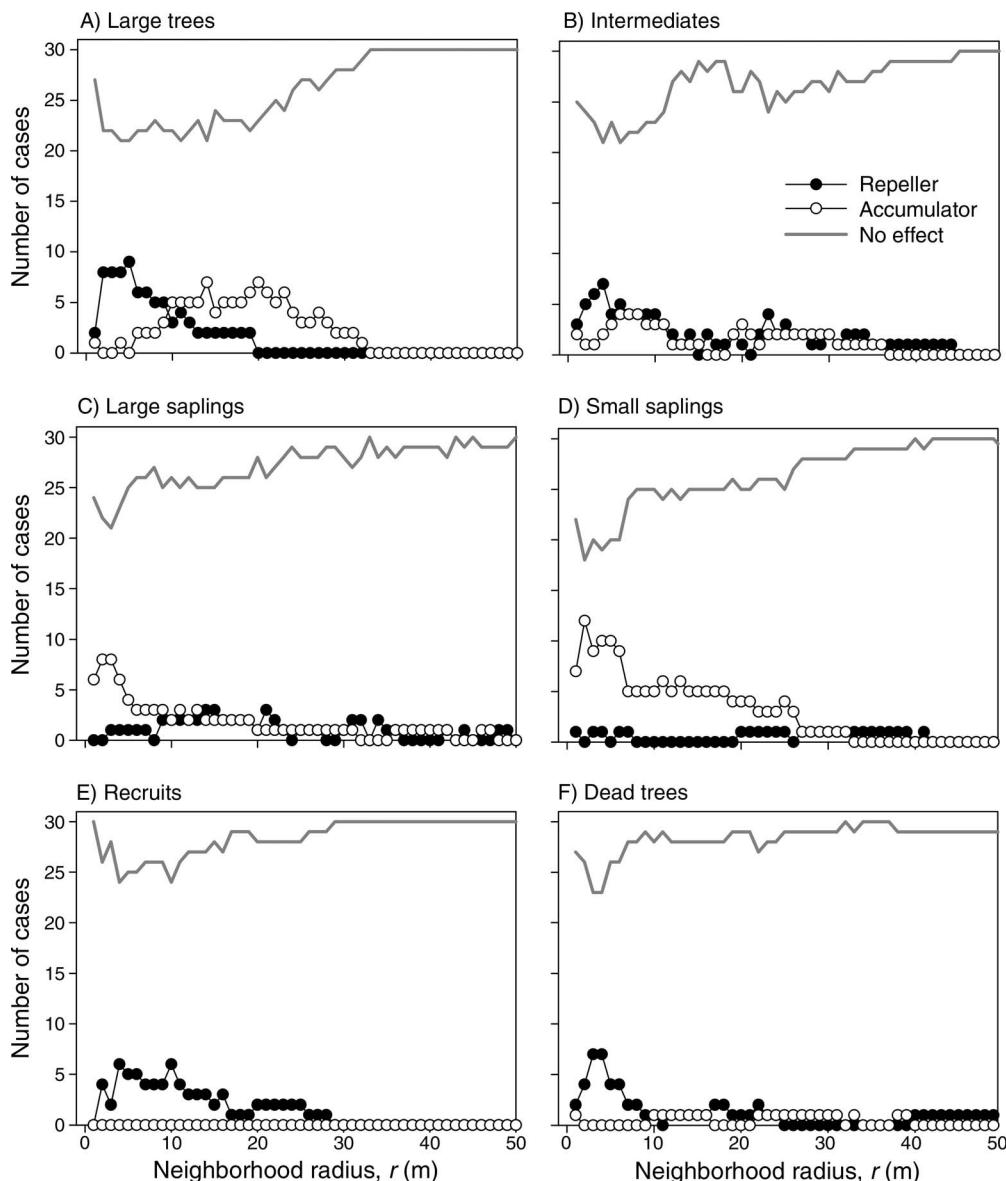


FIG. 2. Number of focal species (with ≥ 50 individuals and $\text{dbh} \geq 20$ cm) that act for the community of respective size classes as repeller species (solid circles), accumulator species (open circles), or show no effect (gray line). Size classes are defined in Appendix: Table A1. The classification as repeller or accumulator species is based on the species richness of the different size classes in the 1–50 m neighborhoods of the large individuals of a focal species relative to the independence null model. Results are for the third census.

strong and negative effects on the neighborhood species richness of large trees at neighborhoods between 2–20 m (Appendix A: Fig. A2c) with effect sizes up to -7 (Appendix A: Fig. A2f). Consequently, the large individuals of *M. nagassarium* are mostly located in local minima of the landscape of local species richness at the 10 m neighborhood (i.e., the blue areas in Fig. 1B). This species is a dominant canopy species with 1055 individuals with $\text{dbh} > 20$ cm, and its seeds are dispersed by gravity near their parent trees (Table 2). In general, the effect-size-transformed results show the departures of the ISAR functions from the null model more clearly than

the ISAR plot and provide a standardized measure of effect size (e.g., Appendix A: Fig. A2d–f).

When analyzing the species richness of large trees in the neighborhood of large trees, we found that the majority of the focal species did not show any significant departure from independence at 20–50 m spatial scale (Fig. 2A) and that departures from the null model were weak in most cases (Appendix A: Fig. A3). Overall, this result confirms the stochastic dilution hypothesis. However, the few departures from the null models point to distinct changes in species interactions with size class (Fig. 2). First, the community of large trees retained a signal of positive effects (Fig. 2A) that formed at the

small sapling stage (Fig. 2D). Second, the community of large trees also showed a signal of negative effects at small neighborhoods (1–10 m; Fig. 2A). However, when looking at successively smaller tree classes, this signal gradually weakened for intermediates (Fig. 2B) and disappeared for saplings (Figs. 2C, D). Interestingly, the peak of the proportion of negative departures from the $ISAR_f$ for the community of large trees coincides approximately with the average nearest neighbor distances to heterospecific large trees, measured from large trees of the focal species (3.1 m; Fig. 2A).

Large trees showed a tendency to be surrounded at the third census by a lower species richness of recruits (Fig. 2E), which however did not persist into the sapling and tree stages. This may be an effect of interspecific clustering of recruits close to their parent trees following episodic recruitment events. This result is also compatible with Janzen-Connell effects where heterospecific recruits in the neighborhood of large trees survive more often into the sapling stage than conspecific recruits, thereby increasing local species richness. For the community of dead trees, we found a peak of 20% repeller species at 3-m neighborhoods (Fig. 2F), which means that dead trees in the neighborhood of large trees originate from a smaller subset of species than expected under the independence null model. The peak coincides with the peak of negative departures found for large trees (Fig. 2A). In general, the results of the two censuses are in good agreement (cf. Fig. 2 and Appendix A: Fig. A4).

Species-specific results

Concerning the species-specific results, the number of scales at which a significant effect (accumulation or repulsion) was observed for large trees (i.e., N_{r1-r2}) was negatively associated with the abundance of the focal species at the 1–10 m interval (Fig. 3, Table 1B). The same result was found for the analysis of small saplings around large trees (Table 1D). In other words, more abundant focal species were more likely to show effects of small-scale species interactions for both large trees as well as small saplings.

The indices NN_c and NN_h of spatial structure of large trees were strongly associated with the variables D_{r1-r2} and N_{r1-r2} at the small 1–10 m scales (Table 1A, B). Focal species with smaller conspecific nearest-neighbor distances (NN_c) were more likely to be repellers, and focal species with more heterospecific crowding and smaller distances to the nearest heterospecific neighbor (NN_h) were more likely to be accumulators. These correlations are likely to be the geometric consequence of competition for space. However, no such correlations were found for the analysis of small saplings around large trees (Table 1C, D).

We found a highly significant relationship between dispersal mode and accumulator and repeller effects with respect to large trees at the 11–30 m spatial scale but not at smaller 1–10 m or larger 31–50 m neighborhoods (Table 1A, B). Animal-dispersed focal species (coded 2;

Appendix A: Tables A2 and A3) tended to show at the 11–30 m scales accumulator effects (i.e., over the 11–30 m variable D_{11-30} tended to show more positive than negative values), whereas gravity-gyration focal species (coded 1) tended to show repeller effects. However, no such effects were detected for the community of small saplings around large trees (Table 1C, D).

Very few species left unique neighborhood diversity patterns at spatial scales of 1–25 m (e.g., *M. nagassarium* and *M. dactyloides*; Appendix A: Table A5). Our results indicate that repeller and accumulator effects of a given focal species are not consistent across size classes (Appendix A: Table A6), thus outlining the stochasticity in the species associations with respect to individual focal species, which supports the stochastic dilution hypothesis.

DISCUSSION

We used data from the 25-ha Sinharaja tropical forest dynamics plot and analyzed the species richness of trees of different size classes in the neighborhood of large trees of different focal species to assess if the net effects of species interactions translate into identifiable spatial patterns in local species richness around large trees. Our analysis across size classes was motivated by earlier studies that found in the spatial patterns of species-rich communities only few indications of interspecific interactions among large trees (e.g., Lieberman and Lieberman 2007, Wiegand et al. 2012, Perry et al. 2014) and neighborhood analyses that found significant effects of large trees on growth and survival of saplings (e.g., Hubbell et al. 2001, Uriarte et al. 2004, 2005). The range of possible outcomes of our expanded analysis across size classes is therefore bounded by two possible extreme cases: signals of species interaction in spatial patterns of local species richness are frequent for smaller trees, but fade away with increasing size class, or alternatively, all size classes show few and weak signals of species interactions in the spatial patterns (stochastic dilution).

The overarching result of our study is that only a low proportion of the focal species showed signals of species interactions with trees of the different size classes (Fig. 2) and they were generally weak (Appendix A: Fig. A3). We found that significant departures of large trees and of small saplings from the null model were more likely if the focal species were more abundant. There was also little consistency of focal species with respect to the accumulator/repeller property during the ontogeny. These results largely confirm the stochastic dilution hypothesis. However, the few signals of species interactions detected by our analysis are consistent with expectations of the effect of competition for space and the dispersal syndrome on spatial patterns. A signal of competition for space found for large trees (Fig. 2A) built up gradually with increasing size; it was not yet present for large saplings (Fig. 2C) but visible for intermediates (Fig. 2B). Animal-dispersed focal species tended to show higher than expected species richness of large trees just outside the canopy of large focal trees,

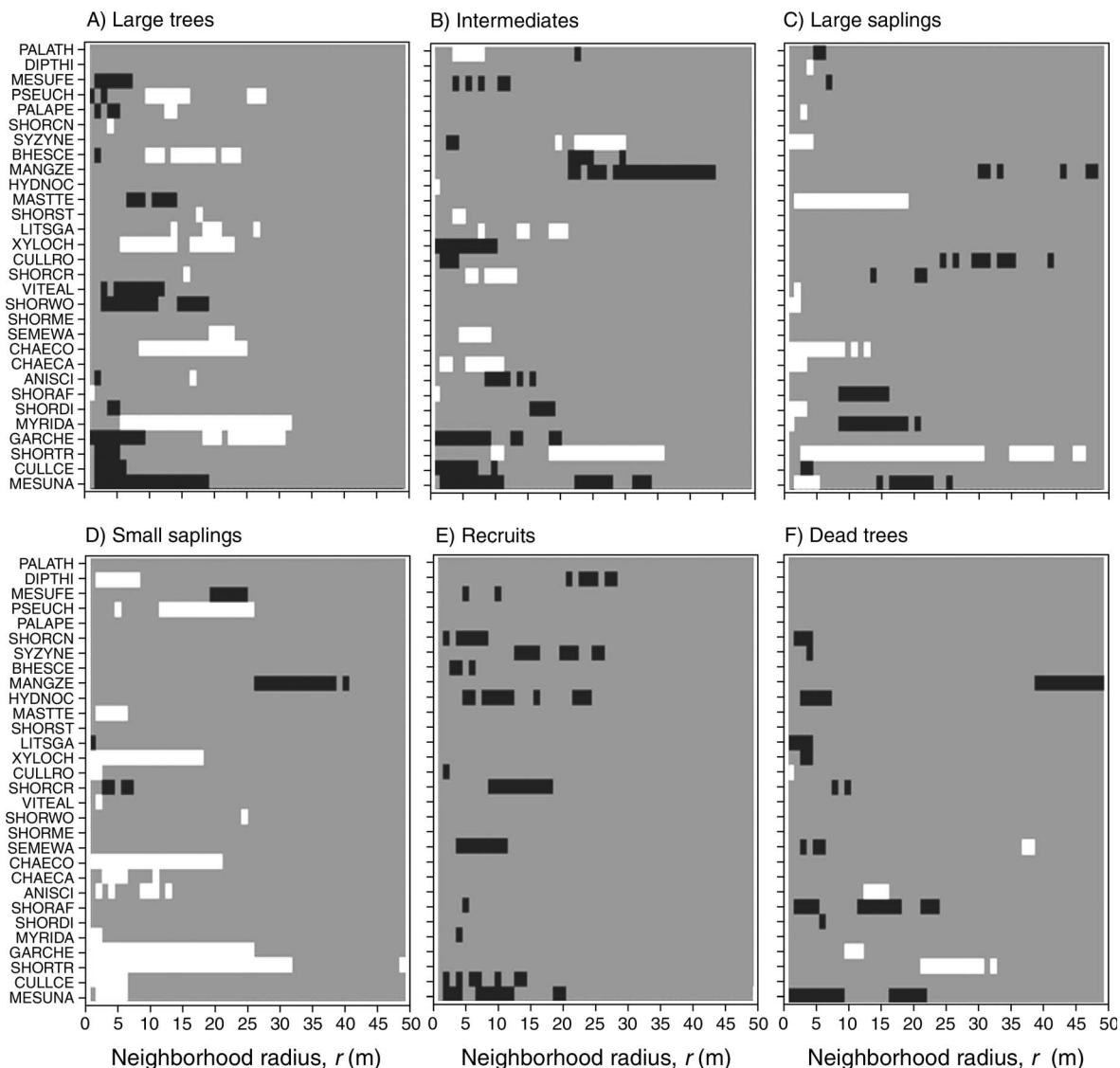


FIG. 3. Summary of the results for individual focal species for the third census. Neighborhoods r , for which the species richness of the given size class was larger than expected (accumulator species), are indicated by white, those with less than expected species richness (repeller) are indicated by black, and gray indicates no effect, i.e., no departure from the independence null model. Full species names are given in Table 2.

whereas gravity-gratation focal species tended to show at this scale lower than expected species richness. Thus, our results suggest that the Sinharaja forest is situated close to the stochastic dilution end of the continuum spanned by the two extreme possible outcomes of our expanded size-class analysis, but that species interactions are largely, but not completely, overpowered as pattern generating mechanisms by stochastic effects.

Stochastic vs. deterministic effects

The majority of the focal species did not show detectable effects of species interactions. This result is somewhat surprising because we adopted a plant's-eye view of the community (Turkington and Harper 1979),

which was explicitly designed to analyze the neighborhoods of individual trees where interactions may occur. This result is also surprising because statistical neighborhood models that relate the performance of individuals (e.g., growth and survival) to their biotic neighborhood found strong evidence for effects of large trees on the performance of small trees (e.g., Hubbell et al. 2001, Peters 2003, Uriarte et al. 2004, 2005). This makes the hypothesis that the focal species exerts no or only weak interactions less likely. The second hypothesis to explain weak and insignificant interactions is that stronger positive and negative species interactions of the focal species with other species just average each other out. This mechanism may contribute to the weak observed

TABLE 1. Rank correlation coefficients between species properties and individual species–area relationship (ISAR) results (shown in Appendix: Tables A2 and A3).

Scales	<i>n</i> correlation	NN _c correlation	NN _h correlation	Dispersal mode, chi-square value
A) Large vs. large trees, calculated for variable $D_{r_1-r_2}$ from Appendix: Table A2				
1–10 m	−0.18	0.35†	−0.68***	0.059
11–30 m	0.02	0.23	−0.30†	6.768***
31–50 m	0.14	−0.06	−0.06	0.383
B) Large vs. large trees, calculated for variable $N_{r_1-r_2}$ from Appendix: Table A2				
1–10 m	−0.33†	0.51**	−0.66***	0.059
11–30 m	−0.22	0.00	−0.08	6.402***
31–50 m	−0.14	0.06	0.06	0.383
C) Small saplings vs. large trees, calculated for variable $D_{r_1-r_2}$ from Appendix: Table A3				
1–10 m	0.39*	−0.06	−0.07	2.011
11–30 m	−0.03	0.20	0.19	2.487
31–50 m	0.10	0.12	0.29	0
D) Small saplings vs. large trees, calculated for variable $N_{r_1-r_2}$ from Appendix: Table A3				
1–10 m	−0.37*	0.03	0.07	1.8763
11–30 m	−0.20	0.02	−0.10	0.3452
31–50 m	0.03	−0.20	−0.17	1.342

Notes: Rank correlation coefficients measured by the variables $D_{r_1-r_2} = \sum_{r=r_1}^{r_2} D_r$ and $N_{r_1-r_2} = \sum_{r=r_1}^{r_2} N_r$ for different spatial scales (r_1, r_2). D_r can take values 0 (for no effect species), 1 (for accumulator species), and −1 (for repeller species) at distance r . The variable N_r can take values 0 (for no effect species) and 1 otherwise. Variables are species abundance (n), mean nearest neighbor distance to conspecifics (NN_c), and mean nearest neighbor distance to heterospecifics (NN_h).

† $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

interaction effects, but it is somewhat unlikely that such a delicate balance would occur for many focal species.

The third hypothesis to explain this apparent contradiction (the stochastic dilution hypothesis) is based on the stochastic geometry of biodiversity and states that species interactions may be overpowered in species-rich communities by stochastic dilution effects (Volkov et al. 2009, McGill 2010, Wiegand et al. 2012). In species rich systems, the identity of the nearest neighbors of individuals of a given species are largely unpredictable (Hubbell 2006), and each individual may be surrounded by a different set of competitors (Hubbell and Foster 1986, Hubbell 2006). While the outcome of local species interactions for individuals of a given species can be governed, as expected, by deterministic fitness and niche differences, the net outcome of competition with the nearest neighbors may differ at the level of virtually every individual, and focal species may only rarely show consistent interactions with their neighbors that would translate into detectable spatial patterns. A similar mechanism has been proposed to explain convergence on similar, competitively equivalent, life-history strategies on evolutionary timescales (e.g., Goldberg and Werner 1983, Hubbell and Foster 1986).

Note that neighborhood models relate the variability in the biotic neighborhood of individuals of a focal

species to their performance, whereas our approach compares the average biotic neighborhood of individuals across a focal species to that of random locations within the plot. Thus, the observed patterns in plant performance may not translate into detectable spatial patterns on the species level, especially if the variability in the biotic neighborhoods is large.

Mechanisms leading to elevated or reduced neighborhood biodiversity

Large trees physically occupy a certain area that allows only for little overlap with other large trees. Thus, competition for space will slightly reduce the number of large trees, and therefore, the number of species in the close neighborhood of large trees (Wiegand et al. 2007b, Perry et al. 2009), thereby producing repeller species. We have approximately 6800 large trees at the 25-ha plot, and thus an average area of 36.8 m² is available to each large tree (which corresponds to an average neighborhood with a 3.4 m radius). Thus, the peak in repeller effects (Fig. 2A) coincides just with the average neighborhood occupied on average by one large tree. Our results therefore confirm this competition mechanism, although only for few focal species (Fig. 2A). However, a similar analysis showed that such repeller effects occurred for two-thirds of the focal species

TABLE 2. Name of the species, dispersal mode, neighborhood diversity at 1–50 m for second census, and species abundance of large trees of focal species.

sp.	Species name	Acronym	Dispersal mode	Abundance C2	Abundance C3
1	<i>Camposperma zeylanica</i>	CAMPZE	Zoochory	50	§
2	<i>Palaquium thwaitesii</i>	PALATH	...	55	54
3	<i>Dipterocarpus hispidus</i>	DIPTHI	Anemochory	58	63
4	<i>Mesua ferrea</i>	MESUFE	Barochory	66	64
5	<i>Dysoxylum championii</i>	PSEUCH	Zoochory	68	74
6	<i>Palaquium petiolare</i>	PALAPE	Zoochory	70	75
7	<i>Shorea congestiflora</i>	SHORCN	Anemochory	70	77
8	<i>Syzygium neesianum</i>	SYZYNE	Zoochory	71	70
9	<i>Bhesa ceylanica</i>	BHESCE	Zoochory	71	69
10	<i>Mangifera zeylanica</i>	MANGZE	Zoochory	79	80
11	<i>Hydnocarpus octandra</i>	HYDNOC	Zoochory	81	81
12	<i>Mastixia tetrandia</i>	MASTTE	Zoochory	83	79
13	<i>Shorea stipularis</i>	SHORST	Anemochory	100	104
14	<i>Litsea gardneri</i>	LITSGA	...	102	87
15	<i>Xylopia championii</i>	XYLOCH	Zoochory	110	118
16	<i>Durio rosayroana</i>	CULLRO	Zoochory	121	138
17	<i>Shorea cordifolia</i>	SHORCR	Anemochory	120	130
18	<i>Vitex altissima</i>	VITEAL	Zoochory	123	125
19	<i>Shorea worthingtonii</i>	SHORWO	Anemochory	131	143
20	<i>Shorea megistophylla</i>	SHORME	Anemochory	137	133
21	<i>Semecarpus walkeri</i>	SEMEWA	Zoochory	143	137
22	<i>Chaetocarpus coriaceus</i>	CHAECO	Zoochory	159	147
23	<i>Chaetocarpus castanocarpus</i>	CHAECA	Zoochory	165	161
24	<i>Anisophyllea cinnamomoides</i>	ANISCI	...	176	184
25	<i>Shorea affinis</i>	SHORAF	Anemochory	221	222
26	<i>Shorea disticha</i>	SHORDI	Anemochory	234	246
27	<i>Myristica dactyloides</i>	MYRIDA	Zoochory	335	340
28	<i>Garcinia hermonii</i>	GARCHE	Zoochory	358	376
29	<i>Shorea trapezifolia</i>	SHORTR	Anemochory	409	420
30	<i>Durio ceylanica</i>	CULLCE	Zoochory	670	718
31	<i>Mesua nagassarium</i>	MESUNA	Barochory	1055	973

Notes: Ellipses indicate data was not available. C2 is second census, and C3 is third census.

§ Species with <50 individuals with dbh \geq 20 cm were not considered.

analyzed in the tropical forest at Barro Colorado Island, Panama (Wiegand et al. 2007b). At Sinharaja, this signal of competition for space built up gradually with increasing life stage; it was not yet present for large saplings but visible for intermediates (Fig. 2).

Seed dispersal by animals can create elevated species richness around tree species, such as *M. dactyloides* (Fig. A2b), that have fruits eaten by bats, Myna (*Gracula ptilogenys*), and Hornbills (*Ocyrceros gingalensis*), which often defecate or drop seeds of other species around these trees (Table 2; Jayasekara et al. 2007). We found positive accumulator effects for roughly one-third of the focal species where the species richness of small saplings in the 1–25 m neighborhood of large trees was larger than expected by the null model. These positive effects were maintained up to the community of large trees, except for small neighborhoods where they were replaced by negative effects. Correlation of species properties with the ISAR results showed that species richness of large trees was only associated to the dispersal syndromes of the focal species (i.e. animal vs. gravity-gyration; Table 1A) at medium spatial scales. Focal species with animal-dispersed seeds tended to have higher species richness of large trees in their neighborhood than the gravity- and gyration-dispersed species. This suggests that frugivores, which eat the fruits of the focal species, but also defecate

or drop seeds of other species around the trees of the focal species, can generate higher species richness in the neighborhood of these focal species. These results agree with Seidler and Plotkin (2006), in that the dispersal mode is important for establishing the long term community structure of tropical forests. However, species richness of small saplings did not differ with respect to dispersal syndrome of the focal species (Table 1C). One explanation for this is that animals strongly contributed in the past to seed dispersal and therefore to the spatial distribution patterns of the large trees, but that seed-dispersing animals declined thereafter and could not provide the same seed dispersal service for the trees which are now small saplings and recruits (Harrison et al. 2013).

Recruits from the third census showed reduced species richness in the neighborhood of large trees, which points to an effect of aggregation of conspecific recruits below the canopy of large trees. This is expected because several of the dominant species at the Sinharaja forest plot show strong seed-dispersal limitations due to their seed dispersal by gyration and gravity where most seeds land close to their parents. Such reduced species richness of recruits can also originate from low recruitment success under low light and strong competition for space in the neighborhood of large trees.

CONCLUSIONS

Our results suggest that deterministic effects of species interactions in the tropical forest at Sinharaja were largely diluted by stochastic effects caused by the unpredictable biotic neighborhood of individuals of a given focal species. We hypothesize that this effect prevented establishment of consistent interactions of focal species with their neighbors that would translate into detectable spatial patterns. The stochastic dilution hypothesis suggests a mechanism based on stochastic geometry of biodiversity (McGill 2010) that can explain the repeated finding that communities of large trees in species-rich tropical forests show only few indications for species interactions (e.g., Lieberman and Lieberman 2007, Wiegand et al. 2012, Perry et al. 2014) and why major theories of biodiversity can neglect species interactions when predicting macroscopic community patterns, such as SAR, species-abundance distributions, and decay of similarity (McGill 2010).

Nevertheless, our analysis across the entire ontogeny from recruits to large trees could detect a noisy signal of species interactions in the pattern of local species richness around large trees. It is therefore likely that stochasticity did not fully dilute the effects of species interactions at the Sinharaja forest. Rather than being competing, these two extreme cases can be conceptualized as a continuum in function of species richness, where effects of species interactions are relatively more important for species-poor communities, and relatively less important for species-rich communities.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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