Spatial patterns of tree species distribution in New Guinea primary and secondary lowland rain forest

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Abstract

Questions: How do spatial patterns of tree distribution and species co-occurrence differ between primary and secondary tropical rain forests? What signatures of ecological processes might be discerned by comparing the spatial patterns of trees between primary and secondary forest plots?

Location: Tropical rain forest vegetation, lowlands of Papua New Guinea.

Methods: All trees over 5 cm DBH were surveyed in two non-replicated 1-ha plots situated in primary and secondary forest. Grid location, DBH, height and species identity were recorded for all surveyed trees. Analysis of the spatial pattern and the autocorrelation of tree sizes and identities were used to assess the structure of the forest found within the plots. Functions combining Ripley's K and the individual species–area relationship were applied to study the spatial distribution of trees and species diversity.

Results: The spatial distribution of common species, and all stems collectively, was aggregated in the secondary forest plot but not different from random in the primary forest plot. Diameter and height were also strongly spatially auto-correlated in the secondary forest plot but not in the primary forest plot. Conspecific aggregations were more common in the secondary forest plot. Finally, the secondary forest plot was characterized by the presence of diversity-repelling species and lower diversity than the primary forest plot, where diversity-accumulating species were present.

Conclusions: We attribute the weaker autocorrelation of tree size in the primary forest to the development of size hierarchies throughout the course of stand aging. The conspecific aggregation and low local diversity within the secondary forest plot are likely caused by dispersal limitation during a brief period of establishment after disturbance. The higher local diversity of the primary forest can be explained by the reduction of species aggregation through increased mortality of conspecifics. This is caused by strong intraspecific competition, supporting the spatial segregation hypothesis (interspecific spatial segregation).

Introduction

As sedentary organisms, most plants interact mainly with their immediate neighbours, and as such, current spatial patterns could preserve an imprint of past ecological processes and interactions in the neighbourhood. When different processes yield similar patterns, linking spatial distributions to ecological mechanisms is not straightforward, but this link remains an important goal in ecology (Lepš 1990; Law et al. 2009; McIntire & Fajardo 2009). For

example, the spatial aggregation of individuals in patches could be a consequence of limited dispersal ability, environmental heterogeneity (such as topographic or edaphic variability), positive interactions among individuals, or some combination of these factors (Ripley 1987). Identifying the processes responsible for aggregation in forests is further complicated by disturbance, where patchy distributions could be due to regeneration in gaps (Perry et al. 2008). On the other hand, a regular spatial pattern (i.e. evenly spaced individuals) is often ascribed to local density-dependent effects including mortality caused by species-specific natural enemies (pests and pathogens; Janzen 1970) or competition among conspecific neighbours (Lepš & Kindlmann 1987; Stoll & Bergius 2005). Furthermore, different ecological processes may prevail at different spatial scales. Biotic interactions, for example, operate mostly at the neighbourhood scale (mostly up to 10–20 m radius) whereas processes such as dispersal and abiotic filtering due to environmental heterogeneity (e.g. topography and slope) operate at scales ranging from the neighbourhood to the landscape (Wiegand et al. 2007b; Getzin et al. 2008). New spatial statistics (e.g. Wiegand & Moloney 2014) have been developed for the purpose of inferring the scale dependence of the relative roles of biotic interactions, environmental heterogeneity, dispersal limitation and their combined effects on community composition (Comita et al. 2007; Wang et al. 2013).

Spatial patterns of forest stem distribution also change during stand development. Spatial change often begins with the aggregation of species or individuals in young stands that develop into randomly or evenly spaced patterns in more mature stands (Lepš & Kindlmann 1987; Stoll & Bergius 2005). This pattern of successional change has even been observed in non-forest pioneer communities, where abiotic stress or disturbance strongly influences biotic interactions (Malkinson & Kadmon 2007; Velázquez et al. 2014). When studying the developmental changes of forest stands, changes in the sizes of trees provide an additional clue to ongoing processes (Moeur 1997; Comita et al. 2007). For example, the spatial autocorrelation of tree sizes is expected to decrease over time due to competition among similarly-sized individuals; positive spatial autocorrelation in young stands or early successional stages may be interpreted in terms of individuals having dispersed to a site and successfully established at a common point in time (Getzin et al. 2006; Suzuki et al. 2008). Assessing spatial patterns at a given point in time may of course be insufficient to detect ongoing processes, but it provides a necessary first step.

Spatial patterns can also affect community processes. It has been hypothesized that spatial segregation (or intraspecific aggregation) in multi-species communities can increase the importance of intraspecific competition relative to interspecific competition (Pacala & Levin 1997).

Interspecific spatial segregation may promote the survival of weaker competitors (Stoll & Prati 2001; Fibich & Lepš 2011) and thereby increase local co-existence of species in communities (Pacala & Levin 1997; Raventos et al. 2010). Analysis of data from the 50-ha Barro Colorado Island Forest Dynamics Plot (Volkov et al. 2009) suggests that interspecific interactions between the most common species are weaker than intraspecific interactions. Moreover, in diverse tropical forests, common species that are significantly less aggregated than rare species may experience less intraspecific competition and density-dependent mortality (Condit et al. 2000; Comita et al. 2010).

The analysis of multi-species associations may also provide insights into the mechanisms of community assembly. Conspecific aggregations (when nearby individuals belong to the same species more often than expected by chance) could result from limited dispersal or from differential establishment across environmental gradients due to topography, slope or soil conditions (Ripley 1987; Getzin et al. 2008). On the other hand, the pattern when close neighbours belong to different species more often than expected by chance could be due to stronger negative interactions among conspecific neighbours than among heterospecific ones. Analysis of multi-species spatial patterns at several scales and the incorporation of individual-level properties may help to disentangle the effects of past and ongoing processes in communities (Podani & Czárán 1997; Shimatani 2001). The individual species–area relationships function (ISAR; Wiegand et al. 2007a) uses the popular species–area relationship (SAR) to evaluate the expected number of species in a circular area defined by the radius around a particular individual drawn at random from a species population. This method enables the assessment of scale-dependent patterns of diversity in the neighbourhood of the individual. For example, positive deviations in ISAR values from null expectations for rare species can support the 'safety in diversity' hypothesis (Wills et al. 1997), where presence in highly diverse clumps should be advantageous in comparison with intraspecifically aggregated individuals, e.g. due to a lower chance of being attacked by natural enemies. ISAR varies according to the spatial distribution of populations, such that the signature of biotic interactions can be confounded by the influence of environmental heterogeneity, which filters species among neighbourhoods and across the landscape (Queenborough et al. 2012).

In the tropics, most studies have focused on mature forests (e.g. Condit et al. 2000; Brown et al. 2013). Comparisons among successional stages are rather scarce (Greig-Smith 1952) even in other habitats (but see Malkinson & Kadmon 2007; Felinks & Wiegand 2008; Velázquez et al. 2014), nevertheless, these comparisons might help to understand the processes maintaining high tropical forest

Table 1. Main hypotheses, applied point pattern analyses and null models with corresponding figures.

Hypotheses	Point-pattern analyses, null models and figures
(H1) Hypothesis 1 – General spatial patterns	
Tree individuals are randomly or regularly distributed due to competition in the primary forest plot. A clumped pattern prevails in the secondary forest plot because of strong dispersal and establishment limitation processes. The patterns remain even after filtering out of inhomogeneous density of individuals in both forests	Pair-correlation function (g) with the null models 'complete spatial randomness' (NM1; Fig S2–S4) and inhomogeneous pair-correlation function considering inhomogeneous density of trees (NM2; Figs 2, S5)
(H2) Hypothesis 2 – Size hierarchies	
Shorter time for development of size hierarchies leads to more spatially correlated DBH and height of trees in the younger secondary forest plot than in the older primary forest plot	Mark correlation function (κ_{mm}) and mark variogram (γ) with the null model of random labelling of tree sizes (DBH and height; NM3; Fig. 3)
(H3) Hypothesis 3 – Species diversity	
Species will be more randomly distributed in the primary forest plot than in the secondary forest plot, because in the primary forest, conspecific clumps have been thinned by intraspecific competition, which has been stronger than interspecific competition. As a consequence, species number and species diversity (Shannon and Simpson indices) will be higher and there will be more species around the most common species in the primary forest plot than in the secondary forest plot	Mark correlation function (κ_{id}) comparing species identities (NM2; Fig. S7) and 'spatialDiversity' function with two null models: (1) inhomogeneous density of trees (NM2; Fig. S8) (2) random shifting of conspecific patterns (NM4; Figs 4, S9)

diversity. Our aim is to track how the legacy of dispersal processes and plant–plant interactions over succession can be observed in current spatial patterns by combining information on the location of individuals with their species identity and size (Table 1). Our study is based on two contrasting plots of different ages, an early successional forest in an abandoned garden and a nearby mature (primary) forest, in relatively homogeneous terrain (Whitfeld et al. 2012a). Because the time scale at which individual processes operate differs between young and mature forest, our comparison should enable us to deduce the relative importance of these processes in determining the spatial pattern formation in the two contrasting successional stages.

Methods

Field plots

Two 1-ha plots near Wanang village (145°10′55″ E, 5°13′51″ S), Madang Province, Papua New Guinea, were sampled, one in primary and one in secondary lowland tropical forest vegetation (Fig. 1). Plots were located in mixed evergreen rain forest, <1 km apart from each other and on relatively level (flat) ground approx. 140 m a.s.l. The primary plot was dissected by a small drainage channel and had an entirely closed canopy, and the plot in secondary forest included a small patch of grassland (<2% of the plot). The climate of the research sites can be described as moist tropical with mean annual rainfall of 3500 mm and mean monthly temperature between 26.2 and 26.7 °C. Mean monthly rainfall exceeds 100 mm throughout the year (Novotny & Basset 1998). The plot in primary forest had not been affected by human disturbance for at

least 60 yr before our study was conducted (Whitfeld et al. 2012a); although we cannot exclude the possibility that the plot was disturbed earlier. The plot in the secondary forest was located in a former mixed crop food garden, which was created by clear felling of the primary forest as a part of traditional slash-and-burn agricultural practice. Our secondary forest plot had been abandoned and overgrown with secondary succession for ca. 10 yr before our study was conducted. In both plots, all trees with DBH ≥ 5 cm were recorded with their coordinates (*x-y* positions), DBH, height and species identity. Woody climbers were excluded from the analysis. For more information on plant surveys see Whitfeld et al. (2012b).

Spatial analysis

Spatial patterns of trees were described using the pair and mark correlation functions (Wiegand & Moloney 2014). We used the pair correlation function (PCF, g(r), also known as neighbourhood density function) defined as:

$$g(r) = K'(r)/2\pi r \qquad (1)$$

where $K'(r)$ is a derivation of Ripley's K function (Ripley 1987). PCF avoids the cumulative characteristic of Ripley's K function, and thus allows the separation of clustering at different spatial scales (Wiegand & Moloney 2014). Values of g(r) = 1 suggest a random point process (or so-called 'complete spatial randomness' (CSR)), g(r) < 1 suggest regularity (uniform pattern), and g(r) > 1 suggest clumping (aggregated, patchy pattern) at the scale defined by a given radius, *r* (Table 1: H1).
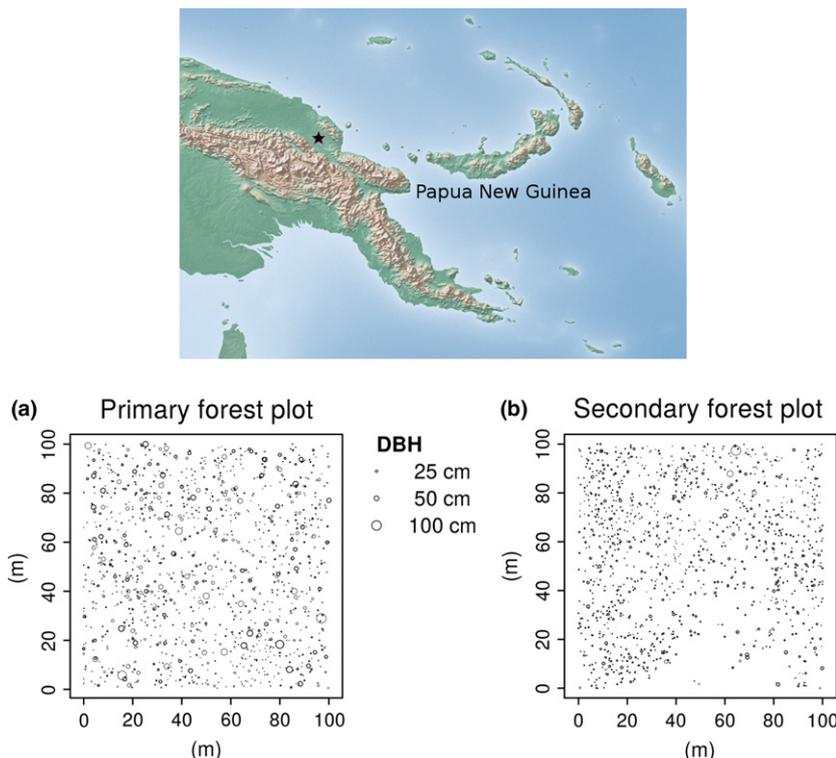
Fig. 1. Geographic position of the plots in Papua New Guinea and map of all stems within (**a**) primary and (**b**) secondary forest plots. Points with black colour corresponds to individuals of species having 20 or more individuals, grey colour is for individuals of less common species.

Various characteristics of spatial pattern might be ascribed to various underlying mechanisms (Table 1). Specifically, we tested whether the qualitative and quantitative marks of individuals, including species identity, DBH and height, are spatially aggregated/segregated using a mark correlation function κ (Stoyan & Stoyan 1994; Wiegand & Moloney 2014). κ(r) is defined as the mean value of a test function $f(m_1, m_2)$ at a distance r. The similarity of DBH or height of two individuals is quantified by the normalized mark correlation function κ_{mm} with the test function:

$$f(m_1, m_2) = m_1 * m_2 \qquad (2)$$

where m_1 and m_2 are DBH or height values of two neighbouring individuals. Values of κ_{mm} (r) higher or lower than 1 signify that within a given spatial scale r, individuals tend to have higher, or lower, DBH – or height – than the plot-wide mean value (Table 1: H2). For quantitative marks, such as DBH and height, we also used a normalized mark variogram γ(r) (Wiegand & Moloney 2014) to test for spatial autocorrelation. Lower than 1 γ(r) values signify that at a given spatial scale r, individuals with the same DBH (or height) tend to be found together; values higher than 1 indicate that individuals with different DBH (or height) are more likely to be found together. The spatial similarity of

species identity is evaluated by the non-normalized mark correlation function κ_{id} with the test function:

$$f(m_1, m_2) = m_1 \;==\; m_2 \qquad (3)$$

where m_1 and m_2 are species identities of two neighbouring individuals, i.e. the function value equals 1 for two con-specific individuals, and 0 for two heterospecific individuals. Higher than mean or lower than mean $\kappa_{id}(r)$ values signify that at a given spatial scale r, individuals of the same species are more (positive) or less (negative) likely to be found together, respectively. κ_{id} relates to the distance-decay (similarity) function (Chave & Leigh 2002; Wiegand & Moloney 2014) and equals 1 − α, where α is the spatially explicit Simpson index (Shimatani 2001).

The number of species and species diversity on different scales in the plots were compared (Table 1: H3) using our bespoke 'spatialDiversity' R function (R Foundation for Statistical Computing, Vienna, AT; see source code and usage in Appendix S2). This function computes mean species number and species diversity (e.g. as Simpson's diversity index) with increasing spatial scale. It is similar to the cumulative Ripley's K function, but counts the number of species or species diversity of the individuals. An edge correction for given scale s (value in m) was implemented using only individuals with x-y positions

and scales, *s* that do not reach the border of the plot. By specifying a parameter `fun`, our function can compute: (1) an ISAR function (Wiegand et al. 2007a) that is able to predict species number around the individuals of the focal species or around all individuals (overall spatial diversity), (2) a distance dependent Simpson index $\alpha(r)$ (Shimatani 2001) defined as the probability that a randomly selected pair of individuals within a distance *r* belong to different species, and also (3) a distance-dependent Shannon index that can evaluate species diversity or species number around an arbitrary group of individuals (e.g. big individuals, rare species, etc.).

To deduce the importance of various processes (e.g. competition), we need to know whether the values of the above functions differ from those expected by null models. For this purpose, we designed three hypotheses, which enable us to test whether the values of the above functions deviate from those expected under various null models (Table 1). We compared the results from the two contrasting plots with the aim of evaluating current mechanistic hypotheses (Table 1) on the processes governing spatial patterns in the primary and secondary forest plots.

Hypothesis 1 – General spatial patterns

In order to investigate the spatial pattern of individuals in both plots, we applied a homogeneous pair correlation function (PCF, g(*r*)) together with complete spatial randomness as a homogeneous Poisson null model (NM1) (Table 1). Further, to account for possible large-scale spatial inhomogeneity of density at the individual level we used an inhomogeneous PCF ($g_{inhom}(r)$) with an inhomogeneous (heterogeneous) Poisson null model (NM2). Here, a density gradient of individuals is non-parametrically estimated by a Gaussian smoothing function with SD (bandwidth) of 30 m (Law et al. 2009), which accounts for possible inhomogeneous density of individuals over the plot (e.g. it removes virtual aggregation in the secondary forest due to the small patch of grassland). However, the high value of bandwidth we chose is not able to reflect inhomogeneity on the scale of the neighbourhood distance, and so it does not filter out the effect of neighbour–neighbour interactions. Inhomogeneous density is often the effect of environmental gradients that are usually considered the most likely causes of broad-scale patters, although dispersal cannot be excluded either.

Both null models were applied to all individuals and to individuals of common species, i.e. species with at least 20 individuals in a plot. There were only 12 common species in each plot, but none of them was common in both plots, and consequently, we were not able to compare spatial patterns of any particular species between the primary and secondary forest.

Hypothesis 2 – Size hierarchies

To investigate the spatial association of tree DBH and height, we applied two tests, using mark correlation function (κ_{mm}) and mark variogram (γ) (Table 1). For both, we used the null model (NM3) that assumed random labelling (i.e. random permutations of DBH or height) while keeping positions of individuals fixed (Goreaud & Pelisier 2003). Identical for both functions, the null hypothesis assumed that the DBH and height values are independent of spatial positions of individuals within the plot, i.e. the size of neighbours is independent. Both functions were applied to all individuals.

Hypothesis 3 – Species diversity

We applied the mark correlation function (κ_{id}) to obtain an overall pattern of similarity of species identities along different spatial scales (distance decay similarity) with the inhomogeneous NM2 (see Hypothesis 1 for details) (Table 1). The null model filters out the effects of inhomogeneous density of individuals of the species (individuals of a single species were generated according to their observed density) and this hypothesis assumed that individuals within species are not spatially associated.

Our 'spatialDiversity' function computed species diversity around trees with increasing spatial scale. It was applied with a random shifting null model (NM4), in which the relative spatial positions of conspecific individuals are conserved, but the coordinates of all individuals of each species are shifted by the same random direction and distance within the plots (which is assumed to be torus-shaped), independently of the other species (independence null model; Goreaud & Pelisier 2003). The values of the function for the observed pattern will be under the null model values if the species are spatially segregated, and higher than expected if the species are more intermingled than expected by chance. The latter situation suggests that interspecific interactions are less negative than intraspecific interactions, which should promote species co-existence. NM4 was applied to filter out the possible mechanisms causing individual species patterns (e.g. the effects of clumping due to dispersal). We also used our 'spatialDiversity' function to investigate patterns in species numbers and species diversity after filtering out the inhomogeneous density of individuals (NM2). Wiegand et al. (2007a) used this null model with ISAR whilst estimating inhomogeneous density for each species separately to distinguish their relationship to the number of species around them; we followed this approach. NM2 allowed us to investigate spatial diversity independently of inhomogeneous individual density (e.g. possi-

ble environmental heterogeneity due to presence of the grassland in the secondary forest).

The 'spatialDiversity' function was applied to all individuals, to the six most common species and to the 190 individuals of rarest species (taking singletons, species with two individuals .. up to 190 individuals). When applied to individual species, this approach enables us to separate species into diversity attractors (i.e. species having more diverse neighbours than expected), diversity neutral species and diversity repelling species (species having less diverse neighbours than expected; Table 1).

For technical details about simulations see Appendix S1.

Results

The primary forest plot was characterized by higher basal area, higher number of species, higher number of singletons (species having only one individual) and lower dominance of the most common species (having ≥20 individuals) than the secondary forest plot, while both plots comprised a similar number of individuals (Table 2, Fig. S1). In the primary forest plot, the most common tree species were *Horsfieldia basifissa* (9.7% of all individuals, 4.1% of total basal area), *Teijsmanniodendron bogoriense* (5.3% of all individuals, 9.9% of total basal area) and *Gymnacranthera paniculata* (4.9% of all individuals, 2.0% of total basal area). In the secondary forest plot, the most common were *Macaranga tanarius* (22.9% of all individuals, 17.8% of total basal area), *Ficus variegata* (18.3% of all individuals, 9.6% of total basal area) and *Trichospermum pleiostigma* (13.7% of all individuals, 25.2% of total basal area). For characteristics of other common species see Table S1.

Table 2. Basic description of primary and secondary 1-ha plots (trees > 5 cm DBH, with climbers excluded). For the number of individuals and their basal areas for the most common species, see Table S1.

Characteristic	Primary forest plot	Secondary forest plot
Number of individuals	1255	1201
Basal area ($m^2 \cdot ha^{-1}$)	29.3	13.5
Number of species	198	88
Number of species with 1 individual	64	36
Number of individuals from spp. with ≥20 individuals	562	974
Number of species with ≥20 individuals	12	12
Number of shared species	45	45
Number of individuals from shared species	579	821

Analysis 1 – General spatial patterns

Overall analysis of all individuals, ignoring their species identity, demonstrated that individuals in the primary forest plot were randomly distributed within the plot, whilst those in the secondary forest plot were aggregated on all spatial scales examined, over the entire range of radii used (NM1; Fig. S2). Both patterns were confirmed also by the inhomogeneous PCF (i.e. after excluding inhomogeneous density of individuals, NM2; Fig. 2). Strong inhomogeneity of tree density was detected in the secondary forest plot, but even apart from this result there was also significant aggregation ascertained up to 8 m distance. Inhomogeneity of tree density was weak or non-existent in the primary forest plot, and the distribution of individuals there was mostly not different from random. The analysis of individual species showed that the majority of the most common species were randomly distributed in the primary forest plot, but aggregated in the secondary forest plot (Figs S3 and S4). In particular, in the secondary forest plot, three quarters of species were aggregated on a scale of up to 13 m radius (Figs S3 and S4 with spatial patterns for individual species). However, when filtering out the inhomogeneity of individual density (NM2) in the secondary forest plot, only a few of the most dominant species were aggregated up to the 8-m neighbourhood (Fig. S5).

Analysis 2 – Size hierarchies

Distributions of heights and DBHs were mostly random in the primary forest plot (Fig. 3A–D). In the secondary forest plot, the expected positive (but not significant) autocorrelation of individuals with similar DBH at 7 and 15 m (Fig. 3E) was observed, together with a significant aggregation of individuals with lower than the mean DBH (Fig. 3F). There was also aggregation of individuals with similar height for the 2–6-m scale (Fig. 3G), finally, individuals up to the 2–13-m scale were taller than average (Fig. 3H) in the secondary forest plot. DBH and height distributions were similar for both plots, although there were more tall trees with large DBH, and more size classes, in the primary forest plot than in the secondary forest plot (Fig. S6).

Analysis 3 – Species diversity

The mean probability that trees 5 m apart were conspecific was 3.2% in the primary forest plot and 21.8% in the secondary forest plot. In the primary forest plot, under the random shifting null model (NM4), we detected both a higher number of species and higher species diversity than expected at the intermediate and large spatial scales. This pattern suggests that some interspecific interactions are
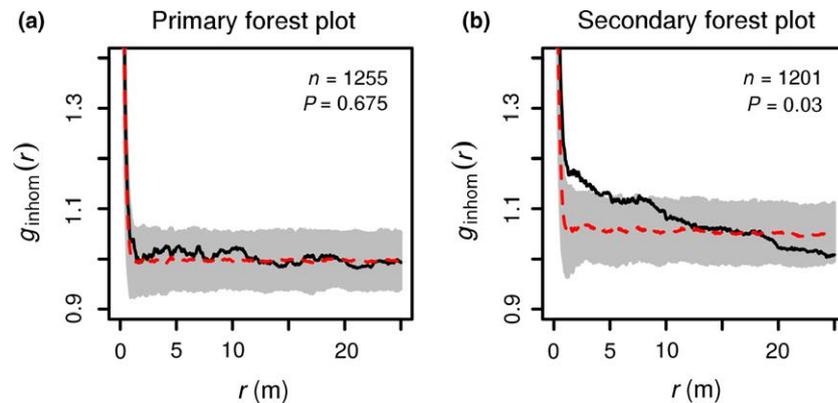
Fig. 2. Inhomogenous pair correlation function $g_{inhom}(r)$ of individuals on both plots. The observed patterns are shown by a solid line, a dashed line denotes the mean confidence (simulation) envelope (CE), and grey areas correspond to confidence (simulation) envelopes (CEs) (solid line outside of CE denotes significant difference from a random pattern along the inhomogeneous density of trees, null model NM2). P corresponds to the goodness-of-fit test (Loosmore & Ford 2006) and n is number of individuals.

positive or less negative than intraspecific interactions (Fig. 4). In contrast, in the secondary forest plot, under the same NM4, the number of species was lower than expected at large spatial scales (>19 m) and species diversity corresponded to the expectation of the null model (NM4) at all spatial scales (Fig. 4). Individuals of the same species were often significantly aggregated in both plots under the inhomogeneous density of trees null model (NM2; Fig. S7). This tendency was much stronger in the secondary forest plot, where aggregation was observed at all scales; in the primary forest plot, the species identity of trees was mostly different up to the 2-m scale (Fig. S7). When compared to a null model that considered an inhomogeneous density of trees (NM2), the number of species and species diversity corresponded to the null model in the primary forest plot and was lower than expected in the secondary forest plot (Fig. S8).

Under the random shifting null model (NM4), the dominant species behaved as diversity-neutral species at most scales, although we observed more diversity-accumulating species in the primary forest plot and more diversity-repelling species in the secondary forest plot at large spatial scales (Fig. S9). Rare species acted as diversity-accumulating species in the primary forest plot on intermediate to larger spatial scales and in the secondary forest plot on smaller spatial scales.

Discussion

Our study clearly demonstrated pronounced differences in spatial patterns of trees between primary and secondary forest vegetation in Papua New Guinea. The fact that the multi-species spatial pattern in tropical forests changes with successional stage was demonstrated in the early 1950s by Greig-Smith (1952), and the same pattern has been observed in pioneer communities elsewhere

(Malkinson & Kadmon 2007; Felinks & Wiegand 2008; Velázquez et al. 2014). The studies of pioneer forests found less aggregated patterns in the later successional or less disturbed communities, than in the early successional or more disturbed communities, where pioneer species facilitated the establishment and growth of the later-arriving species. Competition processes caused decreases in aggregation, i.e. a shift to more regular or random patterns. Differences between our primary and secondary forest plots fit this general trend very well. Our analyses, by taking into account the properties of individuals, provide a more detailed picture. The associations of tree size and tree identities with diversity, and differences between primary and secondary forest plots, point towards some mechanisms that might explain species co-existence and the extraordinary species diversity of tropical forests (Wright 2002). Our analyses are based only on a comparison of two forest plots. However, it should be noted that our 1-ha study plots are well representative of typical New Guinean lowland rain forest composition (i.e. in number and size of tree individuals, and their species and phylogenetic diversity) when compared to a replicated successional plot series at a smaller spatial scale (Whitfeld et al. 2012a, 2014).

General spatial patterns

A high degree of spatial aggregation among individuals has been observed in most tropical forest plots (Condit et al. 2000; Plotkin et al. 2000; Wiegand et al. 2007b; Bagchi et al. 2011), and such spatial aggregation is lower in environmentally homogeneous plots than heterogeneous ones (see Condit et al. 2000). Large-scale spatial aggregation is usually attributed to environmental heterogeneity, whereas small-scale clustering is often attributed to plant–plant interactions (Wiegand et al. 2007b; Getzin et al.
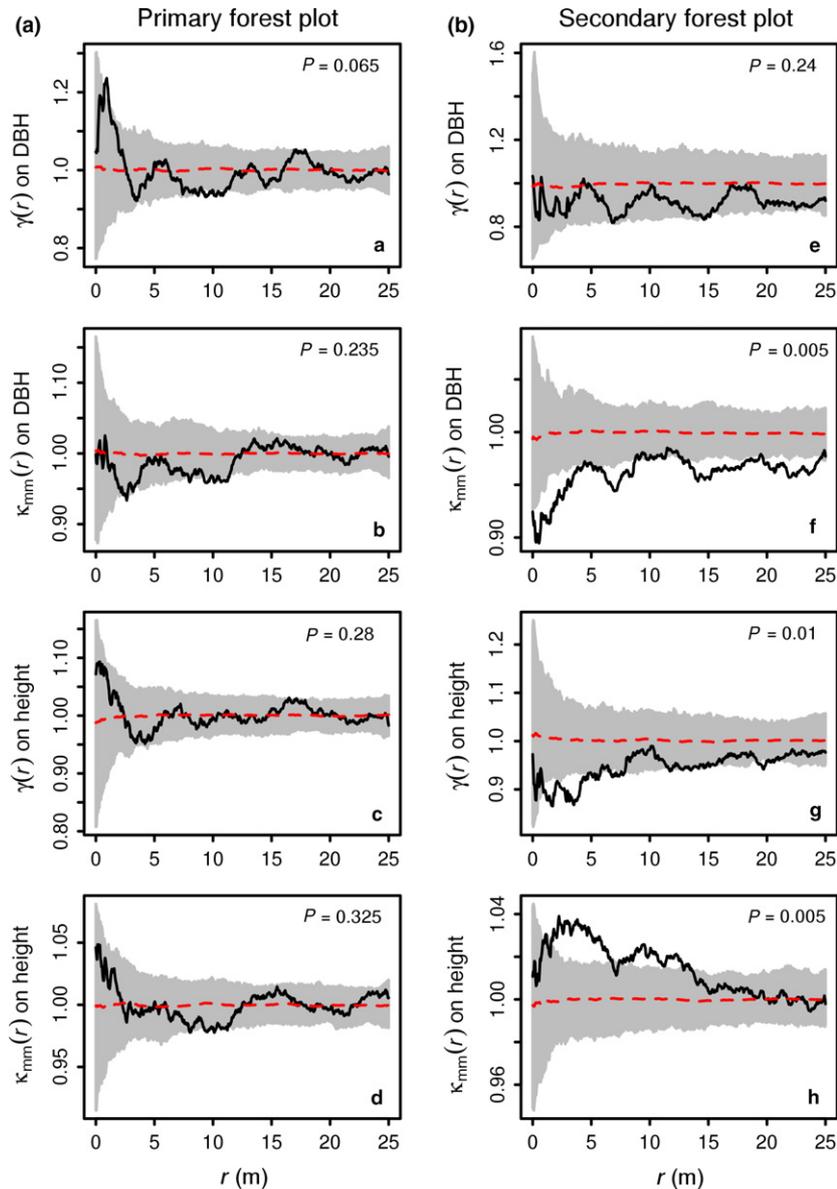
Fig. 3. Mark variogram (γ) and correlation function (κ_mm) of DBH and height of individuals, describing spatial associations of the same/different sizes and lower/higher than mean sizes of individuals, respectively. The observed patterns are shown by solid lines; dashed lines denote mean of results of random labelling and grey areas correspond to CEs (solid line outside CE denotes significant difference from random labelling NM3 by the DBH or height of individuals). *P* corresponds to the goodness-of-fit test (Loosmore & Ford 2006).

2008). Our secondary forest plot was located in close proximity to the primary forest plot, and there is no reason to expect that the secondary forest should be more environmentally heterogeneous (e.g. due to topography, spatial variation of soil quality or water availability) than the primary forest plot, both originally (i.e. before it was cleared for use as a garden) and presently. However, the spatial trends in individual density (i.e. inhomogeneous density) were evident only in the secondary forest plot. As there are no differences in environmental heterogeneity between the plots, the differences in spatial pattern between them

must have been caused by several factors. In the primary forest plot, our results suggest that competition among neighbouring individuals has shaped the spatial pattern much more, and for a longer time than in the secondary forest plot, and consequently led to a more even distribution of individuals. In the secondary forest observed spatial patterns could have resulted from mass colonization, resulting in intraspecific clumping; moreover, species establishment is more sensitive to environmental variability (e.g. topography causing spatial variability in moisture) than growth in later stages of succession. Furthermore, the
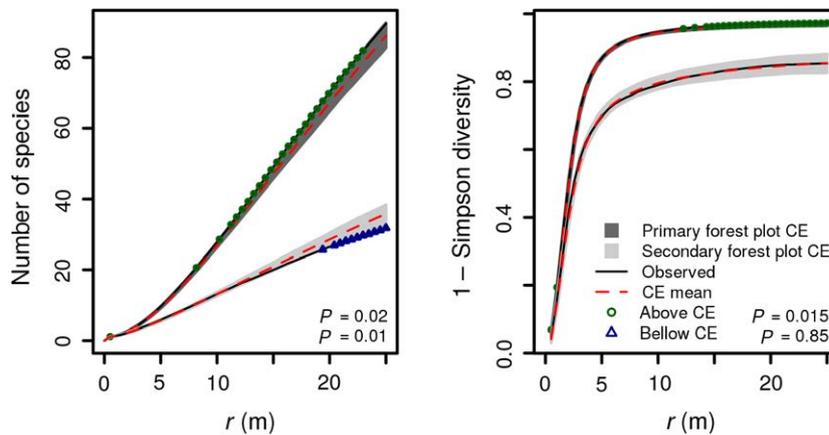
Fig. 4. The number of species and species diversity (1 - Simpson diversity) based on our 'spatialDiversity' function for a random species-shifting model (NM4) around all individuals. Observed patterns are shown as solid lines, dashed lines denote mean of confidence (simulation) envelopes (CEs) and grey areas correspond to CEs (upper dark grey area is for the primary forest and lower light grey area is for the secondary forest). Green circles and blue triangles highlight scales where the observed values lay above and below CE (are significantly different from the null model), respectively. *P* corresponds to goodness-of-fit test (Loosmore & Ford 2006), upper line is for primary forest plot and lower line is for secondary forest plot.

cultivation of various garden crops may have also increased the variability in success of seedling establishment (e.g. due to differential competitive effects of various crops, differences in time of harvesting and differences in management and intensity of weeding required by individual crops). Many of the 'weeds' in the gardens are pioneer tree seedlings, and the weeding is usually abandoned towards the end of the cultivation period (J. Lepš, pers obs). Due to the short time period since the cessation of cultivation, we expect that the legacy of establishment dynamics is still strong. Therefore the most plausible explanations for the aggregated patterns of most species is the effect of dispersal driven by the ability of pioneer species to colonize the plot (i.e. varying availability of seeds according to the proximity of parent trees; Dalling et al. 2002) and differential establishment in garden beds with different crops.

Size hierarchies

It has been shown that the development of local size hierarchies and decrease in size autocorrelation are caused through the regular spacing of trees during stand development in temperate *Abies* forests (Suzuki et al. 2008). Although we did not observe regular spacing of individuals in our forest plots, there were similar trends with respect to the autocorrelation of DBH and height that changed from positive in the young secondary forest plot to no autocorrelation (a random pattern) in the primary forest plot. The positive autocorrelation of DBH and height in the secondary forest plot indicates the presence of patches with similar-sized trees that can most probably be explained by the simultaneous dispersal and subsequent germination of large numbers of seeds (likely originating from the same

parent tree on the edge of the abandoned garden) or by establishment of tree seedlings in a part of garden used for the same crop. In addition, our analysis of the secondary forest plot revealed the presence of non-random patches of individuals with lower than mean DBH and higher than mean height, which again suggests strong competition for light typical of early successional stages (Velázquez & Gómez-Sal 2009). In this situation, trees invest more into vertical growth than diameter growth, because reaching the canopy layer is crucial for survival (Moeur 1997). By contrast, such patches of similarly sized individuals were not observed in the primary forest. Interestingly, the shape of the height spatial autocorrelation functions in the secondary forest was similar to that of an *Abies* stand establishing immediately after a typhoon (Suzuki et al. 2008). Therefore these relationships might be typical features of secondary succession.

Species diversity

In mature tropical forests, the majority of species combinations of nearest neighbour pairs often correspond well to the null model of random mixing of tree species (Lieberman & Lieberman 2007), a pattern that we see in our results. Wiegand et al. (2012) demonstrated that the strength of deviations from random expectations decreased with increasing overall species richness in primary tropical rain forest plots. The higher than expected species richness found in our primary plot compared to the secondary plot supports this trend. Wiegand et al. (2012) interpreted the observed relationship as a result of stochastic dilution effects connected with high species richness. Such an interaction was thought to overpower signals of species

associations and cause approximate/apparent species independence. Although we cannot exclude similar mechanisms, it seems that the distinctions between a more dispersal-influenced pattern in the secondary, and a more competition-influenced pattern in the primary forest is a more plausible explanation in our case. We also detected diversity accumulation around rare species over a much larger range of scales in the primary plot in comparison to the secondary forest plot (see also Wiegand et al. 2007a). Thus, we can expect that rare species were intermingled in a larger area of high diversity within the primary than within the secondary forest. This conclusion was also supported using the mark correlation function on species identities (distance decay similarity). The species accumulator role played by the rare species in the primary forest plot could be explained by the 'safety in diversity' hypothesis (Wills et al. 1997), according to which the presence of rare species in highly diverse clumps should be an advantageous distribution in comparison to intraspecifically aggregated individuals that are more likely to attract natural enemies (e.g. pathogens or herbivores). Our results suggest that these effects will be much stronger in primary forest in comparison to secondary forest.

In general, primary forest plots often show more positive deviations of local diversity than expected under null models, and secondary forest more often shows negative deviations. Our use of the mark correlation function demonstrated that conspecific clumps were more common across a wide range of scales in the secondary forest plot in comparison to the primary forest plot. We also found several diversity-accumulating species in our primary forest plot (such as the common species *Pometia pinnata*, *Pimelodendron amboinicum* and *Mastixiodendron pachyclados*). The presence of diversity-accumulating species suggests that negative intraspecific interactions were stronger than negative interspecific interactions (Comita & Hubbell 2009), which can be interpreted as stronger negative density dependence within species than between species. The relative strength of negative density dependence within species is a process that is considered fundamental to the maintenance of diversity in tropical forests (Wright 2002), and as support for the segregation hypothesis (Pacala & Levin 1997). Our findings that within-species interactions prevail over between-species interactions are also concordant with observations from other old-growth tropical forests (Volkov et al. 2009).

The spatial segregation hypothesis of Pacala & Levin (1997) suggests that intraspecific encounters will be more frequent than interspecific ones, and also suggests that the effect of intraspecific competition will be much more pronounced than the effect of interspecific competition. This greater role of intraspecific competition should support species co-existence, and therefore also an increase in diversity during the course of succession (Murrell et al. 2001). As such, it is in perfect agreement with the patterns we have observed.

In all of our analyses, the comparison with the species shifting null model NM4 led to more diversity-attracting or neutral species, and accordingly to higher than expected local diversity than with the inhomogeneous NM2. This shows that if we are to demonstrate spatial diversity or species interactions, we need to keep the individual species patterns fixed (as in NM4, not in NM2) as ascertained in the field. Otherwise, the processes leading to clumped patterns (mostly those connected with dispersal) will overpower the diversity signal. In our young secondary forest, negative diversity effects were due to prevailing dense mono-specific clumps of early successional species (e.g. light-demanding short-lived *Macaranga* spp.), which most probably attract natural enemies more strongly than intermingled vegetation (Janzen-Connell type effects; Janzen 1970; Queenborough et al. 2012).

Conclusions

Comparisons of spatial structure between secondary and primary forest plots suggest that these successional stages differ in the most important processes forming their spatial pattern. Dispersal and establishment limitation, like non-homogenous seed dispersal and differential seedling establishment, are determinants of the aggregated pattern in which patches of conspecific individuals occur early in succession. Competition among neighbouring individuals, with intraspecific interactions being more negative than interspecific ones, results in well-mixed species patterns with highly species-diverse patches of individuals in primary (old) forest. Here, stronger negative density dependence within species than between species is expected to support the spatial segregation hypothesis (Pacala & Levin 1997). Our results, demonstrating higher than expected local diversity, underpin the importance of Janzen-Connell effects for the maintenance of species diversity. Also, our novel usage of species identities in spatial pattern analysis has shown high spatial accumulation of species around rare species, which follows the 'safety in diversity' hypothesis (Wills et al. 1997). The relative abundance of species in the primary forest plot studied here was similar to the recently censused large-scale 50-ha plot in a primary forest of Papua New Guinea (V. Novotný, unpubl data), which suggests that these patterns hold across larger areas. Whereas data from mapped primary forest plots are becoming more and more available for analysis, the data needed for corresponding analyses of secondary plots in similar locations are mostly missing. Whereas re-surveys of primary forest plots are increasingly available (e.g. Comita et al. 2007), for the secondary forest, the spatially explicit

data for dated successional series are missing. Our study demonstrated that comparison of spatial patterns between contrasting successional stages, using novel methods of spatial pattern analysis taking into account the properties of individual trees, could provide support for mechanistic hypotheses explaining maintenance of species diversity over time.

Acknowledgements

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Supporting Information

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

Appendix S1. Simulations of hypotheses, null models and software used for analyses. Table S1 and Figs S1–S9.

Appendix S2. Source code of 'spatialDiversity' function and examples of its usage.