High frequency of positive inter-specific interactions revealed by individual species–area relationships for tree species in a tropical evergreen forest

Nguyen H. Hai[1], Ion C. Petritan*[2] and David F.R.P. Burslem[3]

[1]*Department of Forest inventory and Planning, College of Forestry, Vietnam National University of Forestry, Hanoi, Vietnam;* [2]*Transilvania University, Brasov, Romania,* [3]*School of Biological Sciences, University of Aberdeen, Aberdeen, Scotland, United Kingdom*

*Corresponding author. Email: *petritan@unitbv.ro*

Abstract

Background: The spatial structure of tree species diversity may help to identify the relative importance of positive, negative and neutral interactions among species and contribute to understanding the processes that maintain high species richness in tropical forest communities.

Aims: We tested the hypothesis that common species accumulate higher species richness at small spatial scales than expected from a null model of complete spatial randomness, and that the strength of this signal decays when tested against a null model that reflects plot-wide environmental heterogeneity.

Methods: We computed individual species–area relationships (ISARs) to examine the accumulation of tree species richness with distance around 18 abundant species on a fully mapped 2-ha plot in a tropical evergreen forest in Vietnam.

Results: Thirteen species displayed ISARs that suggested that they accumulated a higher than expected species richness of trees when tested against a null model assuming complete spatial randomness, but this total dropped to eight species after accounting for non-random species distributions by applying a heterogeneous Poisson null model. Only one species, the pioneer *Macaranga denticulata*, showed lower than expected species richness in local neighbourhoods when tested against the heterogeneous Poisson null model.

Conclusions: These patterns suggest that environmental heterogeneity contribute to the distribution of species diversity at small spatial scales, and must be accounted for using an appropriate null model when analysing point pattern data. The accumulation of higher than expected counts of species richness in the local neighbourhoods of eight species may reflect facilitation, species herd protection, habitat heterogeneity, or overlap in frugivore diets. Low species richness in local neighbourhoods surrounding *M. denticulata* stems is linked to its early colonisation of canopy gap sites.

Keywords: Accumulators, neutral and repellers; Spatial diversity; Spatial pattern; Tropical evergreen forest; Vietnam.

Introduction

Understanding the mechanisms that generate and maintain spatial structure in community properties is a fundamental goal of ecology. This goal has been facilitated by the emergence of large spatially explicit data-sets and new statistical tools for analysing them (Illian et al. 2008; Law et al. 2009, Wiegand and Moloney 2014). Interactions among species and with abiotic environmental conditions may contribute to the emergence of heterogeneity in the spatial distribution of individuals and species richness patterns. Positive interactions, such as shared responses to abiotic conditions (Debski et al. 2002; John et al. 2007) or dispersal by the same vector (Kwit et al. 2004; Clark et al. 2005; Carlo and Morales 2008), might lead to local hotspots of species richness, while interspecific competitive interactions or habitats with low resource availability might result in spatial patterns displaying over-dispersion of species and species richness (Wiegand et al. 2009). Exploiting the power of new statistical methods to uncover evidence for these interactions requires spatially explicit data from a range of plant communities to provide independent case studies for testing these hypotheses. In this paper we present an analysis of data from a fully-mapped tree community on a 2-ha plot in a tropical evergreen forest in Vietnam to add an additional site to the small number of locations globally where such spatial analyses have been conducted.

The majority of studies that describe spatial structure in tropical tree communities have used techniques that compare the univariate and bivariate structures within and between species (Debski et al. 2002; Wiegand et al. 2007a; Wiegand et al. 2007b; Brown et al. 2016). Different measures are required to integrate data across multiple coexisting species for the description of spatial structure of community properties. Species richness is most simply characterised using the species–area relationship (SAR), which quantifies the increase in counts of species as a function of sample area (Connor and McCoy 1979). However, the SAR ignores spatial heterogeneity in patterns of species richness arising from characteristics of the biotic or abiotic environment and is not well-suited for characterising spatial structure within local neighbourhoods. Consequently, the individual species area relationship (ISAR) was proposed to analyse species specific effects on local diversity (Wiegand et al. 2007a; Wiegand et al. 2014). The ISAR computes changes in species richness as a function of area and distance from individuals of a target species and integrates both spatial structure of individuals and the accumulation of species number with sample area (Wiegand et al. 2007a; Wiegand et al. 2014).

The ISAR approach allows species to be classified according to the characteristics of their local biotic neighbourhoods. Therefore, it can be used to distinguish species that display significantly higher than expected species counts (diversity accumulators) from those within (neutral) or below (diversity repellers) expectation in terms of species numbers at a given distance, where expected species richness is defined by a null model (Wiegand et al. 2007a). These contrasting patterns can be

used to test hypotheses of the mechanisms of local community assembly based on species traits and interspecific interactions (Rayburn and Wiegand 2012). For example, higher than expected accumulation of species richness within the local biotic neighbourhood might be indicative of net positive facilitative interactions or shared use of resources at fine spatial scales, while low neighbourhood richness may result from competition for space or environmental filtering (Punchi-Manage et al. 2015). Accounting for environmental heterogeneity across the study site is also important, especially where variation linked to topography or soils across plots creates heterogeneity in the distribution of species and species diversity (Valencia et al. 2004; Gunatilleke et al. 2006). Consequently, species that are differentially associated with relatively species-rich valley habitats may display a higher species richness in local neighbourhoods than species associated with species-poor ridge habitats because of this larger-scale heterogeneity rather than local-scale processes. Neighbourhoods that do not differ from the null model in terms of species richness may either reflect a predominance of neutral interactions between species or a net balance of positive and negative interactions, and the ISAR approach cannot distinguish between these underlying mechanisms (Punchi-Manage et al. 2015).

The ISAR approach has now been applied to communities of subtropical and tropical trees in Panama, Sri Lanka, Taiwan, New Guinea and Thailand (Wiegand et al. 2007a; Punchi-Manage et al. 2015; Tsai et al. 2015; Fibich et al. 2016; Chanthorn et al. 2017), as well as temperate forests and shrubland communities (Rayburn and Wiegand 2012; Zhang et al. 2014; Chacón-Labella et al. 2016). A majority of species analysed in these studies have displayed evidence of accumulation of higher species richness in local neighbourhoods than expected under the null hypothesis of complete spatial randomness in the distributions of species, especially at small spatial scales (generally $< 10 – 30$ m), with exceptions for tree species growing in a secondary forest and some shrubs (Rayburn and Wiegand 2012; Fibich et al. 2016). One explanation for the pervasive signal of diversity accumulation in local neighbourhoods is that species share common habitat associations, which is manifested in large-scale heterogeneity in species distributions across the sampling arena (Rayburn and Wiegand 2012). Under these circumstances a null model that assumes complete spatial randomness at the plot scale is inappropriate for analysing the spatial signal of species richness within individual neighbourhoods, while a heterogeneous null model can account for the effects of habitat association and isolate local interactions (Wiegand et al. 2007a; Rayburn and Wiegand 2012; Tsai et al. 2015; Espinosa et al. 2016). Comparing the outcomes of parallel analyses using homogenous and inhomogeneous null models is a useful complementary technique for identifying effects of large-scale species–habitat associations on fine-scale spatial structuring of species richness (Tsai et al. 2015). A strong signal of habitat associations should also be reflected in positive autocorrelation in community

metrics such as species richness and diversity at the scale of variation in important variables defining tree habitats (Lundholm 2009; Laanisto et al. 2013; Stein et al. 2014).

In this paper we computed individual species-area relationships for common species growing in a tropical evergreen forest in north-central Vietnam that is recovering from historic disturbance resulting from application of defoliants in the late 1960s. A previous study on tree distributions at this study site has provided evidence of spatial structuring driven by environmental heterogeneity, dispersal limitation and species herd protection (Hai et al. 2016). In this study, we tested the hypothesis that common species would accumulate higher species richness at small spatial scales than expected from a null model of complete spatial randomness, and that the strength of this signal would decay when tested against a null model reflecting plot-wide environmental heterogeneity. We addressed the secondary hypothesis that autocorrelation in species richness and diversity would match the spatial scale of heterogeneity in species distributions.

Materials and methods

Study site and plot establishment

A 2-ha study plot (200 x 100 m) was established in tropical evergreen forest in Aluoi district, Thuathien-Hue province, north-central Vietnam ($16°08.35'$N, $107°16.68'$E). Mean annual temperature is $25°$C, and 70-80 % of the mean annual precipitation of about 3500 mm falls during the wet season from September to December, while the dry season lasts from January to August (stnmt.thuathienhue.gov.vn). Soils are mainly light yellow to dark yellow ferralic acrisols (Sterling and Hurley 2008). The elevation of the plot ranges from 625 to 660 m a.s.l, with an average slope of 25 degrees (Hai et al. 2016).

All live trees with a diameter at breast height (dbh) ≥ 2.5 cm were mapped and recorded for species and dbh. Multiple stems on the same tree were recorded separately if the branching occurred below a height of 1.3 m. The relative coordinates (x, y) of each tree were recorded via a grid system of 200 subplots (10 m × 10 m) using a Leica Disto D5 laser distance meter and compass. A total of 3,154 individual trees were recorded belonging to 81 species in 37 families. Species richness per 20 m x 20 m subplot ranged from nine to 30 species (mean 20 ± 5 species), and stem density per subplot ranged from 14 to 108 individuals (mean 63 ± 24 individuals). The most abundant species was *Syzygium zeylanicum* with 514 individuals, which includes some large individuals with a diameter at breast height up to 100 cm, and a total of 18 species were represented by more than 50 individuals on the plot and were therefore sufficiently abundant for analysis (Table 1). This sample includes 12 species that, on the basis of previous work (Chinh et al. 1996), are known to be light demanding and fast growing.

Data analysis

Individual species–area relationships (ISAR) were computed for the 18 focal species with $\geq$ 50 individuals in the sample (Table 1). The ISAR(r) function is the expected number of species within circular areas of radius r around an arbitrarily chosen individual in the target sample (Wiegand et al. 2007a). This function combines the theoretical principles inherent in the species area relationship and the focus on spatially mapped individuals that underpins point pattern analyses, and is a suitable approach for analysing the spatial structure of species richness in tree communities (Brown et al. 2016). For species t growing in a community of N species, the ISAR function can be estimated as:

$$ISAR(r) = \sum_{j=1}^{N} [1 - P_{tj}(0,r)]$$

where $P_{tj}(0,r)$ is the bivariate emptiness probability that species j was not present in the circle with radius r around individuals of the target species t. Using the transformation of r to the area of the equivalent circle, the ISAR function can be expressed in terms of sample area a to resemble the common species area relationship (Wiegand et al. 2007a). The ISAR functions were computed using the software ISAR version 2013 (Wiegand and Moloney 2014), including the default method for edge correction.

Two null models were used for comparison to observed fits of the ISAR function. The first (complete spatial randomness, CSR) assumes that stem density for the target species was homogeneous across the plot and was fitted by randomising the locations of individuals of the target species across a map that retained fixed locations for the stems of all other species. In addition, to accommodate the constraint that homogeneity in species distributions is unrealistic because of dispersal limitation and habitat associations, we also generated realisations of the distribution of each species, using a heterogeneous Poisson null model (Wiegand et al. 2007b). To estimate the density of species (or intensity) functions under the assumptions of a heterogenous Poisson distribution we used a non-parametric kernel estimation based on the Epanechnikov kernel with a bandwidth, R, of 50 m. A kernel function provides an expression of spatial displacement between points in continuous space and is required to smooth the inevitable spikes that occur in the raw data (one spike per pair of points). The Epanechnikov kernel is a popular choice in plant ecology and includes a free smoothing parameter or bandwidth R that determines the extent of smoothing (Stoyan et al. 1995; Law et al. 2009). We estimated ISAR functions up to 50 m, which is half the smallest dimension of the plot and therefore the radius of the largest circle that could be superimposed on the plot without crossing an edge. For both null models the ISAR function was fitted to 199 realisations of the distribution of each target species, generated by Monte Carlo simulations to derive a confidence envelope for comparison with the observed fit to the ISAR function across values of r from 0 to 50 m in steps of 1 m.

Goodness-of-Fit (GoF) tests were used to reduce type I error inflation due to multiple simulations (Loosmore and Ford 2006). The index u_i was computed to evaluate the accumulated deviation of observed values of the ensemble statistic $\bar{H}(r)$ from an expected value derived from the null model realisations. Values of u_i were summed over all distances from 1 m (r_{min}) to 50 m (r_{max}) as follows:

$$u_i = \sum_{r=r_{min}}^{r_{max}} (\hat{H}_i(r) - \bar{H}(r))^2$$

where $\hat{H}_i(r)$ is the observed ($i=0$) or simulated ($i=1$-199) ISAR$_f(r)$ function and $\bar{H}(r)$ is the averaged ensemble statistic excluding the ith function. The rank of the u_i statistic for the observed ISAR among all values of u_i was used as a Goodness of Fit test based on an approximate α level of 0.05, therefore the ranks of all $u_i \geq 190$ were assessed. All ISAR analyses and Goodness of Fit tests were conducted using the ISAR software (Wiegand and Moloney 2014).

Finally, spatial autocorrelation in species richness and total stem abundance at the 20 m x 20 m scale was determined from values of local Moran's I plotted as a correlogram. Approximate 95% confidence envelopes were constructed based on 199 Monte Carlo permutations of species richness and stem abundance. Spatial autocorrelation analyses were made using the Spatial Analysis in Macroecology (SAM) software v. 4.0 (Rangel et al. 2010).

Results

Spatial autocorrelation in species richness and stem density

Species richness and stem density both displayed positive spatial autocorrelation at spatial scales of 0 - 40 m, but were generally independent at larger scales (> 45 m) except for a tendency towards negative autocorrelation at scales of 100 - 120 m for species richness and 130 – 150 m for stem density (Figure 1). Moreover, species richness and abundance were positively correlated ($P<$ 0.001) among subplots (Figure S1).

Individual species-area relationships

Based on goodness of fit tests, 14 of the 18 species displayed significant spatial structuring of species richness when compared to a null model of complete spatial randomness, but for six of these species this disappeared after accounting for large-scale heterogeneity in stem density using the heterogeneous Poisson null model (Table 1). Only one species (*Microcos paniculata*) displayed significant spatial structuring of species richness assuming heterogeneity in stem density but not when stem density was assumed to be distributed randomly, while species richness was distributed at random in the local neighbourhoods under both null models for only three species (*Dillenia scabrella, Nephelium melliferum* and *Quercus platicalyx*)

The observed ISARs suggest that individuals of all species have a similar number of species (15 – 19) in local neighborhoods of 10 m radius, but species number within neighborhoods of a radius of 35 m diverged to 44 – 49 among species (Figure 2a, 2c). At neighborhood distances of up to 35 m, between 8 and 12 of the 18 species accumulated a significantly greater neighborhood species richness than predicted by the null model of complete spatial randomness (Figure 2b), but this number dropped to 3 to 8 species that were significant accumulators based on the heterogeneous poisson null model (Figure 2d). Only one species in each case had significantly lower than expected counts of species richness in local neighborhoods and the scale of this response (10 – 40 m vs 4 – 19 m) depended on the null model chosen (Figure 2b, 2d).

The curves plotting values of $ISAR_f(r)$-$ISAR_{exp}(r)$ extended above the 95% confidence envelope derived from simulations assuming the heterogeneous poisson null model across a range of spatial scales dependent on species, and only extended below the 95% confidence envelope for *Macaranga denticulata*, at scales of 4 – 19 m (Figure 3). For *Adina pilulifera, Diospyros eriantha, Litsea vang, Polyalthia nemoralis, Syzygium zeylanicum* and *S. wightianum, ,* species richness was significantly greater than the null expectation in local neighbourhoods only up to distances of 25 to 35 m, while *Microcos paniculata* and *Ormosia balansae* displayed higher than expected species richness in neighbourhoods up to 40 m or 45 m (Figure 3). *Macaranga denticulata* showed a switch from lower than expected species richness at low distances to higher than expected species richness at distances of 22 - 50 m (Figure 3). By contrast, when assessed against a null model of complete spatial randomness (CSR), which obscures large-scale heterogeneity in stem distributions, an additional five species appeared to display significant accumulation of species richness in local neighbourhoods, and one additional species displayed a significant reduction in species richness in local neighbourhoods (Table 1). In these tests assuming CSR the maximum spatial scales at which species richness appeared to accumulate in local neighbourhoods increased in most cases, and the signal of significant repulsion of species richness at small scales in *M. denticulata* was lost (Figure 4).

Discussion

In this study of 18 species growing on a 2-ha plot of tropical evergreen forest in Vietnam, a high proportion of species displayed a tendency towards accumulating higher species richness in local neighbourhoods than would be expected based on random assembly from the local community. When assessed against a null model of complete spatial randomness, 13 species were diversity accumulators, and this tally reduced to eight species when the null model assumed the heterogeneous Poisson distribution, which attempts to account for large-scale heterogeneity and shared habitat

associations (Wiegand et al. 2007a; Rayburn and Wiegand 2012; Tsai et al. 2015; Espinosa et al. 2016). In contrast, only one species displayed evidence of lower than expected species richness in local neighbourhoods for either null model. Significant accumulation of species richness was observed in both common (e.g. *Syzygium zeylanicum*, 514 individuals on 2 ha) and rare (e.g. *Ormosia balansae*, 50 individuals on 2 ha) species among those that had at least 50 stems on the 2 ha plot, and there is no clear evidence that species abundance was a strong driver of this pattern (Tsai et al. 2015). Similarly, significant accumulation of species richness was displayed in species of both small and large trees, and for both shade tolerant and light demanding species (Table 1), which suggests that these traits are also unrelated to the mechanisms that drive this pattern (Tsai et al. 2015; Chanthorn et al. 2017).

This study therefore supports research from a small number of other sites where similar analyses have been conducted, showing that about half of tree species analysed in subtropical and tropical tree communities display evidence of non-random species accumulation in local neighbourhoods (Wiegand et al. 2007a; Punchi-Manage et al. 2015; Tsai et al. 2015; Fibich et al. 2016; Chanthorn et al. 2017). These patterns are indicative of several non-mutually exclusive mechanisms, which include facilitation, species herd protection, spatial structuring of species richness associated with habitat heterogeneity, and overlap in frugivore diets leading to contagious patterns of seed deposition (Chanthorn et al. 2017). The positive spatial autocorrelation in species richness at a scale of 40 m, coupled with negative autocorrelation at 90 m, provides evidence of habitat heterogeneity across the plot that is sufficient to drive spatial structuring of species richness (Stein et al. 2014). On this plot, habitat heterogeneity may be linked to the occurrence of a rock outcrop and an intermittent stream, which may affect hydrological regimes and soil nutrient availability. Habitat heterogeneity may give rise to opportunities for species habitat associations, which are commonly observed among tropical tree species (Harms et al. 2001; Gunatilleke et al. 2006; John et al. 2007; Baldeck et al. 2013). Species habitat associations combined with variation among habitats in species richness are predicted to generate evidence of significant accumulation of species richness in the local neighbourhoods of specialists of more species-rich habitats across a heterogeneous enviornment (Wiegand et al. 2007a; Rayburn and Wiegand 2012; Tsai et al. 2015; Espinosa et al. 2016). This interpretation may help to explain the reduction in the scale and prevalence of species accumulation in the neighbourhoods of species when large-scale habitat heterogeneity was accounted for using a heterogenous poisson null model. We conclude that the loss of the signal of species accumulation in local neighbourhoods of *Archidendron balansae, Ardisia lindleyana, Aphanamixis polystachya, Endospermun sinensis, Schefflera octophylla* and *Sterculia lanceolata,* when the null model was switched from complete spatial randomness to the heterogeneous poisson distribution may be indicative that these species were aggregated in the more species-rich habitats on the plot.

Only one species, *M. denticulata*, displayed a lower than expected accumulation of species richness in local neighbourhoods when tested against the heterogeneous poisson null model (Figure 3), and this signal changed to positive diversity accumulation across all scales up to 50 m when tested against complete spatial randomness (Figure 4). The distribution map for this species shows that it occurred almost exclusively in the more species-rich western half of the plot (Figure S2), which explains why it appears to be a diversity accumulator when tested against complete spatial randomness. The emergence of the opposite signal after accounting for large-scale heterogeneity may reflect the specialisation of this species to recently created canopy gap sites (biotik.org/laos/species/m/macde/macde_en.html), reflecting the pioneer strategy of other *Macaranga* species across tropical Asia (Davies et al. 1998; Slik et al. 2003). The distribution map for *M. denticulata* on this plot (Figure S2) suggests a high degree of spatial aggregation, which would support the hypothesis that recruitment reflects the distribution of former canopy gaps. Pioneer species such as *M. denticulata* possess adaptations to colonise and tolerate the relatively exposed and dessicating conditions of new canopy gaps, but pioneers represent a small component of the tree flora (Whitmore 1984; Swaine and Whitmore 1988). Therefore tree species richness of early successional vegetatin in canopy gaps is low relative to that of the surrounding vegetation, and this pattern may explain the lower than expected number of species in local neighbourhoods of *M. denticulata* after accounting for large-scale heterogeneity. The only other species that showed a lower than expected count of species richness was *Sterculia lanceolata*, and in this case the non-randomness was observed at intermediate spatial scales (10 – 40 m) and only when tested against complete spatial randomness. The cause of this pattern is unclear, but it may be related to an association of this species to species-poor habitats across the plot or to seed dispersal limitation.

Eight species displayed evidence of diversity accumulation in local neighbourhoods even after accounting for large-scale habitat heterogeneity. Spatial analyses cannot distinguish among the potential mechanisms that might explain these patterns, but one intriguing possibility is that contagious distributions arise when fruigivores generate species-rich seed rain close to their preferred food plants (Kwit et al. 2004; Clark et al. 2005; Carlo and Morales 2008; Chanthorn et al. 2017). The dispersers of these eight species are unknown at our study site, but in most cases their fruit morphology is indicative of dispersal by birds or primates (Hai et al. 2016). Two species analysed in this paper were also present on a 30-ha permanent tropical forest plot at Mo Singto in Thailand, where they are dispersed by gibbons, macaques and terrestrial mammals (*Nephelium melliferum*) and by hornbills (*Aphanamixis polystachya*) respectively (Chanthorn et al. 2017). Similar analyses to those presented here show that on the Mo Singto plot *Nephelium melliferum* is a strong diversity accumulator across a wide range of spatial scales, while *Aphanamixis polystachya* is a weak diversity accumulator and this signal only emerges for communities of small trees in the neighbourhoods of

large trees. At our study site in Vietnam, neither species displayed any evidence of diversity accumulation at any scale after accounting for habitat heterogeneity. The cause of these differences in spatial structure between the two study sites is unknown, but it is consistent with differences in the abundance or community structure of resident frugivores between the two sites. Further research at the Vietnamese study site should address the status of frugivore populations following the impact of defoliants in the late 1960s.

Conclusions

About half of the abundant species in our sample were accumulated species diversity local neighbourhoods after accounting for large-scale heterogeneity and shared habitat associations. These patterns suggest that environmental heterogeneity contribute to the distribution of species diversity at small spatial scales, and must be accounted for using an appropriate null model when analyzing point pattern data. The accumulation of higher than expected counts of species richness in the local neighbourhoods of eight species may reflect facilitation, species herd protection, habitat heterogeneity, or overlap in frugivore diets. Low species richness in local neighbourhoods surrounding *M. denticulata* stems is linked to its early colonisation of canopy gap sites.

Notes on contributors

Nguyen Hong Hai is a forest ecologist with a background in spatial ecology and species diversity in tropical forests.

Ion Catalin Petritan is a forest ecologist researching the processes occurred in temperate old-growth forests.

David F.R.P. Burslem is an ecologist with interests in the processes that maintain diversity in tropical forests and the mechanisms that control the distribution of tropical tree species and communities.

Declaration of interest statement

No potential conflict of interest was reported by the authors.

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Table 1. Tree properties and rank of the Goodness-of-Fit (GoF) test for the observed ISAR functions compared to null models assuming complete spatial randomness (CSR) or a heterogeneous Poisson distribution (HP). Ranks ≥ 190 indicate a significant departure from the null models ($p \leq 0.05$), while "n.s." refers to tests that are non significant.

| Species	Shade tolerance	No. individuals	Mean dbh (cm)	Under HP null model		Under CSR null model	
				Rank	p values	Rank	p values
Syzygium zeylanicum	Intermediate	514	10.05	200	<0.05	200	<0.05
Syzygium wightianum	Light demanding	351	9.54	200	<0.05	200	<0.05
Litsea vang	Intermediate	266	18.35	191	<0.05	198	<0.05
Microcos paniculata	Light demanding	189	21.37	198	<0.05	185	n.s.
Polyathia nemoralis	Light demanding	171	5.61	200	<0.05	200	<0.05
Sterculia lanceolata	Shade tolerant	157	11.94	150	n.s.	200	<0.05
Diospyros eriantha	Shade tolerant	112	5.33	200	<0.05	200	<0.05
Endospermun sinensis	Light demanding	90	25.26	173	n.s.	196	<0.05
Aphanamixis polystachya	Intermediate	81	14.79	176	n.s.	198	<0.05
Ardisia lindleyana	Shade tolerant	79	3.78	148	n.s.	200	<0.05
Macaranga denticulata	Light demanding	76	14.23	199	<0.05	200	<0.05
Schefflera octophylla	Light demanding	71	14.43	182	n.s.	200	<0.05
Nephelium melliferum	Light demanding	64	19.53	137	n.s.	188	n.s.
Quercus platicalyx	Light demanding	63	29.96	121	n.s.	139	n.s.
Dillenia scabrella	Light demanding	62	14.32	79	n.s.	124	n.s.
Adina pilulifera	Shade tolerant	61	8.90	191	<0.05	199	<0.05
Archidendron balansae	Intermediate	54	12.35	35	n.s.	195	<0.05
Ormosia balansae	Light demanding	50	29.71	194	<0.05	200	<0.05
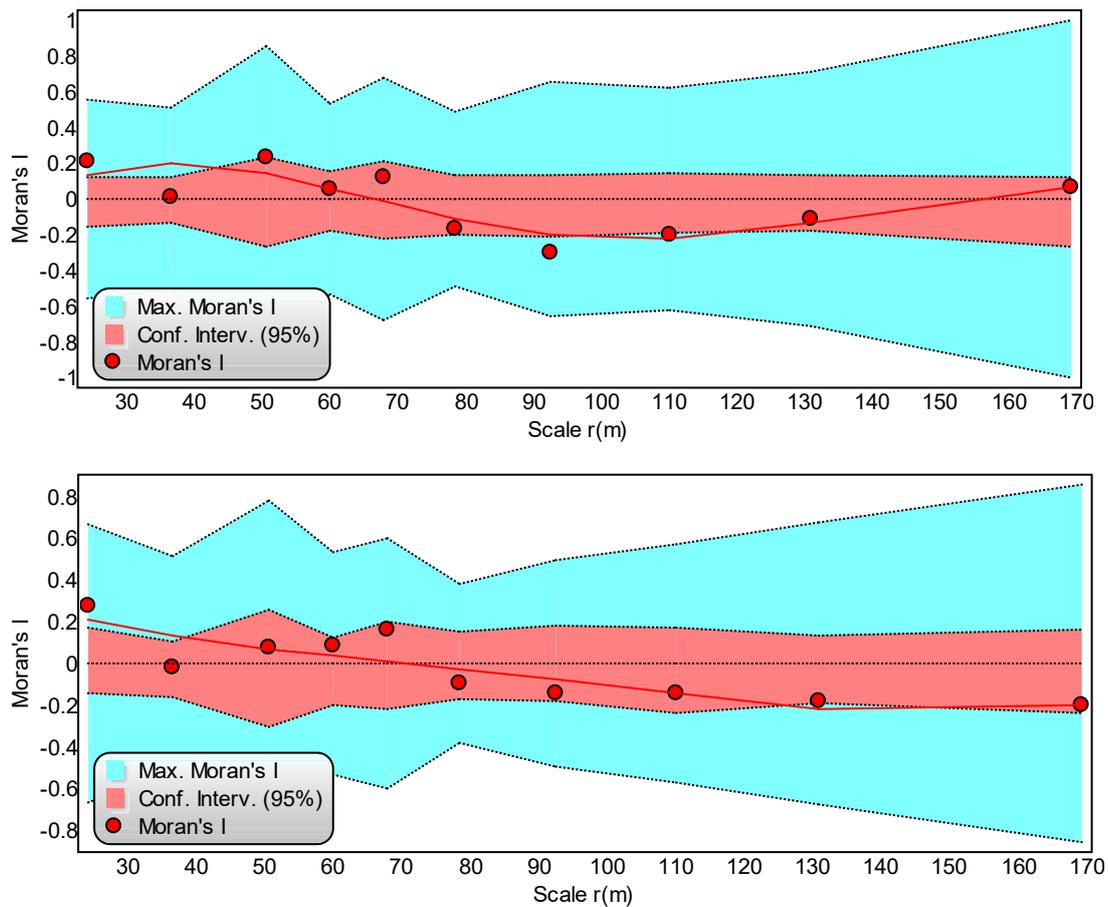
Figure 1. Correlograms displaying the spatial structuring of species richness (a) and stem density (b) based on values of Moran's I for trees growing on a 2-ha plot of tropical evergreen forest in Vietnam. The correlograms were constructed based on 10 distance classes set up according to a criterion of equal numbers of pairs within each class. Significant values were identified through 199 permutations and p-value at $\alpha < 0.05$.
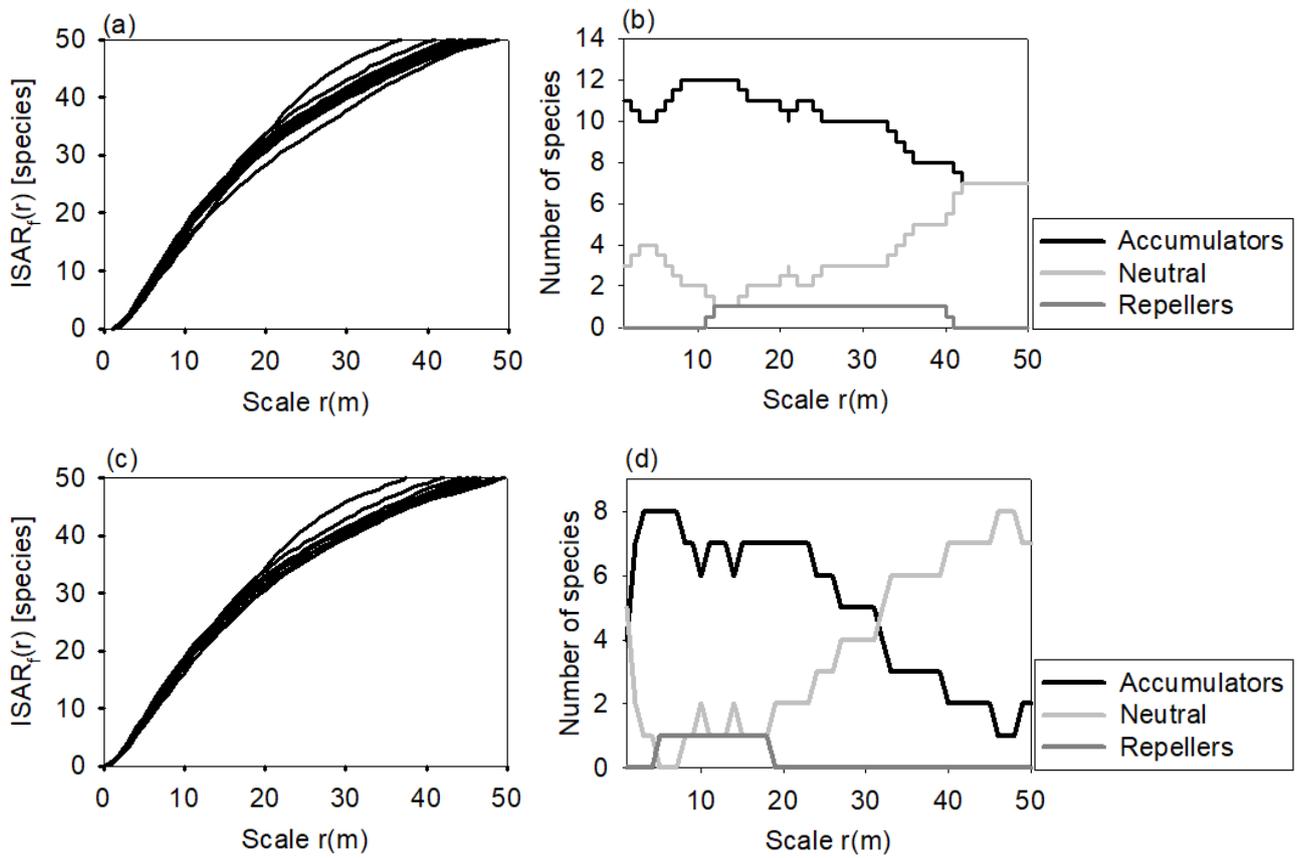
Figure 2. The ISAR function analyses with $p \leq 0.05$ assuming null models based on complete spatial randomness of 14 species (a) and heterogeneous distributions of nine species (c). In (a) and (c) the black lines show the observed ISAR function - $ISAR_f(r)$, while (b) and (d) summarise the number of species that show patterns of diversity accumulation (Accumulators), repulsion (Repellers) or no pattern (Neutral).
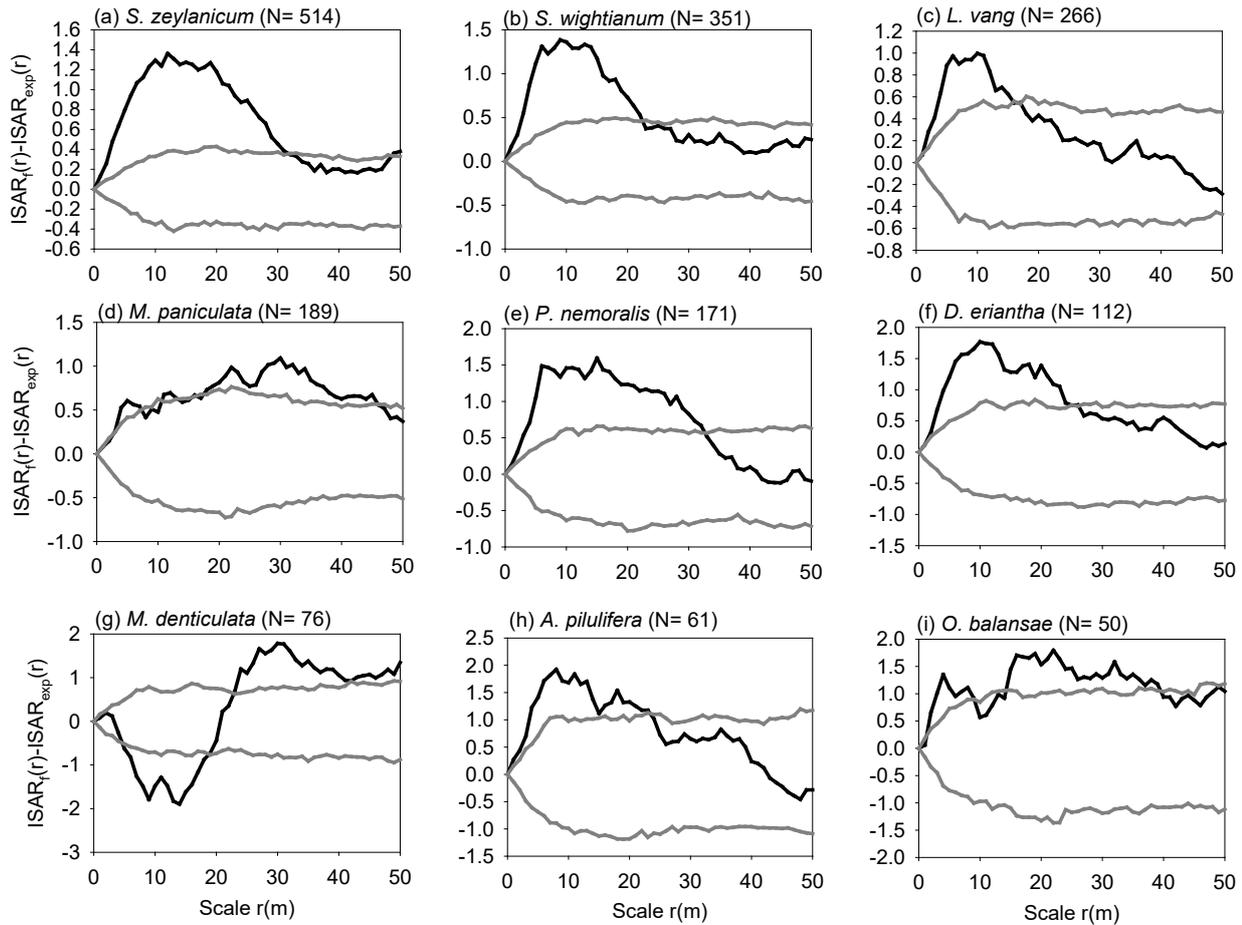
Figure 3. Results of ISAR analyses for the nine species that displayed a significant departure from the null model based on simulations assuming a heteregenous poisson distribution (p ≤ 0.05). Black lines show $ISAR_f(r)$-$ISAR_{exp}(r)$, which represents the observed ISAR function minus the expectation under the heterogeneous poisson null model. The grey lines show the simulated 95% confidence envelopes assessed by the Goodness-of-fit test over the 0-50 m interval. N is number of individuals.
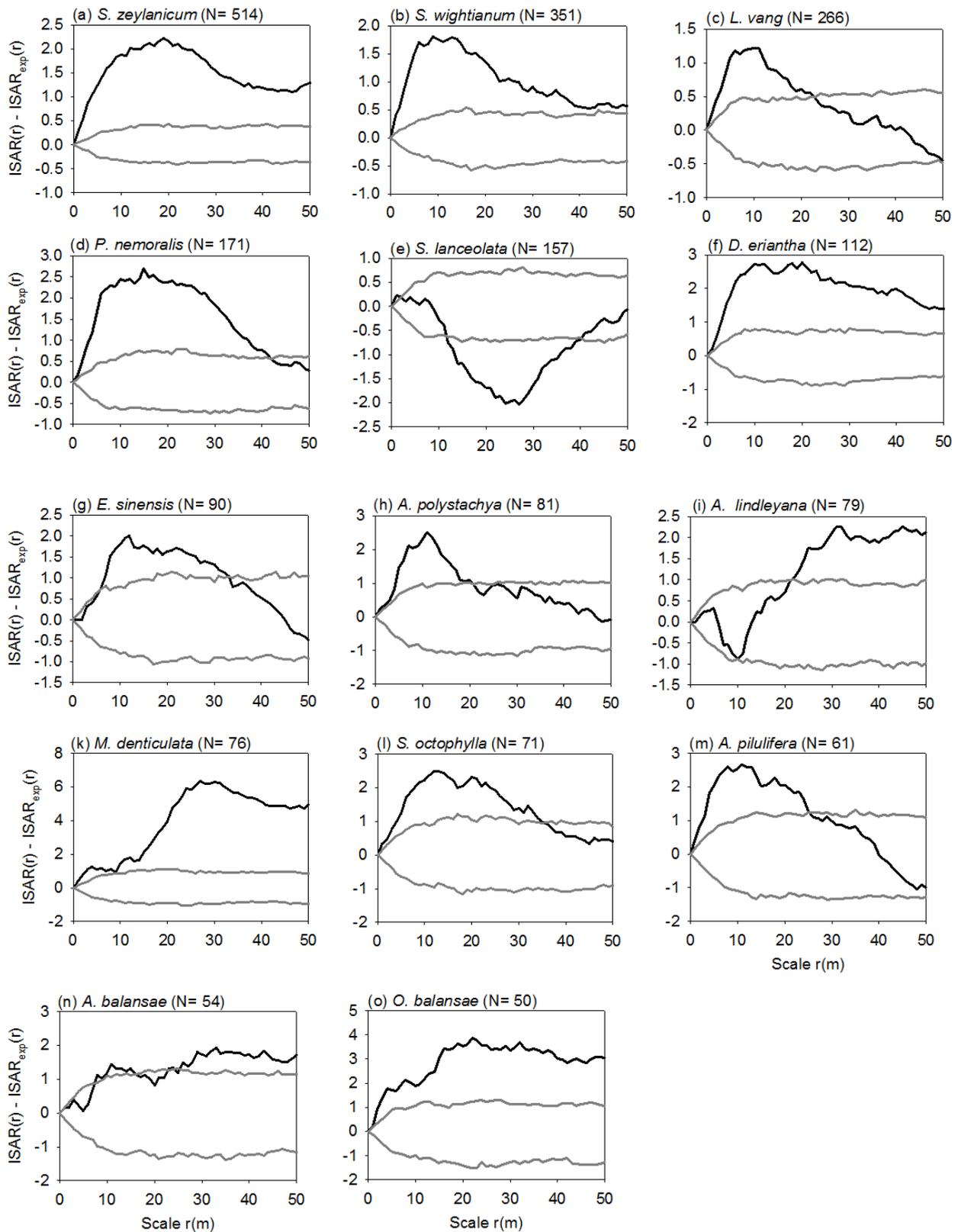
Figure 4. Results of ISAR analyses for the 14 species that displayed a significant departure from the null model based on simulations assuming complete spatial randomness (p ≤ 0.05). Black lines show ISAR$_f$(*r*)-ISAR$_{exp}$(*r*), which represents the observed ISAR function minus the expectation under the null model of complete spatial randomness. The grey lines show the simulated 95%

confidence envelopes assessed by the Goodness-of-fit test over the 0-50 m interval. N is number of

individuals.

Supplementary material

Figure S1. Spatial correlation between Species richness and abundance (p< 0.001)
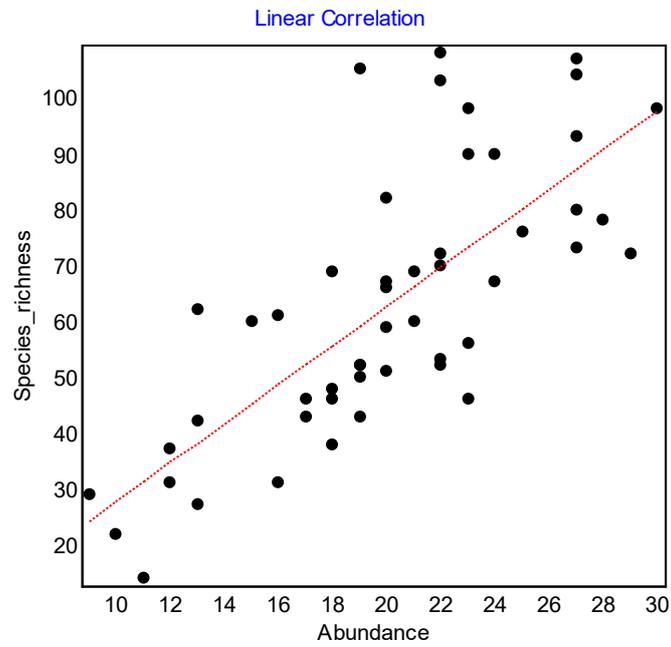
Figure S2. The spatial distributions of 18 studied species. N is number of individuals.