



Linking intraspecific trait variability and spatial patterns of subtropical trees

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Abstract

The importance of intraspecific trait variability (ITV) to the spatial distribution of individual species is unclear. We hypothesized that intraspecific trait dispersions underlying niche processes deviate more from null model expectations, by reducing their spread (range and variance), kurtosis, and standard deviation of near-neighbor distance, for species with aggregated than those with random distributions. The link between species' spatial distributions and ITV patterns was examined using an individual tree-based trait data set, in which specific leaf area, mean leaf area, leaf dry matter content, and diameter at breast height were measured for 18,773 stems of 45 species in a 4.84 ha mapped subtropical forest plot in China. The nearest-neighbor distance analysis showed that, of 45 species, 14 species were distributed in random and 31 species were distributed in aggregation, while no species was distributed in uniform in the plot. The dispersions of all studied traits in species with an aggregated distribution on average deviated more strongly from the null expectation than those in species with a random distribution and that the extent of deviation was negatively associated with the degree of spatial randomness across species. Our results indicate that niche processes are primarily responsible for the spatial structure of species with aggregated distributions, while stochastic processes drive those with random distributions. Our results highlight the fundamental role of ITV in shaping spatial patterns of co-existing species.

Keywords Aggregated distribution · Environmental filtering · Evergreen broadleaved forest · Niche differentiation · Stochastic processes

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Introduction

Most tree species in nature distribute as aggregates or in a random manner over a given spatial scale; few are distributed in a regular pattern (Pielou 1960; He et al. 1997; Condit 2000). Understanding the ecological processes underlying the spatial patterns of individual species has long been one of the central foci of community ecology (Clark and Evans 1954; Condit 2000; Dale 2002; Réjou-Méchain et al. 2011). The spatial distribution of an individual species is a result of multiple ecological processes associated with its resource use strategies (Dale 2002; Clark 2010). Functional ecology has demonstrated that plant traits are crucial for shaping the presence/absence as well as abundance of species under specific environmental conditions (Poorter et al. 2008; Cornwell and Ackerly 2010; Wright et al. 2010; Benitez-Lopez et al. 2014; Li et al. 2015), and that trait variations among species drive the distribution of plant species and their interactions across spatial scales (Escudero and Valladares 2016; Kunstler et al. 2016). Increasing evidence shows that

interspecific trait differences are closely related to environmental filtering and determine the functional niche occupancy of plant communities (Li et al. 2017); whereas, simultaneous niche differentiation occurs through competitive exclusion among species (Kraft et al. 2008). These niche-based processes, therefore, shape occurrence and abundance of individual species at a given location (Cornwell and Ackerly 2010; Yan et al. 2013), and may further structure the spatial distribution of individual species. However, when compared with the effects of interspecific trait variability on occurrence, abundance, and assemblage of co-existing species, little is known about the role of intraspecific trait variability in niche and stochastic processes controlling the spatial distribution of individual species.

Individual specialization is widespread and can vary widely among species due to a diverse array of physiological, behavioral, and ecological mechanisms (Schlichting and Levin 1986; Bolnick et al. 2003), and intraspecific trait variations have profound implications for species distributions and community dynamics (Araujo et al. 2011; Fajardo and Siefert 2016). Recent evidence suggests that, as a result of phenotypic plasticity (Laforest-Lapointe et al. 2014; Turcotte and Levine 2016), intraspecific trait variations are sensitive to niche and stochastic processes (Jung et al. 2010; Albert et al. 2011; Bolnick et al. 2011; de Bello et al. 2011; Siefert 2012a; Umaña et al. 2015), and both biotic interactions and environmental fluctuation act on species as a consequence of environmental filtering on individuals (Paine et al. 2011; Siefert et al. 2015). Intraspecific trait variability allows individual plants to adjust in response to environmental fluctuation (i.e., phenotypic plasticity, see Clark 2010; Ravenscroft et al. 2014; Spasojevic et al. 2016). Moreover, individuals can modify their traits through phenotypic plasticity in response to the activity of their closest neighbors of the same species (Violle et al. 2012; Le Bagousse-Pinguet et al. 2015; Chacon-Labelle et al. 2016).

What are the consequences of niche and stochastic processes on the patterns of intraspecific trait dispersions among spatially aggregated, random and uniform species? Aggregated distribution of tree species is a widespread spatial pattern observed in natural forests owing to local stochasticity of recruitment and/or to the specific history and environmental filtering of each site (Condit 2000; Réjou-Méchain et al. 2011). Among the many processes that contribute to the spatial aggregation, environmental filtering is a predominant driver clustering conspecific individuals in areas with favorable conditions (Pielou 1960; Wang et al. 2010; Ravenscroft et al. 2014; Umaña et al. 2015). Environmental filtering acts to select for individuals with different phenotypes (Laughlin et al. 2015) with a similar fitness as a response to particular set of environmental condition. As such, relative to the trait variation in populations across sites, environmental filtering reduces the variance/range and increases the

kurtosis of trait values among conspecific individuals at a specific location (Le Bagousse-Pinguet et al. 2017) (Fig. 1a). We, therefore, expected that species with aggregated distribution would have a greater probability of reduced range and variance of the functional traits than from those with random distributions. Although uniform distribution is uncommon in natural forests (He et al. 1997; Condit 2000; Dale 2002; Li et al. 2009; Wang et al. 2010), competition induced by self-thinning (Greig-Smith 1979; Chapin et al. 1989; Dale 2002; Stoll and Bergius 2005; Wang et al. 2010), and/or Janzen–Connell spacing effects (Janzen 1970; Connell 1971) could result in niche differentiation with an outcome of trait divergence (or over dispersion of trait values) among conspecific individuals. Niche differentiation and/or plasticity in functional traits may limit the similarity of trait values through partitioning of the spacing of trait values more regularly among conspecific individuals (Kraft et al. 2008; de Bello et al. 2016), regardless of whether competition is symmetric or not (Le Bagousse-Pinguet et al. 2015). In this case, relative to those traits expected by chance, reduced kurtosis (i.e., fat-tailed distribution) and standard deviation of nearest-neighbor distances of a trait (SD.NND, i.e., spaced more evenly along the trait axis) occur for conspecific individuals (Jung et al. 2010) (Fig. 1a). Accordingly, we expected that species with uniform distribution would have a greater probability of reduced kurtosis and SD.NND than expected by random. By contrast, random distribution of tree species may result from stochastic processes that assume that individuals distribute independently from each other (Dale 2002; Gotzenberger et al. 2012), such as chance colonization, random extinction, and ecological drift. Therefore, we predict that stochastic processes shape a random distribution of conspecific individuals, with trait values being neither under- nor over-dispersed (Fig. 1b).

Across a range of spatial distribution from aggregated to random, we expect a greater extent of intraspecific trait dispersion for species with more aggregated distribution (shaped by niche processes) than species with random distribution (shaped by stochastic processes), i.e., a negative association between the extent of intraspecific trait dispersions and the degree of the spatial randomness across spatially aggregated and random species (Fig. 1c). Here, the extent of intraspecific trait dispersion refers to a measure of the degree to which the observed range, variance, kurtosis, and SD.NND of trait values deviating from the null expectations (Kraft et al. 2008; Violle et al. 2012). The degree of the spatial randomness represents a continuous measure of nearest-neighbor distance index values among conspecific individuals across species (Clark and Evans 1954).

In this study, we measured four plant traits: leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), and diameter at breast height (d.b.h), for

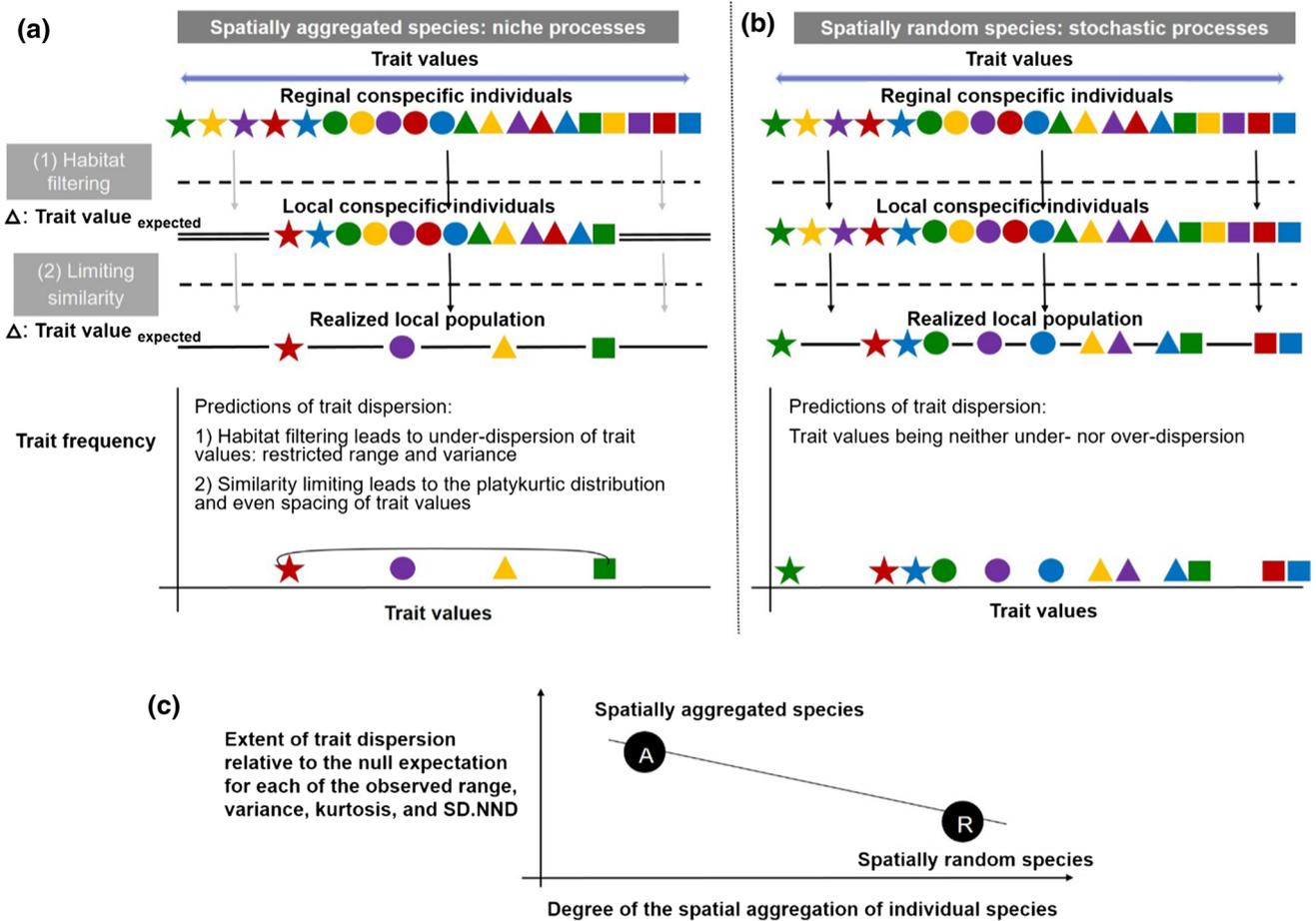


Fig. 1 Conceptual framework outlining the role of intraspecific trait variability in regulating the spatial distribution of individual species in **a** species with aggregated distribution structured by niche processes and **b** species with random distribution shaped by sto-

chastic processes. **c** Hypothesized relationship between the extent of intraspecific trait dispersion and the degree of the spatial randomness across spatially aggregated (A) and random (R) species. Color version of this figure is available online

all individual trees of 45 species in a spatially mapped 4.84 ha subtropical evergreen broadleaved forest plot in Eastern China. Although these traits do not represent the full aspects of plant ecological strategies, they may be employed as robust indicators for elucidating the spatial patterns of tree species (Cornelissen et al. 2003). Specifically, we tested the hypotheses that: (1) species with aggregated distributions would have greater probabilities with significantly reduced spread (range and variance), kurtosis and SD.NND of intraspecific traits compared with those with random distributions, while species with uniform distributions (if existed) would have greater probabilities with significantly increased interspecific trait dispersions and (2) the extent of spatial distribution from aggregation, random to uniform would be associated with the extent of the deviation of intraspecific trait dispersions from stochastic expectations across a diverse

array of tree species in a species-rich subtropical forest in Eastern China.

Materials and methods

Study plot and species

This study was conducted in a spatially mapped 4.84 ha subtropical forest plot in Tiantong National Forest Park (29°48'N, 121°47'E, 200 m a.s.l), located in Ningbo city, Zhejiang Province, in Eastern China. The climate of this region is subtropical monsoon with a hot, humid summer and a cold, dry winter. The mean annual temperature is 16.2 °C, and the mean annual precipitation is 1374.7 mm, the majority of which occurs between May and August (Yan et al. 2013). The vegetation within the Park is characterized as a subtropical evergreen broadleaf forest, which

has been severely disturbed in recent history, with only small intact and semi-intact tracts remaining in close proximity to a Buddhist temple. The primarily loam-textured soils of this area belong to Ferralosols with pH values that range from 4.4 to 5.1. The parental material is composed of Mesozoic sediments and intrusive acidic rocks, including quartzite and granite (Song and Wang 1995).

A 20 ha (400 × 500 m) forest plot was established in the intact area of the Park in 2009 and 2010 by following the protocols from the CTFS-ForestGEO network (Condit 1998). The forests in this area had not been subjected to logging or other human disturbances for at least a century (Yan et al. 2013). In this study, we selected 4.84 ha in the center of the 20 ha forest plot for mapping functional traits of individual trees. The topography of the functional trait plot was heterogeneous and rugged with elevations varying from 310 to 480 m a.s.l. and slopes of 121 20 × 20 m quadrats from 15 to 56°. The changes in elevation were more pronounced in the northern section than in the southern section of the plot (Fig. S1). Western and eastern edges of the plot extended through two north–south-oriented valleys, with the interior of the plot spanning two small northwest-to-southeast-oriented ridges, approximately 100 m apart.

The vertical structure of community and species composition changed with topography. In the ravine area, the canopy tree layer (~ 15–20 m in height) was dominated by deciduous *Choerospondias axillaris*, the sub-canopy tree layer (4 m ≤ height < 15 m) was dominated by evergreen *Machilus leptophylla*, and dominant species in the understory layer (< 4 m in height) included evergreen *Litsea elongata* and *Eurya loquaiana*. On slopes and ridge areas, dominant species in the understory layer were similar to those in the ravine area, but the canopy tree layer was occupied by evergreen species including *Lithocarpus harlandii* and *Cyclobalanopsis nubium*, while the sub-canopy tree layer was dominated by evergreen species such as *Lithocarpus harlandii*.

Within the functional trait plot, all trees with diameters at breast height (d.b.h., tree diameter at 1.3 m above root collar) ≥ 1 cm were tagged, species identified, measured, and geo-referenced in the summer of 2009. There were a total of 20,253 stems from 108 species, 76 genera, and 43 families. In the plot, to obtain a relatively large number of quadrats including representatives of conspecific individuals of a given species in the analysis of trait dispersion, 45 species, each with more than 25 individuals, were selected for the quantification of their spatial patterns and intraspecific trait variability (Table 1). Among them, *Eurya loquaiana* was the most abundant species, accounting for 29.6% of the total number of individuals under study (i.e., 18,773 stems for 45 species). This work was conducted based on Forestry Standards for ‘Observation

Methodology for Long-term Forest Ecosystem Research’ of the People’s Republic of China (LY/T 1952-2011).

Trait measurements

We determined leaf traits in the summer (i.e., June–August) of 2010–2013. We measured four traits for each of the 18,773 individuals, including SLA (projected leaf area per unit leaf dry mass, cm² g⁻¹), LA (cm²), LDMC (%), and d.b.h. (cm; used to represent variation in plant size). Field sampling for leaf traits was carried out between morning and early afternoon. Since leaf life stage strongly affects plant nutrient use strategies, leaf traits were measured in mature leaves. For each individual tree, following the d.b.h. measurement, three branches were cut from the upper, mid, and lower positions on the sunlit side of the tree crown. Approximately 20–30 mature leaves (with full light and without apparent physical damage) were collected from each branch. The leaves from the three branches of the same individual were subsequently combined to form a composite sample. The leaves were wrapped in a moist paper towel, placed into a sealed plastic bag, and stored in a cooler until they were processed in the laboratory.

In the laboratory, leaf functional traits were measured within 12 h (i.e., in the afternoon and evening of the same day of field sample collection). Twenty leaves were randomly selected from each composite sample and scanned using a leaf area meter (LI-3100C, Li-Cor, USA) to determine mean LA for each sample tree. The masses of these fresh leaves were then immediately taken. The samples were then dried at 75 °C for 48 h in an oven to determine leaf dry mass, toward calculating SLA and LDMC.

Spatial distribution of individual tree species

We quantified the spatial pattern for each of the 45 tree species within the 4.84 ha plot using the nearest-neighbor distance index (R) described by Clark and Evans (1954) (Eq. 1):

$$R = \frac{\bar{r}_A}{\bar{r}_E}, \quad (1)$$

where \bar{r}_A is the mean distance from an individual to its nearest conspecific neighbor in the 4.84 ha plot and \bar{r}_E is the expected mean distance to the nearest conspecific neighbor when conspecific individuals were randomly distributed. Following the Poisson distribution with stand density λ , \bar{r}_E was calculated according to

$$\bar{r}_E = \frac{1}{2\sqrt{\lambda}}. \quad (2)$$

R provides a measure of the degree to which the observed distribution of individuals within a given area departs from

Table 1 Number of stems, number of quadrats, nearest-neighbor distance index (R), and the spatial distribution patterns for the 45 tree species within a 4.84 ha spatially mapped subtropical forest plot in the Tiantong National Forest Park, Eastern China

Species	Number of stems	Number of quadrats	R	P	Spatial pattern
<i>Machilus leptophylla</i>	388	33	0.56	< 0.001	Aggregated
<i>Clerodendrum cyrtophyllum</i>	59	4	0.59	< 0.001	Aggregated
<i>Symplocos laurina</i>	143	18	0.59	< 0.001	Aggregated
<i>Photinia glabra</i>	173	23	0.64	< 0.001	Aggregated
<i>Syzygium buxifolium</i>	120	17	0.64	< 0.001	Aggregated
<i>Illicium lanceolatum</i>	247	48	0.67	< 0.001	Aggregated
<i>Distylium myricoides</i>	1349	68	0.70	< 0.001	Aggregated
<i>Rhododendron ovatum</i>	333	40	0.72	< 0.001	Aggregated
<i>Daphniphyllum oldhami</i>	139	23	0.76	< 0.001	Aggregated
<i>Symplocos anomala</i>	428	69	0.76	< 0.001	Aggregated
<i>Eurya loquaiana</i>	5559	120	0.77	< 0.001	Aggregated
<i>Laurocerasus phaeosticta</i>	203	30	0.77	< 0.001	Aggregated
<i>Osmanthus cooperi</i>	103	24	0.77	< 0.001	Aggregated
<i>Cyclobalanopsis sessilifolia</i>	231	55	0.81	< 0.001	Aggregated
<i>Symplocos setchuensis</i>	173	43	0.81	< 0.001	Aggregated
<i>Eurya rubiginosa</i>	189	46	0.83	< 0.001	Aggregated
<i>Castanopsis fargesii</i>	199	46	0.84	< 0.001	Aggregated
<i>Neolitsea aurata</i>	693	97	0.84	< 0.001	Aggregated
<i>Alniphyllum fortunei</i>	107	25	0.85	< 0.001	Aggregated
<i>Sassafras tzumu</i>	82	20	0.85	0.01	Aggregated
<i>Adinandra millettii</i>	478	94	0.86	< 0.001	Aggregated
<i>Cinnamomum subavenium</i>	205	54	0.86	< 0.001	Aggregated
<i>Litsea elongata</i>	3061	114	0.86	< 0.001	Aggregated
<i>Styrax confusus</i>	88	22	0.86	0.01	Aggregated
<i>Camellia cuspidata</i>	1684	114	0.87	< 0.001	Aggregated
<i>Lithocarpus henryi</i>	329	75	0.87	< 0.001	Aggregated
<i>Eurya muricata</i>	125	30	0.88	0.01	Aggregated
<i>Symplocos lancifolia</i>	167	42	0.88	< 0.001	Aggregated
<i>Machilus thunbergii</i>	387	77	0.90	< 0.001	Aggregated
<i>Symplocos sumuntia</i>	306	66	0.90	< 0.001	Aggregated
<i>Choerospondias axillaris</i>	235	56	0.92	0.01	Aggregated
<i>Castanopsis carlesii</i>	69	13	0.91	0.17	Random
<i>Cyclobalanopsis myrsinifolia</i>	132	36	0.92	0.07	Random
<i>Ilex buergeri</i>	93	24	0.92	0.12	Random
<i>Acer pubinerve</i>	47	7	0.95	0.55	Random
<i>Carpinus viminea</i>	90	17	0.96	0.43	Random
<i>Lindera rubronervia</i>	30	4	0.99	0.89	Random
<i>Litsea coreana</i>	47	9	1.00	0.98	Random
<i>Ilex kengii</i>	31	6	1.03	0.79	Random
<i>Symplocos stellaris</i>	27	3	1.05	0.60	Random
<i>Vernicia fordii</i>	67	12	1.05	0.47	Random
<i>Ilex latifolia</i>	45	9	1.07	0.38	Random
<i>Ilex rotunda</i>	44	6	1.12	0.14	Random
<i>Fraxinus insularis</i>	40	5	1.13	0.11	Random
<i>Liquidambar formosana</i>	28	3	1.13	0.20	Random

that of a random expectation. An R value being less than, equal to, or greater than 1 indicates aggregated, random, or uniform distribution, respectively (Clark and Evans 1954).

We used a z test to examine whether the observed spatial distribution of a given species differed significantly from the null expectation that all conspecific individuals are randomly

distributed. With the z test, spatial randomness, aggregation, or regularity for each species was determined based on a critical $\alpha = 0.05$ (Table 1). The value of the nearest-neighbor distance index (R) was calculated using the R package ‘*spatstat*’ by applying Ripley’s isotropic edge correction (Baddeley and Turner 2016). We assessed whether nearest-neighbor distance index was associated with species frequency distribution (number of quadrats presented) and abundance (number of stems), and found that spatial structure was neither significantly related to frequency nor abundance of the 45 species (Fig. S2).

Quantification of intraspecific trait dispersions

We used a null model approach to quantify trait dispersion patterns underlying niche and stochastic processes of the 45 species within the 4.84 ha plot. Similar to Kraft et al. (2008), our focus is to infer the processes of niche differentiation and environmental filtering at the local scale, we combined trait information with species abundance (number of stems) to estimate trait distribution in the 121 20×20 m quadrats. For each species present in a quadrat, we calculated observed and null model expected trait dispersion indices including range, variance, kurtosis, and SD.NND, and we derived null model expected trait dispersion indices for each species by creating 999 randomly assembled populations of an equal number of individuals (i.e., maintain the same abundance for each species) to the sample quadrat by drawing individuals at random from all conspecific individuals within the 4.84 ha plot. In this step, at least five individuals were used to calculate the within-quadrat statistics for each species. Environmental conditions such as soil properties, slope, and topography were considered as the random factors to satisfy the nature of the stochastic processes.

We tested the differences between the observed and null model expected trait dispersion patterns for each species at each quadrat using Wilcoxon signed rank test. We used reductions in range and variance, compared with null model expected, as measures sensitive to environmental filtering, and we used reductions in kurtosis and SD.NND as measures sensitive to limiting similarity or niche differentiation (Kraft et al. 2008). In all analyses, we used one-tailed tests based our priori predictions of environmental filtering and niche differentiation, and judged significantly non-random if the observed metric fell into the extreme 5% of the null distribution. Because environmental filtering may yield either larger or smaller mean trait values in observed than in null model expected (Jung et al. 2010), we did not include trait means into our trait metrics. Similar to Kraft et al. (2008), we used percentage of the quadrats in which the observed trait values significantly ($\alpha = 0.05$) deviated from the null expectations as a measure of the degree to which observed

trait distribution departs from random in the 4.84 ha forest plot.

Statistical analysis

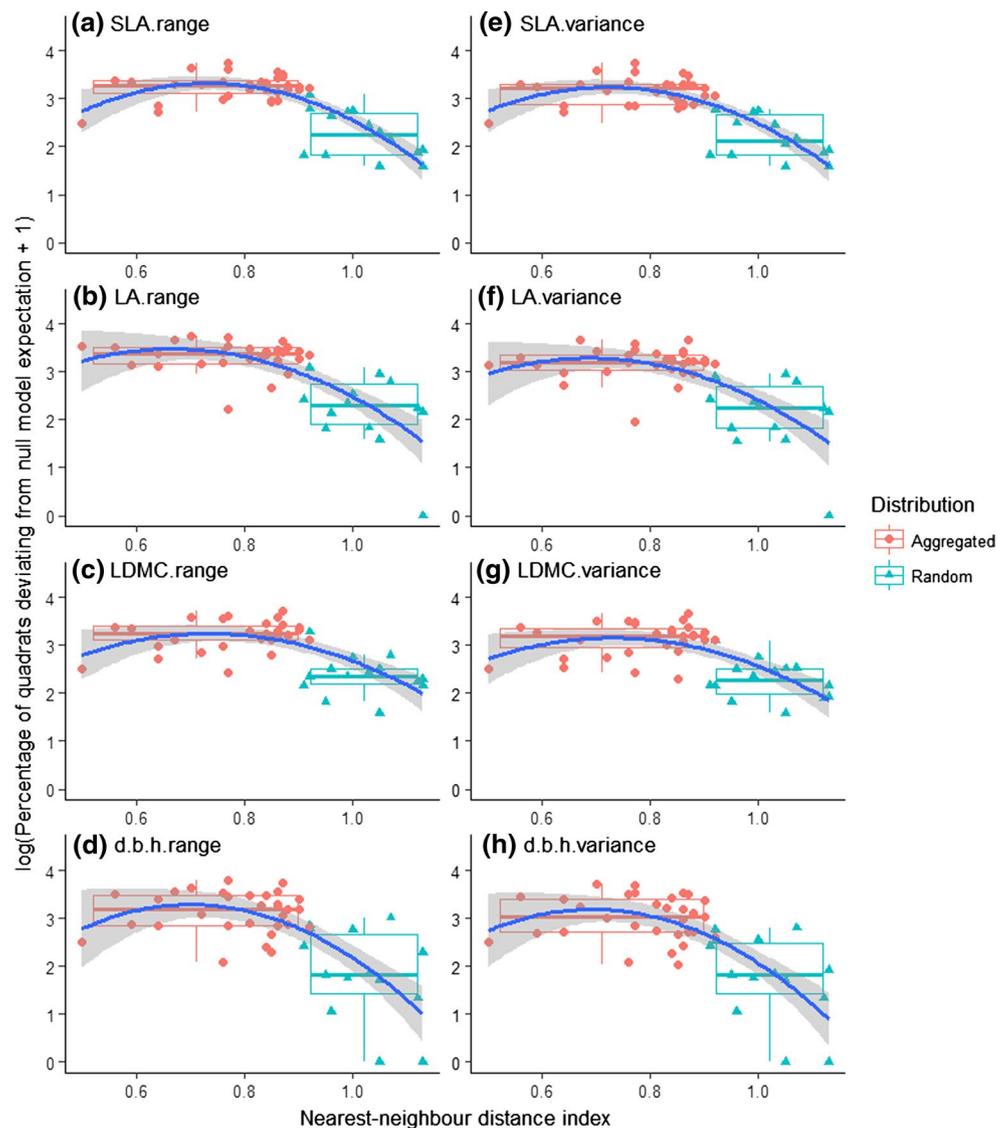
We tested the difference in the percentage of quadrats in which observed range, variance, kurtosis, and SD.NND of measured traits significantly deviated from the null model expectations between spatially aggregated and random species groups, using a Mann–Whitney test. We also examined the association between the percentage of quadrats and spatial structure across all species by treating the nearest-neighbor distance index as a continuous measure of spatial distribution. In this analysis, we log-transformed the percentages of quadrats as recommended (Warton and Hui 2011). To assess potential nonlinear associations between the percentage (log-transformed) and the nearest-neighbor distance index, we compared five alternative models (linear, quadratic, third-order polynomial, logarithm, and exponential). Based on Akaike information criterion (AIC), the quadratic function was consistently the best except the association between the kurtosis of LDMC and nearest-neighbor distance index, which was best described by the cubic function (Table S1), but the cubic function produced qualitatively similar patterns as the quadratic function. For consistency, we presented all associations by quadratic functions. All analyses were carried out with R 3.3.1 (R Core Development Team 2016).

Results

The nearest-neighbor distance analysis showed that, of 45 species, 14 species were distributed in random and 31 species were distributed in aggregation, while no species was distributed in uniform in the studied 4.84 ha forest plot (Table 1). The Mann–Whitney test showed that the percentages of quadrats with significant reductions in range and variance of the four studied functional traits from null model expectations were significantly greater in species with aggregated distributions than those in species with random distributions (Fig. 2, $P < 0.001$ in all cases). In addition, species with aggregated distributions had greater percentages of quadrats with significant reductions in kurtosis and SD.NND than those with random distributions for all studied traits (Fig. 3, $P < 0.001$ in all cases).

The percentages of quadrats deviated from the null expectations for each of range and variance of the four traits were all significantly negatively correlated with the nearest-neighbor distance index across the 45 species (Fig. 2). Similarly, significantly negative relationships were found between the percentages of quadrats deviated from the null

Fig. 2 Relationships between nearest-neighbor distance index and percentage of quadrats with significantly reduced **a–d** range and **e–h** variance of four studied traits [specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), and diameter at breast height (d.b.h.)] than expected from null models. Dots in red circle and blue triangle represent species with aggregated and random distributions, respectively, and each dot represents percentage of quadrats of a given species deviated from the null model expectation. Fitted regressions and their 95% confidence intervals are in blue lines and grey shades, respectively. The inserted box plots show the median (line within the box), 25th and 75th percentiles (the boundaries of the box), 95th and 5th percentiles (error bars), and observations outside 95th and 5th percentiles (black dots) by aggregated and random species. Color version of this figure is available online



expectations and nearest-neighbor distance index for kurtosis and SD.NND of all four studied traits (Fig. 3).

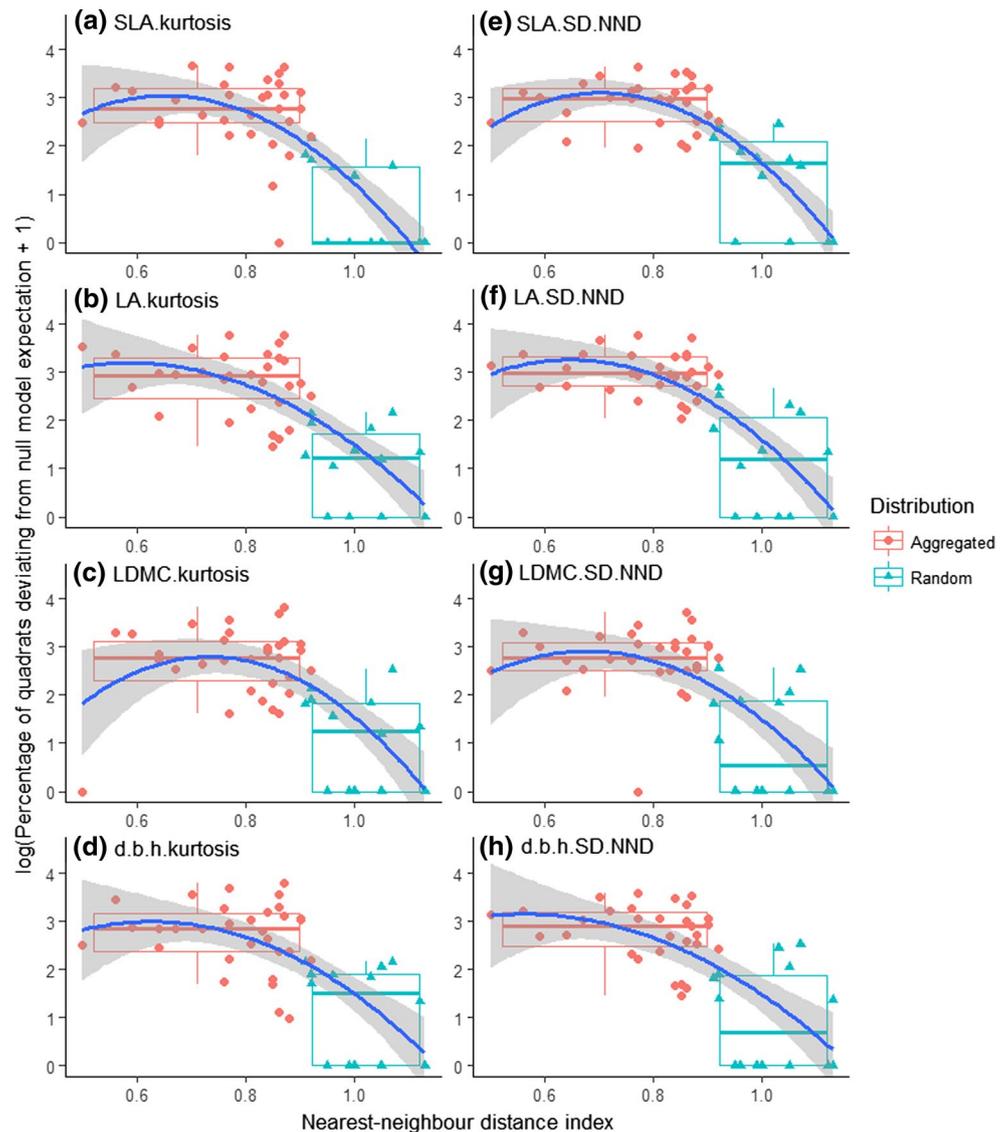
Discussion

We found that the intraspecific dispersions of all studied traits in species with aggregated distribution had greater probabilities with reduced range, variance, kurtosis, and SD.NND, compared with null expectations, than those in species with random distribution. Particularly, the percentages of quadrats with reduced range, variance, kurtosis, and SD.NND decreased continuously with the change from aggregation to randomness across our 45 studied species. While most previous studies have shown that niche processes play an important role in community assembly based on interspecific and intraspecific trait variability (Kraft et al.

2008; Jung et al. 2010; Siefert 2012a), our results indicate that niche processes drive the spatial structure of the species with aggregated distributions, while stochastic processes are more responsible for those with random distributions. Our results extend the link between trait variability and community assembly to that between intraspecific trait variability and spatial distribution of individual species.

Intraspecific trait dispersion patterns for which particular ecological processes play out are predictable with respect to the spatial structure of individual species (Violle et al. 2012). Compared with the null model expectations, the greater extent of reductions in ranges and variances of the four studied traits in aggregated than random species are consistent with the role of environmental filtering. Environmental filters, which pose a barrier to species establishment and/or survival at specific sites (Clark 2010), drive optimal trait values and in turn select for appropriate species mixtures

Fig. 3 Relationships between nearest-neighbor distance index and percentage of quadrats with significantly reduced **a–d** kurtosis and **e–h** SD.NND of four studied traits [specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), and diameter at breast height (d.b.h.)] than expected from null models. Dots in red circle and blue triangle represent species with aggregated and random distributions, respectively, and each dot represents percentage of quadrats of a given species deviated from the null model expectation. Fitted regressions and their 95% confidence intervals are in blue lines and grey shades, respectively. The inserted box plots show the median (line within the box), 25th and 75th percentiles (the boundaries of the box), 95th and 5th percentiles (error bars), and observations outside 95th and 5th percentiles (black dots) by aggregated and random species. Color version of this figure is available online



(Laughlin et al. 2015; Li et al. 2017). By the same token, environmental filters select for the appropriate individuals for a given species, resulting in a trait-mediated aggregation of conspecific individuals (Jung et al. 2010; Violle et al. 2012). Alternatively, the greater reduction in ranges and variances of the four studied traits in aggregated than random species suggests a smaller phenotypic plasticity in species with aggregated distributions than those with random distributions. In other words, environmental filtering selects for conspecific individuals with more fixed trait values in species with aggregated than those with random distributions (Fajardo and Siefert 2016; Le Bagousse-Pinguet et al. 2017). In this study, the greater effects of environmental filtering on the convergence of the four traits for aggregated than for random species are attributable to the heterogeneous topography of the plot, where two valleys and ridges varied in elevations, convexity, and slopes (Fig. S1). For example,

individuals of *Lithocarpus henryi* tend to be clustered in valley areas with high SLA, large LA, small LDMC, and large d.b.h. (Fig. S1).

We also found that greater percentages of quadrats had reduced kurtosis and SD.NND of our four studied traits, compared with null model expectations, in species with aggregated distribution than those with random distribution. Reduced kurtosis (fat-tailed distributions) and reduced SD.NND (even spaced) of trait values in aggregated species may have resulted from niche differentiation among conspecific individuals (Turcotte and Levine 2016) and/or plastic responses to increased trait distance from neighbors (Jung et al. 2010; Le Bagousse-Pinguet et al. 2015). The ‘niche variation’ of individuals within a species allows individuals to specialize behaviors to forage for alternative resources (Laughlin and Messier 2015; Abakumova et al. 2016). Biotic interactions with neighboring individuals can impose

selection on functional trait plasticity, which may feedback through trait divergence and niche differentiation (Araujo et al. 2011; Le Bagousse-Pinguet et al. 2015). Therefore, congruent with limiting similarity that acts on locally co-existing species, localized competition may also serve to select for conspecific individuals with divergent trait distributions (Abakumova et al. 2016) through ‘niche variation’ and/or phenotypic plasticity (Fajardo and Siefert 2016), and thus limit the similarity of closest neighbors of conspecific individuals of species with an aggregated distribution (Uriarte et al. 2010; Violle et al. 2012; Le Bagousse-Pinguet et al. 2015).

When spatial arrangement of conspecific individuals is affected by only stochastic processes, their trait values are expected to be randomly dispersed (Kraft et al. 2008; Paine et al. 2011). We found that the percentages of the quadrats with trait dispersion deviating from null model expectations were low for randomly dispersed species, with a large number of the measures of trait dispersion identical to null model expectations in all quadrats. This result is consistent with the prediction of neutral stochasticity theory, i.e., individuals occur independently of each other, regardless of the properties of habitats (Vellend et al. 2014). Our results suggest that random distribution is driven primarily by ‘neutral’ assembly such as chance colonization and ecological drift.

The negative relationships between the extents of intraspecific trait dispersion deviated from the null model expectations and the degree of the spatial randomness across species for all studied traits in this study highlight that the strength of niche and stochastic processes, which acted on plant traits, is associated with a wide range of spatial patterns of individual tree species. The larger extent of intraspecific trait variability deviating from the null model reflects the greater influences of niche processes than those of stochastic processes on the spatial distribution of individual tree species. Therefore, the negative relationship suggests that the effects of niche processes decrease relative to stochastic processes with an increasing extent of spatial randomness and that niche and stochastic processes jointly serve as a stabilizing effect to determine species coexistence by acting on the contrasting dimensions of spatial distributions for individual species in a local community.

We note that, consistent with the observations in other forests (He et al. 1997; Condit 2000; Dale 2002; Li et al. 2009; Wang et al. 2010; Réjou-Méchain et al. 2011), we did not find species with uniform distribution in the studied forest. This might be attributable to the high degree of topography heterogeneous, with which none of species have an ability to tolerate the varied habitat conditions. Rather, individuals of a given species are preferred to clump to the optimally particular set of locations, where they can survive with different phenotypes (Laughlin et al.

2015). In addition, the uniform distribution of plant species tends to be an ideal spatial pattern controlled by a single dominant regime such as competition in ecosystems of tundra (Chapin et al. 1989). However, in tropical forests, multiple controlling mechanisms, for instance, intra- and interspecific competition, suitability of locations, stochastic recruitment, niche differentiation, and dispersal limitation, tend to drive the spatial distributions of tree species toward to aggregation and randomness (Greig-Smith 1979; He et al. 1997; Réjou-Méchain et al. 2011).

In conclusion, our study represents the first to address the link between intraspecific trait variability and the spatial arrangement of conspecific individuals among co-existing tree species. Our results indicate that niche processes drive the spatial structure of species with aggregated distributions, while stochastic processes are responsible for those with random distributions. The strong negative relationships between the extent of intraspecific trait dispersion deviated from the null model expectations and spatial randomness across a diverse array of species suggest that the relative strength of stochastic versus niche processes increases with the extent of spatial randomness of conspecific individuals among co-existing species in a local community.

We note that in addition to niche processes such as environmental filtering and niche differentiation, dispersal limitation and other processes such as intra and interspecific competition can also generate a spatially aggregated distribution of tree species (Weiher and Keddy 1995; Levine and Murrell 2003; Gotzenberger et al. 2012; Siefert 2012b). Although we cannot assess the contribution of dispersal limitation on the trait dispersion pattern for aggregated species, it is more likely that spatial patterns of tree species are subjected to multiple mechanisms. We encourage future studies to focus on the relative importance of environmental filtering, niche differentiation, dispersal limitation, and stochastic processes on the relationship between intraspecific trait variability and spatial pattern of tree species.

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Author contribution statement ERY and HYHC designed the study and wrote the manuscript. ERY, LLZ, XHW, and XYL conducted the study. LLZ and HYHC analyzed the data.

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