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Authors

McFadden, Ian R
Bartlett, Megan K
Wiegand, Thorsten
et al.

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Disentangling the functional trait correlates of spatial aggregation in tropical forest trees

Ian R. McFadden [ID],[1,8] Megan K. Bartlett,[1,2,3] Thorsten Wiegand,[4,5] Benjamin L. Turner,[6] Lawren Sack,[1] Renato Valencia [ID],[7] and Nathan J. B. Kraft[1]

[1]*Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Charles E. Young Drive South, Los Angeles, California 90095 USA*
[2]*Princeton Environmental Institute, Princeton University, 129 Guyot Hall, Princeton, New Jersey 08544 USA*
[3]*Department of Ecology and Evolutionary Biology, Princeton University, 106 Guyot Hall, Princeton, New Jersey 08544 USA*
[4]*Department of Ecological Modeling, UFZ Helmholtz Centre for Environmental Research, PF 500136, Leipzig DE-04301 Germany*
[5]*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig 04103 Germany*
[6]*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama*
[7]*Laboratory of Plant Ecology, School of Biological Sciences, Pontifical Catholic University of Ecuador, Apartado 17-01-2184, Avenida 12 de Octubre 1076, Quito, Ecuador*

Abstract. Environmental filtering and dispersal limitation can both maintain diversity in plant communities by aggregating conspecifics, but parsing the contribution of each process has proven difficult empirically. Here, we assess the contribution of filtering and dispersal limitation to the spatial aggregation patterns of 456 tree species in a hyperdiverse Amazonian forest and find distinct functional trait correlates of interspecific variation in these processes. Spatial point process model analysis revealed that both mechanisms are important drivers of intraspecific aggregation for the majority of species. Leaf drought tolerance was correlated with species topographic distributions in this aseasonal rainforest, showing that future increases in drought severity could significantly impact community structure. In addition, seed mass was associated with the spatial scale and density of dispersal-related aggregation. Taken together, these results suggest environmental filtering and dispersal limitation act in concert to influence the spatial and functional structure of diverse forest communities.

Key words: community assembly; dispersal limitation; diversity maintenance; environmental filtering; leaf hydraulics; leaf toughness; spatial point process modeling.

Introduction

Explaining species coexistence in diverse communities is a perennial challenge for ecologists (Hart et al. 2017), and this challenge is particularly acute in tropical forests, where hundreds of tree species may co-occur within a single hectare (Valencia et al. 2004). In plant communities, diversity may be maintained by a variety of mechanisms (Wright 2002), including environmental filtering acting on interspecific variation in abiotic tolerances (Cornwell and Ackerly 2009), as well as limited seed dispersal (Hubbell 2001). Both of these processes aggregate conspecifics and therefore reduce competition with heterospecifics, which can then contribute to species coexistence (Chesson 2000). Intraspecific aggregation is a common feature of many plant communities (Levine and Murrell 2003), including tropical forests (Condit

et al. 2000), which suggests that dispersal limitation, environmental filtering, or both processes are widespread structuring factors of plant assemblages (Shen et al. 2009, Pinto and MacDougall 2010).

Unfortunately, it is often difficult to quantify the relative importance of filtering and dispersal limitation as both can cause the same pattern of intraspecific aggregation when abiotic factors are spatially autocorrelated (Shen et al. 2013). In order to better understand the processes shaping plant communities, it is therefore critical to disentangle the separate contributions of both processes. Intraspecific aggregation in plant communities has most often been studied through the lens of a single ecological process such as environmental filtering, dispersal limitation, or biotic factors such as competition or natural enemies (Harms et al. 2001, Seidler and Plotkin 2006, Mangan et al. 2010), though studies examining multiple processes are becoming more common (Russo et al. 2007, Pinto and MacDougall 2010, Wiegand and Moloney 2014). As multiple processes can drive aggregation, studies that focus on a single mechanism may misinterpret the importance of the mechanism

under study. For example, a species with limited dispersal potential may appear to be associated with spatially autocorrelated abiotic conditions found in its distribution, when in fact it is able to tolerate a far broader range of conditions (Pinto and MacDougall 2010).

One important way forward is to study empirical species distributions with recently developed spatial point process models (SPPMs) that estimate the strength of both environmental filtering and dispersal limitation (Fig. 1; Waagepetersen and Guan 2009, Jalilian et al. 2013). These models allow researchers to estimate associations with environmental variation as well as properties of species clustering independent of any environmental variation. If all major environmental attributes have been included in the model, this residual clustering can be interpreted as a measure of aggregation due to dispersal limitation (Shen et al. 2013). SPPMs have several advantages over nonspatial methods and methods that average occurrences into quadrats. First and most important for the goals of this study is that SPPMs make it possible to control for the influence of dispersal limitation when estimating habitat associations. An additional advantage is that fine-scale spatial variation below the quadrat level is explicitly incorporated (Møller and Waagepetersen 2003).

While SPPMs provide a powerful way to disentangle the causes of species aggregation, SPPMs on their own do not offer easy ways to discover the underlying physiological or functional trait drivers. Conversely, many trait-based ecology studies to date disregard the fine-scale spatial structure of the community in question (reviewed in Wiegand et al. 2017) and focus on a small number of relatively easy to measure traits such as specific leaf area (SLA), plant height, seed size, and wood density (Silvertown 2004, Kraft et al. 2008, Cornwell and Ackerly 2009, Swenson et al. 2012). As the functional traits of plants are known to shape both environmental responses and dispersal ability (McGill et al. 2006, Cornwell and Ackerly 2009, Lowe and McPeek 2014), coupling functional trait analyses with SPPMs offers a promising path toward a more complete understanding of the drivers of spatial structure in plant communities. Specifically, insights into the mechanisms driving aggregation can come from relating spatial properties such as habitat associations and cluster properties with key functional traits (Seidler and Plotkin 2006, Wiegand et al. 2009).

Though the current core plant functional trait list is useful for understanding the mechanisms of species aggregation (e.g., variation in seed size is often implicated in driving variation in dispersal potential among species; Levine and Murrell 2003), it cannot provide the insights that more detailed physiological studies can offer. For example, core plant functional traits offer limited information about drought tolerance (Bartlett et al. 2016), which is critical for understanding how species and communities are distributed with respect to water availability, and how they will respond to anthropogenic changes in water regimes (Bartlett et al. 2012b, Choat

et al. 2015). To address this limitation, we capitalize on recent method developments (Bartlett et al. 2012a) that have made assessing drought tolerance more tractable in high diversity communities.

Here, we integrate spatial process modeling and functional trait approaches to better understand how environmental filtering, dispersal limitation and species traits create variation in the spatial structure of a high-diversity forest in the Ecuadorian Amazon. We first use SPPMs to infer the relative importance of environmental filtering and dispersal limitation as drivers of spatial aggregation for 456 co-occurring tree species. To accomplish this, we used a decision tree (Appendix S1: Fig. S1) to categorize each species based on whether a single process, both processes or neither process is required to describe its spatial aggregation patterns. We then test whether the physiological and functional traits of species are correlated with variation in the strength of processes inferred from the spatial models.

We predict that because of the strong topographic and edaphic heterogeneity within this forest (Valencia et al. 2004), the distribution and aggregation of species will be primarily driven by abiotic gradients, as opposed to dispersal limitation or both in combination (H1). Next, we predict that ridge-associated species will have more resource-conservative traits (e.g., higher leaf drought tolerance, lower SLA, larger seed mass) than valley-associated species (H2). Finally, we predict species with larger seeds and taller statures will be less dispersal limited, i.e., have larger clusters with fewer stems per cluster (H3). This is because most tree species in this forest are dispersed by animals (Bemmels et al. 2018) and, in tropical forests, heavier seeds tend to be dispersed by larger birds and primates with larger home ranges (Holbrook and Smith 2000). In addition, tree height has been shown to influence dispersal distances for wind-dispersed species (Thomson et al. 2011). We find that the majority of species are best described by a model that includes both filtering and dispersal limitation, and that traits related to resource use and seed mass are important drivers of habitat preferences and clustering due to dispersal limitation, respectively.

METHODS

Study area and environmental data

We conducted our research in the Yasuní Forest Dynamics Plot (FDP), a 50-ha tree plot containing over 1,100 tree species in which all stems $\geq$ 1cm diameter at breast height (DBH) have been identified, mapped, and censused at regular intervals (Valencia et al. 2004; R. Valencia, *unpublished data*). Given constraints of existing trait data from the site (Kraft et al. 2008), we focus our analyses on the better sampled western 25 ha. The Yasuní FDP is part of the Smithsonian Forest Global Earth Observatory (ForestGEO) plot network (Anderson-Teixeira et al. 2015). Given the statistical demands
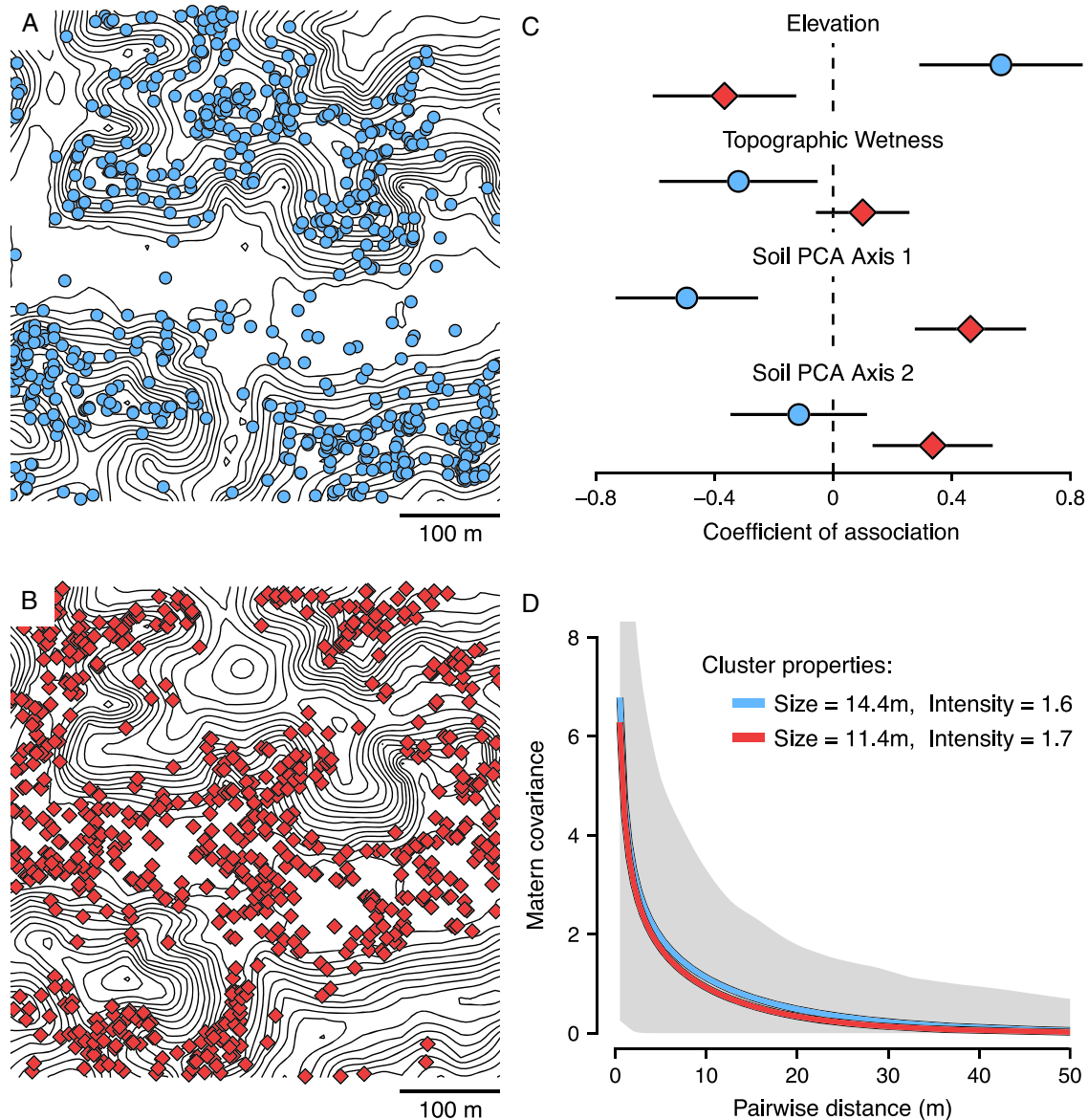
Fig. 1. Visual primer of spatial point process modeling. Panels A and B are plot-wide stem maps, and panels C and D are model parameters for two exemplar species that are associated with different habitats but share similar clustering properties. Contours in panels A and B indicate plot topography. Light blue circles in panel A correspond to individual stems of *Faramea capillipes* (Rubiaceae). Panel C shows this species is positively associated with elevation, and is thus most often found on ridgetops and slopes, and is negatively associated with topographic wetness and soil PCA axis 1 (Appendix S1: Fig. S2). Dark red diamonds in panel B are the stems of *Pentagonia williamsii* cf. (Rubiaceae), which are negatively associated with elevation but positively associated with both soil PCA axes. Horizontal bars in panel C represent 95% confidence intervals. The Matérn covariance function (MCF), which estimates the spatial correlation between pairs of stems within a species in the form of a dispersal kernel, is plotted for both species in panel D. Species cluster size and clustering intensity are used to calculate the MCF over a range of pairwise distances between stems. The gray polygon in panel D represents the 95% confidence interval of the MCF for the 348 species for which it was estimated, i.e., species in the dispersal only or habitat and dispersal categories.

of our spatial analyses, we limited our study to the 456 species with 70 or more individuals in the 25-ha plot, which together account for over 90% of stems. The plot contains significant topographic and edaphic heterogeneity, with two main ridges running east to west separated by a central stream-filled valley (Fig. 1A & B;

Appendix S1: Fig. S2). The forest is aseasonal (Valencia et al. 2004) and is home to a largely intact fauna despite some nearby hunting (Bass et al. 2010). To assess the influence of abiotic environmental factors on tree species distributions (H1), we included four topographic and soil attributes mapped at 5×5 m resolution (Appendix S1:

Figs. S2, S3). Specifically, we used elevation, the topographic wetness index (TWI, Sörensen et al. 2006), and the first two PCA axes from a data set of 15 soil nutrient and chemical properties representing soil cations (axis 1) and major nutrients such as N, P, and K (axis 2, Appendix S2).

Overview of spatial modeling process

We used a two-step approach to determine whether the spatial aggregation of each focal species (using all stems with DBH ≥ 1cm) was driven by environmental filtering alone, dispersal limitation alone, neither process, or both processes in combination (Table 1). First, to place species in one of the four above categories, we implemented a decision tree using two increasingly complex SPPMs (Appendix S1: Fig. S1). Then, to estimate habitat associations and or clustering parameters for species with nonrandom spatial structure (categories C2–C4), we used SPPMs incorporating one or both processes (Table 1). We used goodness-of-fit tests (Loosmore and Ford 2006) to assess nonrandom departures from the SPPMs in the decision tree, and the method of minimum contrast (Diggle and Gratton 1984) to fit cluster parameters. Minimum contrast methods seek to minimize the difference between the observed dispersion of stems (i.e., aggregated, random, disaggregated) and the patterns of dispersion generated by a model used to recreate the species spatial properties (Møller and Waagepetersen 2003). Our analysis generally follows the approach of Shen et al. (2009, 2013), but for clarity below we expand on each step in more detail.

Step one: Determine model category for each species

To assign species to the four spatial aggregation categories (Table 1), we used the decision tree outlined above (Appendix S1: Fig. S1). We first used goodness-of-fit tests with 999 simulations of complete spatial

TABLE 1. Spatial model categories.

Spatial aggregation category	Spatial model	Parameters estimated
C1: Complete spatial randomness	homogeneous Poisson[1]	none
C2: Habitat only	heterogeneous Poisson[1]	coefficients of association (β)
C3: Dispersal only	Thomas cluster process[1]	cluster size (α) and intensity (σ^2)
C4: Habitat and dispersal	log-Gaussian Cox process[2,3]	β, α, σ^2

Notes: Categories used to classify species based on spatial aggregation properties, the spatial models used to estimate parameters for species in each category, and the parameters estimated from each spatial model.
Sources:
1, Baddeley et al. (2016); 2 Jalilian et al. (2013); 3, Shen et al. (2013).

randomness (CSR; Baddeley et al. 2016) as a null model to determine whether species exhibited nonrandom spatial structure over a range of scales. To quantify spatial structure, we used three spatial summary statistics that capture distinct aspects of species aggregation patterns: the pair correlation function, the L-function, and the empty space function. The pair correlation function $g(r)$ is the expected density of stems at distance r from a given stem in the pattern normalized by stem density; the L-function is a transformed version of the K-function, the cumulative number of stems within distance r of a typical stem normalized by stem density, and the empty space function is the expected distance from a random location in the plot to the nearest stem in the pattern (Wiegand and Moloney 2014, Baddeley et al. 2016). We used the Benjamini-Hochberg correction for multiple comparisons when assessing significance.

If a species did not differ significantly from the CSR null model, it was assigned to the complete spatial randomness category (C1), and no habitat associations or clustering parameters were estimated. For species that did exhibit significant nonrandom spatial structure, we used a heterogeneous Poisson model that correlates variation in the density of stems across the plot with the four topographic and soil attributes. We determined the final set of environmental attributes included in the model through backward selection via AIC. Next, we assessed whether species were further aggregated beyond any aggregation due to the environment by testing for departures from the heterogeneous Poisson model via goodness of fit. Species associated with at least one environmental attribute, but without significant departures from the heterogeneous Poisson model were placed in the habitat only category (C2). Next, species with significant departures from the heterogeneous Poisson model but not associated with any environmental attributes were placed in the dispersal only category (C3). Finally, species associated with at least one habitat attribute and showing significant departures from the heterogeneous Poisson model were placed in the habitat and dispersal category (C4). In species with departures from the heterogeneous Poisson model (C3 and C4), aggregation not explained by the abiotic environment is attributed to dispersal limitation, though unmeasured environmental variation such as canopy gaps could also contribute to these patterns.

Step two: Estimate habitat associations and clustering parameters

After placing species into categories based on properties of their spatial aggregation, we next quantified parameters related to habitat associations and or dispersal limitation for species in categories C2–C4 (Table 1). For species in the habitat only category (C2), we used a heterogeneous Poisson model to estimate standardized coefficients of association with the reduced set of environmental attributes. For species in the dispersal only category (C3), a Thomas cluster process model was used

to estimate only average cluster size and clustering intensity via a Matérn covariance function (MCF). Cluster size is an estimate of the spatial radius over which clustering occurs and clustering intensity represents the strength of association between points within a cluster, such that species with higher clustering intensity have more stems within a given cluster. To model negative exponential decay of pair correlation in the MCF, we used a cluster shape value of 0.5, as this function is commonly used to estimate dispersal kernels (Nathan and Muller-Landau 2000). Finally, for species in the habitat and dispersal category, we used a log-Gaussian Cox process (LGCP, Jalilian et al. 2013) model in which the spatial aggregation of stems is modeled by a random intensity function:

$$\log \Lambda(x) = \lambda_H(x) + D(x) = \mu + \sum_i \beta_i H_i(x) + D(x). \quad (1)$$

This function combines (1) a log-linear species distribution model to predict the intensity function $\lambda_H(x)$ of stems at location x as a vector of coefficients of association $\beta_i(x)$ with a vector of environmental attributes $H_i(x)$, and (2) a MCF to describe additional clustering $D(x)$ independent of habitat associations, with μ representing an intercept (Jalilian et al. 2013, Shen et al. 2013). Importantly, the LGCP updates the estimates of coefficients of association for each environmental attribute based on the pair correlation, or additional clustering. See Waagepetersen and Guan (2009), and Shen et al. (2013: Appendix B) for a detailed description of the LGCP modeling process.

Functional traits

To identify the physiological and functional drivers of filtering and dispersal limitation, we used seven leaf, seed, wood, and whole-plant traits related to leaf economics, resource capture, dispersal, and growth–mortality trade-offs. We used previously published values for SLA, leaf nitrogen content, wood density and maximum DBH (as a proxy for maximum height) collected via established protocols (Cornelissen et al. 2003, Kraft and Ackerly 2010, Hietz et al. 2013). In addition, we collected new data on leaf drought tolerance (Bartlett et al. 2012a) and leaf tissue mechanical strength, an important trait for understanding leaf lifespan, herbivore defense, and litter decomposition rates (Onoda et al. 2011). We also included seed mass data from ongoing work in the Yasuní plot (J. Wright and N. Garwood, *unpublished data*). To ensure sufficient sample size for multivariate regressions using all traits, we used wood density and seed mass values for species too rare to sample at Yasuní (45% and 51% of species respectively) compiled from published studies from other sites or estimated from genus or family level means (Fortunel et al. 2016).

We assessed leaf drought tolerance by measuring the turgor loss point (TLP; units: MPa), which is the leaf water potential at which cells lose turgor and the leaf wilts (Bartlett et al. 2012b). We sampled TLP for 28 ridge-associated, 26 valley-associated, and 26 habitat generalist species via the vapor pressure osmometer method (Bartlett et al. 2012a). To minimize damage to the trees and preserve forest dynamics, we modified earlier protocols by collecting leaves instead of entire branches. We collected two leaves from four to six trees per species in double-bagged, humidified, Whirl-Pak bags (Uline, Pleasant Prairie, Wisconsin, USA) and then rehydrated leaves with the petioles in water for 8 h under dark, humid conditions before sampling. We measured leaf osmotic potential using a vapor pressure osmometer (VAPRO 5600; Wescor, South Logan, Utah, USA) and then converted measurements to TLP values following Bartlett et al. (2012a).

We measured leaf mechanical strength for 454 of the 456 focal species using a custom-built penetrometer constructed around a digital force gauge (DS2-11; Imada, Northbrook, Illinois, USA) and test stand (KV-11-S; Imada). We measured the specific force to punch (Units: N/mm^2), or the maximum force required to pass a circular metal rod through a leaf normalized by the circumference of the punch rod and the thickness of the leaf, following established protocols (Perez-Harguindeguy et al. 2013). We sampled two leaves from three individuals per species at three positions along the midrib axis of the leaf (25%, 50%, and 75% of leaf length), avoiding the midrib and secondary veins.

Linking species traits and spatial properties

To determine whether physiological and functional traits are predictive of spatial properties across species, we correlated our trait data set with the six aggregation parameters estimated from the spatial models, specifically the strength of environmental association with the four habitat attributes, cluster size, and clustering intensity. We first examined bivariate relationships between single traits and spatial properties inferred from our two-step decision tree approach. We then used multivariate regressions with all traits to predict spatial properties and model reduction via AIC to find best fitting trait combinations. To ensure sufficient sample size of spatial model parameters in multivariate regressions, we used the LGCP model (C4, habitat and dispersal) for all species. All analyses were done in R 3.4.1 (R Core Team 2016).

RESULTS

Contrary to our first hypothesis that environmental variation alone will structure the majority of species aggregation, we found that most species distributions (75.2%, 343/456) were best described by the LGCP habitat and dispersal model (C4; Fig. 2). Similar numbers of the remaining species (12.1% and 11.6%, or 55 and 53 species, respectively) were placed in the habitat only (C2,

heterogeneous Poisson model) and null model (C1, CSR) categories. Only five species (1.1%) were assigned to the dispersal only category (C3, Thomas cluster process). Alternative analyses focused only on large-statured species (maximum 95th percentile DBH $\geq$10 cm) yielded qualitatively similar results, while restricting the analysis to smaller-statured species (maximum DBH < 10 cm) increased the proportion of species in the habitat and dispersal category (C4; Fig. 2). Most species (67.8%, 309/456) were significantly associated with one or more of the four environmental attributes (Fig. 3; Appendix S1: Fig. S4). For those species in which clustering related to dispersal limitation was estimated (those in the dispersal only and habitat and dispersal categories), most had small clusters (mean α = 25.8 m, SD = 63.6 m) with a mean intensity (σ^2) of 2 (SD = 1.2).

Functional trait differences were related to a number of the spatial patterns that we detected. Species with no detectable aggregation (C1), had higher seed masses and larger maximum DBHs than those in the habitat and dispersal (C4) category (Appendix S1: Fig. S5). Supporting our second hypothesis, we found that species with higher leaf drought tolerance tended to be associated with higher elevations and lower TWI values in the plot (Fig. 4A, R^2 = 0.16, P = 0.002; Appendix S1: Table S1). We found mixed support for other traits. For example, ridge-associated species had lower SLA in bivariate comparisons but the relationship reversed in multivariate regressions, while ridge-associated species had higher seed masses in multivariate regressions but no significant relationship in bivariate comparisons (Table 2; Appendix S1: Table S2). Finally, seed mass and maximum DBH were correlated positively with species cluster size and negatively with clustering intensity (Fig. 4B, C, Table 2), supporting our third hypothesis.

Many of the functional traits in our study were weakly correlated with the six spatial parameters when considered individually (Table 2, Pearson correlation −0.41 to 0.36; Appendix S1: Table S1), while multivariate models using combinations of traits increased predictive power somewhat (Appendix S1: Table S2). For example, species with stronger clustering intensity tended to be smaller in stature and possess traits associated with pioneer strategies (e.g., higher SLA, smaller seed mass, R^2 = 0.24). In addition, species positively associated with elevation (ridge and slope-associated species) had higher drought tolerance, larger seed size and lower leaf nitrogen as may be expected if these environments are resource poor, but also tended to have higher SLA and smaller DBHs (R^2 = 0.3).

DISCUSSION

Most species were best described by a model that included both habitat associations and dispersal limitation, suggesting both mechanisms are important determinants of spatial structure in this forest. This joint effect has also been demonstrated in Asian and Central American forests (Shen et al. 2009, 2013, Jalilian et al. 2013), suggesting it may be a common feature of tree communities given sufficient environmental heterogeneity. While neutral theory (Hubbell 2001) might predict little or no habitat associations given the hyper-diversity of the local and regional tree community (Bass et al. 2010), we instead found consistent effects of environmental heterogeneity on species distributions within the plot, though they were often weak. We also found that dispersal limitation is pervasive in this forest as evidenced by the fact that most species were placed in a model category that included this process, which is
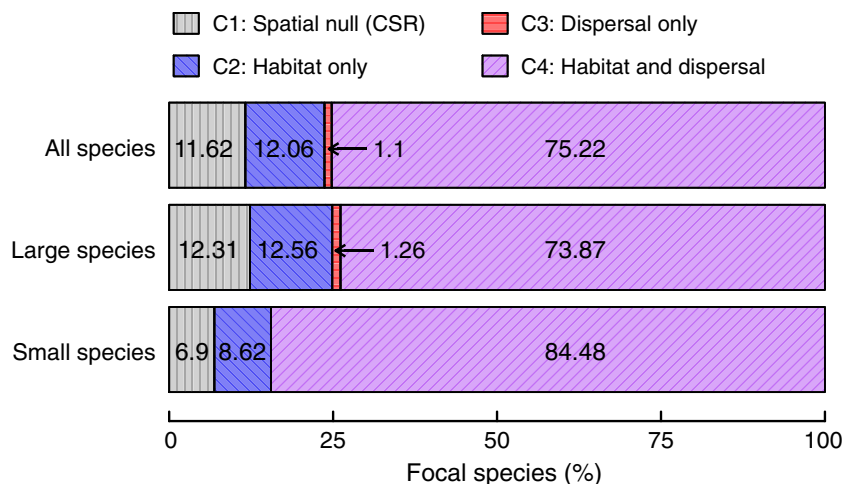

FIG. 2. Percentage of focal species assigned to each of the four spatial aggregation categories (Table 1). The majority of species (75.2%, 343/456) are best described by a model that incorporates both habitat associations and dispersal limitation (habitat and dispersal, C4). Results are similar when only species with maximum DBH $\geq$10 cm are included (large species, N = 398), while when only species with maximum DBH <10 cm are included (Small species, N = 58) no species remain in the dispersal only category (C3) and more fall in the habitat and dispersal (C4) category.
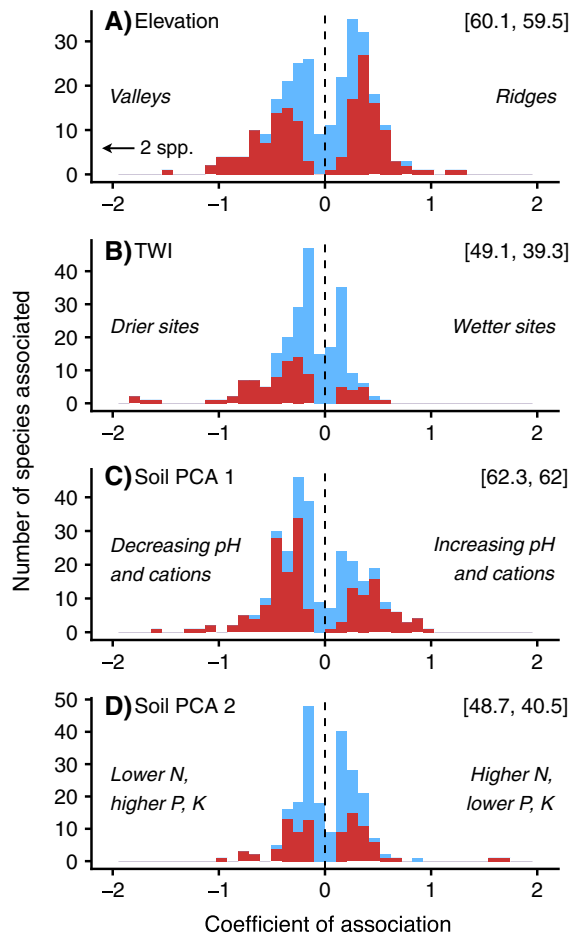
FIG. 3. Frequency distributions of species habitat association coefficients for the four environmental attributes (labeled A–D). Species with significant positive or negative associations (95% confidence interval does not overlap zero) are in dark red, and species without significant association (confidence interval overlaps zero) are in light blue. Numbers in brackets indicate the percentage of species associated with the environmental attribute after model reduction (left), and the percentage of significant associations within this reduced group (right). The environmental attributes of the gradient extremes are noted in italicized text. See appendix S1: Fig. S5 for the complete set of confidence intervals and Data S1 for species-specific values. Note that, in panel A, two species with extreme spatial distributions were excluded for visual clarity and are shown in Appendix S1: Fig. S9.

counter to our hypothesis that the environment alone will be sufficient to describe most species distributions.

In our analyses, we find that physiological and functional traits are correlated with key features of the spatial patterns of species. This broadens the utility of traits in community ecology by connecting them with spatially explicit measures of species distribution. For example, seed size was related to both the size and intensity of species clustering attributed to dispersal limitation. This could be due to seed size vs. number trade-offs, where larger seeded species have fewer offspring and therefore fewer individuals (Muller-Landau 2010). Alternatively,

larger-seeded species in this plot may be preferentially dispersed by larger vertebrates such as toucans, toucanets, and primates, leading to more widespread stem patterns. In line with our results, Seidler and Plotkin (2006) found that tree cluster size increased with seed mass and Russo et al. (2007) found that animal-dispersed tree species were less clustered at the 0–20 m scale than those dispersed by gravity or wind. While dispersal limitation is often modeled as a stochastic process with respect to species (Lowe and McPeek 2014), these results suggest it is determined in part by species traits. It may therefore be possible to predict the degree of dispersal limitation a species experiences using dispersal-related traits alone, which may inform studies of community dynamics, reforestation, and forest management.

One of the strongest associations between traits and spatial properties was that ridge-associated species had more negative leaf turgor loss points than valley-associated species. This suggests that, on average, ridge-associated species may be more drought tolerant, though stomatal responses and stem and leaf hydraulic vulnerability data, which could be used to estimate thresholds beyond which hydraulic function is lost, are lacking. While leaf turgor loss point has been shown to shape topographic associations in seasonal tropical forests (Maréchaux et al. 2015, Bartlett et al. 2016), this study is the first to report this result for an aseasonal forest. Amazonian forests are experiencing increased drought due to stronger and more intense El Niño events (Lewis et al. 2011), which may select for more drought-tolerant species. For example, after the 2010 El Niño drought, slope and ridge-associated species experienced lower mortality than those in valleys in a forest in the Colombian Amazon (Zuleta et al. 2017). This suggests that droughts may cause ridge-associated species to increase in abundance and perhaps expand their elevational ranges.

Despite clear links between traits and species aggregation, many of the bivariate correlations between traits and spatial properties were somewhat weak or not significant. This is not unexpected, as the spatial properties of species are a result of multiple processes acting over a variety of scales; thus, any one functional trait may not be a strong predictor of spatial pattern. This lack of predictive ability could also be because traits with better predictive power have not yet been measured. Predictive power increased somewhat in multivariate trait models, with largely similar results. This suggests that traits act in an integrative way to shape spatial structure. Our analysis of leaf lamina toughness extends previous work in the Yasuní FDP on this trait (Cardenas et al. 2014), which found that leaf toughness, in combination with other leaf mechanical and chemical traits, predicted the degree of herbivore damage for 28 species. Last, our work on single-species models of the most abundant species in the plot contrasts with previous analyses of community-weighted mean (CWM) trait values that compared observed trait distributions with a null model simulating random dispersal (Kraft et al. 2008, Kraft and
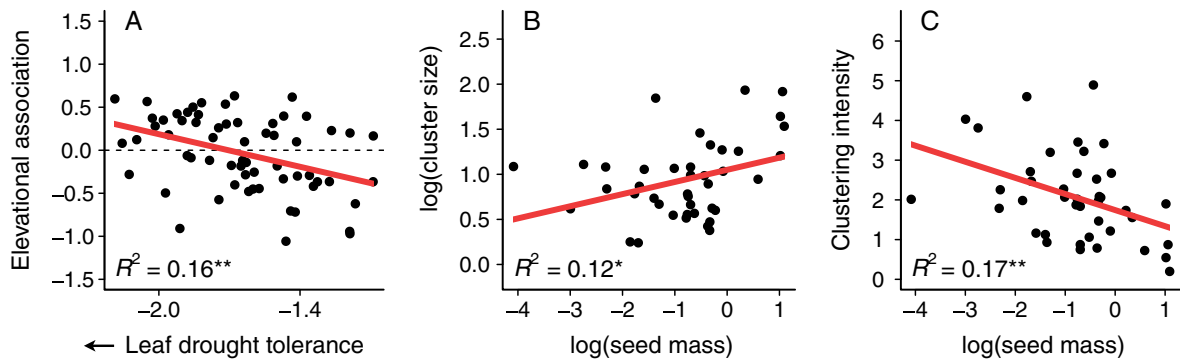
FIG. 4. Functional traits are related to spatial properties across species. (A) Species positively associated with elevation (i.e., ridge associated species) tend to have higher leaf drought tolerances, i.e., a more negative leaf turgor loss point. (B, C) Seed mass is positively related to cluster size and negatively related to clustering intensity, such that larger-seeded species have larger clusters and fewer stems per cluster. (A) $N = 64$, (B, C) $N = 41$. Red lines are linear ordinary least squares (OLS) fits; $**P < 0.01$, $*P < 0.05$. Units: Leaf drought tolerance was measured in megapascals (MPa), seed mass is in grams, cluster size is in meters, and elevational association and clustering intensity are unitless. In panel A, one outlier, *Capparis sola*, was removed for visual clarity, which when included increases R^2 to 0.17.

TABLE 2. Relationships between traits and spatial properties.

Functional trait	Spatial property					
	Elevation	TWI	Soil PCA 1	Soil PCA 2	Cluster size	Clustering intensity
Turgor loss point	**−0.41**	**0.36**	0.13	**0.29**	**−0.31**	0.04
Specific force to punch	**0.18**	**−0.27**	0.03	**−0.17**	**0.18**	**−0.23**
SLA	**−0.24**	**0.20**	0.06	**0.27**	−0.03	**0.20**
Leaf nitrogen concentration	**−0.17**	**0.20**	0.05	**0.18**	0.02	**0.12**
Wood density	**0.25**	**−0.25**	−0.15	−0.17	0.12	−0.12
Seed mass	−0.16	0.16	−0.19	−0.41	**0.35**	**−0.41**
Maximum DBH	**0.14**	0.06	**−0.18**	−0.10	**0.14**	**−0.28**

Notes: Bivariate Pearson correlations between the leaf, wood, seed, and stature traits used in the study and model parameters relating to habitat associations and dispersal limitation. The Benjamini-Hochberg correction for multiple comparisons was used when assessing significance, boldface type indicates a significant relationship. SLA, specific leaf area. See Appendix S1: Table S1 for *P* values and degrees of freedom.

Ackerly 2010). While this study estimated the influence of additional habitat attributes including soil chemistry as well as properties of clustering due to dispersal limitation, these studies together suggest the abiotic environment and species traits have weak but consistent effects on community structure in this hyperdiverse forest.

A key result was that aggregated species with stronger clustering intensity were smaller, more resource-acquisitive species. One possibility is that this result is driven by abundant, shrub-like species that have different spatial properties and traits than larger species. To examine this, we compared the trait values and spatial properties of smaller-statured species ($DBH_{max} < 10$ cm) and larger-statured species ($DBH_{max} \geq 10$ cm; Appendix S1: Figs. S6, S7). Smaller-statured species indeed had smaller and more dense clusters, but we found no difference in the trait values of the two groups. In addition, we examined the relationship between species abundance and spatial properties, and between abundance and traits (Appendix S1: Fig. S8), and found most spatial properties and traits had no relationship with abundance.

Counter to our expectations, more abundant species had lower clustering intensity, though the correlation was weak ($r = -0.26$) and the relationship was triangular. While more abundant species may be expected to cluster more intensely as a simple function of the number of individuals, here we estimated clustering intensity independent of aggregation due to the environment.

The generality of our findings should be further tested via comparisons with other tropical or temperate forests that differ in the strength of local environmental variation and in vertebrate seed disperser and predator community composition. For example, a recent study (Clark et al. 2017) examined whether functional traits of trees and lianas predicted species spatial patterns in the Barro Colorado Island, Panama ForestGEO plot using a wavelet-based approach. While the study did not incorporate topographic or edaphic variation as model predictors and instead used canopy gaps, species with more resource conservative traits and larger statures were less spatially aggregated, which is in line with our results.

One potential limitation of our spatial modeling approach is that species may be aggregated due to unmeasured environmental variation, which could then be attributed to dispersal limitation in our analysis (Baldeck et al. 2013). While we compiled detailed topographic and edaphic data, there is no existing canopy gap or light availability data set for the Yasuní plot, which may be an important driver of aggregation for pioneer species. However, most gaps in Yasuní are small and pioneers make up a small fraction of the species and stems in the plot (Valencia et al. 2004). Further quantification of the abiotic environment including light levels and canopy gaps could be included in future analyses, and may increase the explanatory power of the abiotic environment. Another limitation is that the pattern of seed rain and thus cluster size is not determined solely by seed dispersal vectors such as wind, birds, and mammals, but via topographic features that trap seeds and the distribution of reproductive adults, among other factors (Levine and Murrell 2003). This suggests that the clustering we observe may be shaped by additional factors besides dispersal limitation alone. Finally, it should be noted that conspecific negative density dependence would act to reduce the clustering of stems and is not estimated in this analysis.

Conclusions

Spatial point process models provide tools to separate the effects of environmental filtering and dispersal limitation on community structure, and when combined with functional traits can indicate which aspects of plant morphology and physiology are linked to a specific process.

Physiological traits in particular may better capture species responses to specific resources than traits that integrate multiple responses such as SLA. Additional studies that combine spatially explicit models with species traits to understand biodiversity dynamics are needed as communities become increasingly altered due to habitat loss, hunting, and climate change.

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