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Functional traits of tropical trees and lianas explain spatial structure across multiple scales

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Abstract

1. Dispersal and density dependence are major determinants of spatial structure, population dynamics and coexistence for tropical forest plants. However, because these two processes can jointly influence spatial structure at similar scales, analysing spatial patterns to separate and quantify them is often difficult.
2. Species functional traits can be useful indicators of dispersal and density dependence. However, few methods exist for linking functional traits to quantitative estimates of these processes that can be compared across multiple species.
3. We analysed static spatial patterns of woody plant populations in the 50 ha Forest Dynamics Plot on Barro Colorado Island, Panama with methods that distinguished scale-specific differences in species aggregation. We then tested how these differences related to seven functional traits: growth form, dispersal syndrome, tree canopy layer, adult stature, seed mass, wood density and shade tolerance. Next, we fit analytically tractable spatial moment models to the observed spatial structure of species characterized by similar trait values, which allowed us to estimate relationships of functional traits with the spatial scale of dispersal, and the spatial scale and intensity of negative density dependence.
4. Our results confirm that lianas are more aggregated than trees, and exhibit increased aggregation within canopy gaps. For trees, increased seed mass, wood density and shade tolerance were associated with less intense negative density dependence, while higher canopy layers and increased stature were associated with decreased aggregation and better dispersal. Spatial structure for trees was also strongly determined by dispersal syndrome. Averaged across all spatial scales, zoochory was more effective than wind dispersal, which was more effective than explosive dispersal. However, at intermediate scales, zoochory was associated with more aggregation than wind dispersal, potentially because of differences in short-distance dispersal and the intensity of negative density dependence.
5. *Synthesis.* We develop new tools for identifying significant associations between functional traits and spatial structure, and for linking these associations to quantitative estimates of dispersal scale and the strength and scale of density dependence. Our results help clarify how these processes influence woody plant species on Barro Colorado, and demonstrate how these tools can be applied to other sites and systems.

1 INTRODUCTION

Spatial patterns encode information about the processes that form them. Studying species spatial distributions can therefore yield insight into their ecology. In plant populations, two major processes, dispersal and density dependence, have particularly profound influences on spatial structure. Dispersal reduces clustering by separating reproductive individuals from their offspring. Negative and positive density dependence can reduce or increase clustering, respectively, by either limiting or enhancing recruitment success and survival around existing individuals (Bolker & Pacala, [1999](#)). Negative density dependence and short-distance dispersal can promote high diversity by restricting the abundance of common species (Detto & Muller-Landau, [2016](#); Janzen, [1970](#)). These processes are thought to be particularly important in diverse tropical forests (Bagchi et al., [2011](#); Comita, Muller-Landau, Aguilar, & Hubbell, [2010](#); Harrison et al., [2013](#); Kunstler et al., [2015](#); Seidler & Plotkin, [2006](#)).

While it is easy to predict how individual processes influence spatial structure in theory, determining the relative influences of multiple processes from observed patterns is challenging for a number of reasons. First, similar spatial structure can be generated by different combinations of clustering and disaggregating processes (Bagchi et al., [2011](#); Beckman, Neuhauser, & Muller-Landau, [2012](#); May, Andreas & Wiegand, [2015](#); Muller-Landau,

Wright, Calderón, Hubbell, & Foster, [2002](#); Seabloom, Bjørnstad, Bolker, & Reichman, [2005](#)). For example, spatial aggregation in a population may be indicative of short-range dispersal, positive density dependence or a mixture of both processes (Scanlon, Caylor, Levin, & Rodriguez-Iturbe, [2007](#)). Furthermore, spatial structure varies depending on the scale at which it is observed. For example, a checkerboard is homogeneous at the scale of a single grid cell, aggregated at the scale of a few cells, and uniformly distributed at larger scales. Finally, analyses of spatial patterns of species that are strongly associated with particular environments, such as canopy gaps or specific soil or hydrological conditions, can be confounded by the spatial distribution of the environmental variable (Dalling et al., [2012](#); Seabloom et al., [2005](#)).

Previous studies have attempted to address these challenges in two major ways. First, methods that examine spatial structure across multiple scales are often better able to separate influences of different processes (Detto & Muller-Landau, [2013](#); Getzin, Wiegand, & Hubbell, [2014](#); Seidler & Plotkin, [2006](#)). Second, methods that link functional traits to potential mechanisms that enhance or decrease dispersal and density dependence (Augspurger & Kelly, [1984](#); Kunstler et al., [2015](#); Muller-Landau, Wright, Calderón, Condit, & Hubbell, [2008](#)), or to particular kinds of spatial structure (Getzin et al., [2014](#); Hubbell, [1979](#); Seidler & Plotkin, [2006](#)), can be used to associate differences in spatial patterns with potential underlying mechanisms. These methods have made substantial progress in determining which kinds of processes are important determinants of observed spatial distributions. Nevertheless, few existing studies have used observations from static spatial patterns to quantitatively compare the relative influences of dispersal and density dependence across multiple species.

Studies of spatial structure are particularly well-developed for large-scale surveys of plant species populations, such as the Forest Dynamics Plot on Barro Colorado Island (BCI) (e.g. Bagchi et al., [2011](#); Comita et al., [2010](#); Dalling et al., [2012](#); Getzin et al., [2014](#); Harms, Wright, Calderón, Hernández, & Herre, [2000](#); Seidler & Plotkin, [2006](#)). Data from BCI includes spatially explicit surveys of tree (Condit, [1998](#); Condit et al., [2012](#); Hubbell, [1999](#)) and liana (Schnitzer et al., [2012](#)) distributions, and comprehensive information about species functional traits (Croat, [1978](#); Hubbell & Foster, [1986](#); Muller-Landau et al., [2008](#); Wright, Calderón, Hernández, Detto, & Jansen, [2016](#); Wright et al., [2010](#)). Here, we use these data to detect and quantify associations between functional traits and spatial processes that influence woody plant species distributions on BCI. To do this, we extend recently developed methods for quantifying spatial variability across multiple scales using wavelet variance (Detto & Muller-Landau, [2013](#)) to incorporate covariates based on species functional traits and environmental heterogeneity.

There are several useful features of wavelet variance which help address the challenges outlined above. First, because wavelet variance is calculated from Fourier decompositions of spatial data, processes that influence spatial patterns at one set of spatial scales do not bias estimates at other scales. Thus, large-scale environmental heterogeneity—such as variation in habitat type, topography (Dalling et al., [2012](#)) and soil nutrients (John et al., [2007](#)) that occur at large spatial scales on BCI (generally above 100 m)—does not obscure patterns at smaller scales (see example in Appendix S1, A.1.I). Second, wavelet variance provides an unbiased estimate of spatial variability, even for very rare species. This enables analysis of species with as few as 10 observed individuals (see example in Appendix S1, A.1.II). Finally, wavelet variance can be analytically related to spatial moment models (Bolker & Pacala, [1999](#); Bolker, Pacala, & Levin, [2000](#); Law & Dieckmann, [2000](#)). These models can be fit using standard regression tools (Detto & Muller-Landau, [2013](#)), and provide quantitative estimates of the spatial scales of dispersal, and the spatial scale and intensity of density-dependent interactions.

We analyse spatial structure and fit spatial moment models to test for relationships of aggregation, dispersal and density dependence with seven commonly measured traits: plant growth form, dispersal syndrome, tree canopy layer, adult stature, average seed mass, average wood density and shade tolerance. We test several hypotheses for which there is already empirical support from other studies on BCI (Dalling et al., [2012](#); Ledo & Schnitzer, [2014](#); Muller-Landau et al., [2008](#); Schnitzer et al., [2012](#); Seidler & Plotkin, [2006](#)), both as proof of

concept, and to corroborate existing results using a single set of methods. We also test several hypotheses for which there is currently limited empirical support, such as that species with denser wood should be more resistant to pathogens (Augsburger & Kelly, [1984](#); Chave & Leigh, [2002](#); Kunstler et al., [2015](#); Wright et al., [2010](#)), and that species with larger seeds experience less intense negative density dependence (Lebrija-Trejos, Reich, Hernández, & Wright, [2016](#); Muller-Landau, [2010](#)).

By combining analyses across these traits using consistent methods and spatial data, we clarify how these processes influence tropical tree and liana populations on BCI. In addition to describing differences in aggregation across multiple spatial scales, our results also summarize spatial patterns using simple, analytically tractable models of spatial population dynamics. These models provide quantitative estimates of how functional traits correspond to differences in dispersal and negative density dependence for species on BCI, and demonstrate how these methods can be applied to other sites and systems to address similar questions.

2 MATERIAL AND METHODS

2.1 Study site

Barro Colorado Island is a 15 km² island located on the eastern margin of Gatun Lake in the Panama Canal (9.9°N, 79.51°W, 140 m elevation). The island vegetation is lowland moist tropical forest, characterized by a 4-month dry season (Leigh, [1999](#)). We utilized data from the 50 ha (1,000 m × 500 m) Forest Dynamics Plot on BCI, which includes species-specific data on distributions of individual trees and lianas greater than 1 cm in stem diameter at breast height (DBH) (Condit, [1998](#); Schnitzer et al., [2012](#)). The vast majority of the 50 ha plot (96%) is old-growth forest (Piperno, [1990](#)).

2.2 Census data

For trees, we used data from seven censuses conducted between 1981–1983 and 2010 (Condit, [1998](#); Condit et al., [2012](#); Hubbell, [1999](#)); for lianas, we used data from a single census in 2007 (Schnitzer, Rutishauser, & Aguilar, [2008](#); Schnitzer et al., [2012](#)). For all species, we treated stems that were obviously vegetatively connected (either as rooted clones or branches) as a single individual, centred at the mean coordinates of all combined stems, discretized into a 1 × 1 m grid. To ensure unbiased estimates of our spatial statistics, we excluded from the analysis species with fewer than ten observed individuals in any census year (see power tests in Appendix S1, A.1.II and C.1, and in Figure S3). This yielded 254 tree and 130 liana species (78% and 77%, respectively, of all species surveyed).

We quantified canopy gap locations based on canopy height surveys conducted annually from 1983 to 2010, except for 1994, 1997–1999 and 2002 (Condit et al., [2012](#); Hubbell, Comita, Lao, & Condit, [2014](#)). Surveys from 1983 to 2002 recorded presence or absence of vegetation at the intersections of a 5 × 5 m grid, measured at six heights (0–2, 2–5, 5–10, 10–20, 20–30 and ≥30 m). We classified locations with no vegetation above 2 m as a gap. Surveys from 2003 to 2010 recorded vegetative percent cover across the interior of the same grid (0–10%, 10–25%, 25–50%, 50–75% and 75–100%) with seven height classes (0–1, 1–2, 2–5, 5–10, 10–20, 20–30 and ≥30 m). We classified locations with less than 10% cover in all height classes above 2 m as a gap. Less conservative cut-offs yielded similar results. To analyse spatiotemporal co-occurrence of gaps and species, we discretized stem locations into a 5 × 5 m grid, centred over the grid intersections or the centre of the grid cells, respectively, for the two types of gap surveys. Because gaps can turn over in as little as a year, trees and lianas in each census were marked as being in a gap if they occurred in locations that were recorded as a gap in any of the five surveys during or preceding the tree or liana census. We chose 5 years because it fully captured the conditions between tree censuses, though other lag intervals between 1 and 10 years yielded similar results.

2.3 Trait data

We distinguished trees and lianas following Croat ([1978](#)), and further divided trees by canopy layer based on maximum adult height into canopy (>20 m), midcanopy (10–20 m), understory (5–10 m) and shrub (<5 m) (Hubbell & Foster, [1986](#)). We categorized all species by primary dispersal syndrome as bat, bird, non-volant mammal, wind or explosively dispersed (Muller-Landau & Hardesty, [2005](#); Muller-Landau et al., [2008](#); Wright et al., [2016](#)).

As a continuous proxy for stature, we used maximum DBH, which is strongly and positively related to tree height and crown area (Bohlman & O'Brien, [2006](#); O'Brien, Hubbell, Spiro, Condit, & Foster, [1995](#)). We estimated maximum DBH as the 95th percentile of DBH for each species, calculated using linear interpolation of the empirical cumulative density function with MATLAB's 'quantile' command. For individuals with multiple vegetative stems, DBH was estimated from the combined basal area. Dry seed mass was based on the oven-dried (at 60°C) mass of endosperm and embryo only (Wright et al., [2010](#)). Seed mass and maximum DBH were \log_{10} -transformed for all analyses.

Wood density was defined as wood specific gravity measured after drying at 100°C (Wright et al., [2010](#)). To define a shade tolerance index, we used the first principal components analysis axis derived from relative growth rates and annual mortality rates for tree saplings (1–4.9 cm DBH) in the 50-ha plot, following Wright et al. ([2010](#)). We rescaled and standardized the index with zero mean and unit standard deviation such that larger values specify lower growth and mortality rates, which are associated with greater shade tolerance. Because we only had data for a single liana census, we were unable to calculate the same shade tolerance index for liana species.

Three pairs of continuous traits were significantly correlated: seed mass and wood density (Pearson correlation coefficient $\rho = 0.151$, $p = .05$), seed mass and shade tolerance ($\rho = 0.364$, $p < .001$), and shade tolerance and wood density ($\rho = 0.473$, $p < .001$).

2.4 Quantifying spatial structure

We quantified spatial structure for tree and liana distributions on BCI using normalized wavelet variance, V , *sensu* Detto and Muller-Landau ([2013](#)). V describes the intensity with which aggregation or disaggregation of individuals occurs across spatial scales for a spatial pattern (Bartlett, [1964](#); Dale & Mah, [1998](#); Detto & Muller-Landau, [2013](#)). For a completely random spatial process (e.g. Poisson process), the expected value of V is 1 for all spatial scales. Patterns that are more strongly clustered than the random expectation ('aggregated' patterns) have V greater than one, and patterns that are more spatially dispersed than the random expectation ('disaggregated' patterns) have V between zero and one. For more detailed information on wavelet variance, see the primer in Appendix S1.

For all analyses, we calculated V at each of 40, log-evenly spaced scales between 2 and 115 m. V thus represents the vector of 40 estimates of wavelet variance across all spatial scales tested. For trees, where we had multiple census years, we calculated separate wavelet variance estimates for each survey year, and analysed averages taken across all years to pool information from across the censuses. Note that because all species were observed in all years, this did not lead to differences in year-specific uncertainties. For lianas, we used estimates from the single census.

To quantify co-occurrence of species with canopy gaps, we calculated wavelet covariance, V_{XY} , which measures the degree to which two spatial patterns co-occur, and is calculated in the same manner as univariate wavelet variance, except that it tests for aggregation in the product of two spatial patterns (Detto, Muller-Landau, Mascaro, & Asner, [2013](#); Kumar & Foufoula-Georgiou, [1994](#)). As with V , we averaged V_{XY} across all survey years

for each tree species. Because of lower spatial resolution of canopy gap data, we calculated V_{XY} only for spatial scales above 10 m.

2.5 Testing how traits relate to spatial pattern

To test for associations between traits and specific types of spatial structuring, we employed a series of nonparametric statistical tests. To do this, we calculated a mean estimate of V for each trait value by averaging across spatial patterns from species with similar traits, and tested whether mean V observed across species in each trait-based group was a better predictor of individual species' V than the grand mean observed across all species, regardless of their traits. Similar to a classical ANOVA, smaller within-group than among-group variability in V indicates that the trait-based groups differ in spatial structure.

For categorical traits, we grouped species into nested subdivisions of categories—e.g. zoochoric (i.e. animal vectored) versus abiotic dispersal; zoochoric versus wind versus explosive dispersal, etc. For continuous traits, we calculated locally estimated V for each observed level of the trait by averaging across species with similar trait values (e.g. trees with similar maximum DBH) using a smoothing kernel. This generated estimates for V at each spatial scale as a function of the continuous trait, similar to results from a loess smoother or other nonparametric regression methods. For each candidate grouping of species, we calculated the likelihood of observed spatial variability based on the mean and variance for observed V within each group (e.g. averaged across all species with explosive dispersal, or based on the local estimates from the smoothing kernel for a particular maximum DBH), and compared this likelihood to that of a null model where we randomly shuffled trait values among species. For more details on grouping methods and likelihood calculations, see Appendix S2, B1.

We report grouping results using the difference in log likelihoods $L(H_A) - L(H_0)$, where $L(H_A)$ and $L(H_0)$ are the log likelihoods of the data under the alternate and null models, respectively. We then selected trait-based groupings with the best improvement in likelihood relative to the corresponding null model. If likelihoods of multiple potential groupings did not differ, we chose whichever contained the fewest traits (i.e. the most parsimonious). Finally, we compared mean estimated V from each of these 'best-fitting' trait-based groupings to test for significant differences in V . This determined the significance of differences in spatial structure associated with specific traits measured at specific spatial scales, similar to a post-hoc test for an ANOVA such as a Tukey Test.

2.6 Estimating dispersal and density dependence from spatial structure

We fit three nested spatial moment models (see details and derivations in Appendix S1, A.2) to the estimated V for each trait-defined group selected above. All three are extensions of a simple logistic growth model, with added terms describing effects of the spatial second moment (i.e. proximity among individuals) on recruitment success. However, rather than modelling population size, these models explain differences in spatial structure, summarized by the wavelet variance V . Model I describes a population in which dispersal is spatially structured, but negative density dependence acts 'globally' (i.e. at scales larger than 115 m). Thus, while mean population size depends on both dispersal and density dependence, V in this model depends only on dispersal (Detto & Muller-Landau, **2013**). Model II describes populations where both dispersal and negative density dependence act locally (i.e. dispersal is limited by distance from reproductive individuals, and negative density dependence is more intense when individuals are closer together). Thus, V depends on both dispersal and the scale and intensity of density-dependent interactions. Lastly, Model III accounts for spatially structured dispersal, density dependence and the influence of canopy gaps.

Each of these models incorporates kernels which describe how interaction strength declines with distance, and shape parameters which alter the spatial scale and intensity of interactions predicted by these kernels. For Model I, the expected wavelet variance is related to dispersal as $\hat{V}_1 = 1/(1 - \tilde{D}(c_D))$ where $\tilde{D}(c_D)$ is the Fourier

transformation of the dispersal kernel, and c_D is a dispersal distance parameter, and \hat{V} indicates a model-based estimate of V (Detto & Muller-Landau, **2013**). For Model II, $\hat{V}_{II} \approx 1(1 - \tilde{D}(c_D) + \Pi_1 \tilde{K}(c_K))$ where Π_1 is an index of the intensity of negative density dependence with larger values indicating stronger negative density dependence, $\tilde{K}(c_K)$ is the kernel function describing the spatial scale of density-dependent interactions, and c_K describes the distance at which self-limitation acts. Note that this relationship is only approximate because its derivation relies on a moment closure approximation, and approximates the effects of species abundance on spatial structure assuming long-distance interactions (Detto & Muller-Landau, **2013**). Lastly, in Model III, $\hat{V}_{III} \approx (1 + \Pi_H \tilde{H}(c_H) V_{NM}) / (1 - \tilde{D}(c_D) + \Pi_1 K(c_K))$ where V_{NM} is the wavelet covariance of species (N) with canopy gaps (M), Π_H describes changes in species abundance attributable to the presence of canopy gaps, and $\tilde{H}(c_H)$ is the spatial kernel describing how the influence of canopy gaps declines with distance. In all three models, larger c_D indicates longer-distance dispersal, larger c_K indicates that density dependence acts over larger distances, larger Π_1 indicates stronger effects of negative density dependence, larger c_H indicates that gaps affect species over larger distances, and larger values of Π_H indicate increased abundance of species within canopy gaps.

Model I performed worse than other models for all cases that we tested (based on AIC), and we do not discuss it further here. We therefore report results for parameter estimates using Model II for each trait-based species group. For the distributions of all lianas and of all trees, we also fit and calculated AIC for Model III in order to assess potential influences of canopy gaps on their spatial structure. For all kernels, we scaled parameters to match a Gaussian kernel, for which spatial parameters represent the standard deviation of the distribution (see Appendix S1, A.2.I for details). Thus, roughly 68% of dispersal, self-limitation and canopy gap interactions take place within distance c_D , c_K and c_H of the focal individual, respectively. See Figure S1 in Appendix S1 for examples of how parameter values influence \hat{V} for each model.

2.7 Sensitivity analyses

Because our methods rely on several assumptions, we also conducted a series of sensitivity analyses. First, to test the reliability of our assumptions of moment closure and to test the reliability of long-distance interactions, we simulated spatial patterns with known dispersal and density-dependent characteristics that violated these assumptions, and then fit Model II to each pattern. These tests showed that fitting methods were robust to assumption violations, with the exception of the negative density dependence intensity index, Π_1 , which increased with species abundance regardless of the true magnitude of density dependence. To ensure that this did not bias our results, we tested for differences in species abundance among trait-based groups, and repeated our analysis of the BCI data using a series of weighting methods that sequentially reduced the influence of rare species. Because species of different stature might be expected to have inherent differences in the spatial scale of aggregation, we also repeated our analysis of the BCI data using a subset of tree species with similar maximum DBH, and tested whether the spatial distribution of large and small individuals of the ten most common species differed significantly from that of randomly chosen subsets of individuals. Lastly, because our spatial moment models assume that spatial structure is at equilibrium, we also tested for consistent signals of temporal change in V for each trait-based groups of species.

In general, these analyses showed that our fitting methods worked well across the range of parameters observed in our data, results were not qualitatively altered by differences in species abundances or size, and equilibrium assumptions were not violated. Detailed methods and results of these sensitivity analyses are described in Appendix S3. A small number of cases where the sensitivity analyses suggest potential biases in our main results are described in the discussion.

3 RESULTS

3.1 Lianas versus trees

Lianas were significantly more aggregated than trees across all spatial scales (Figure 1a). The fitted spatial moment model suggested that trees dispersed at significantly larger spatial scales, and experienced somewhat less intense negative density dependence than lianas (Figure 2a). However, the model fit for lianas was relatively poor at spatial scales above 20 m, and estimates for average competitive distance for lianas included very large uncertainty.

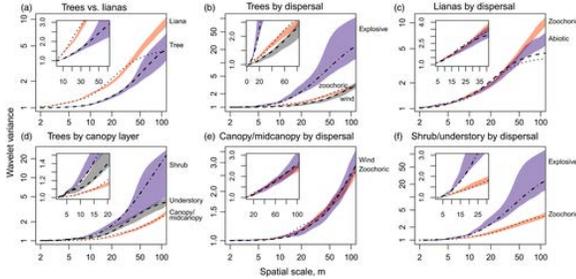


Figure 1 Differences in spatial structure among best-fitting groupings of species based on categorical traits. The wavelet variance (V) describes the degree of aggregation in a spatial process at each of multiple spatial scales, with $V = 1$ indicating random distributions at that scale, larger values indicating aggregation, and smaller values indicating segregation. Species groupings are those with the highest likelihood from nonparametric tests described in the main text (see Figure S4 for likelihoods of all tests). Shaded regions show mean \pm SD for V for species within each trait-based group, with darker shading indicating overlapping distributions. Lines show model-based estimates \hat{V}_{II} from fitting Model II, described in the main text. Figure insets show subsets of each graph on linear axes

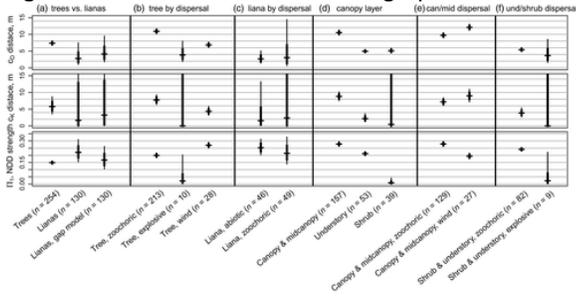


Figure 2 Parameters of spatial moment models (Model II) fitted to the best-fit categorical groupings of species from Figure 1. Parameters c_D and c_K describe, respectively, the spatial scale of dispersal and conspecific negative density effects. Π_1 describes the intensity of negative density dependence, with larger values indicating more intense negative density dependence. Number of species in each trait-based grouping is indicated by n . Intervals show mean \pm SD, and 95% confidence interval. For lianas, coefficients for the ‘gap model’ are also shown, which includes spatial influences of canopy gaps on abundance (Model III). Other parameters for the gap model are shown in Figure 3

Using Model III to account for relationships with canopy gaps improved model fit for lianas ($\Delta AIC_{III-II} = -2.4$), especially at larger scales, though parameter estimates remained relatively unchanged (Figures 2a and 3). Including canopy gap information worsened model fit for trees ($\Delta AIC_{III-II} = 5.1$, with $c_H \neq 0$). Parameter estimates from Model III showed a significant increase in liana abundance within canopy gaps ($\Pi_H = 0.029 \pm 0.012$), and a significant decreased within canopy gaps for trees ($\Pi_H = -0.014 \pm 0.005$).

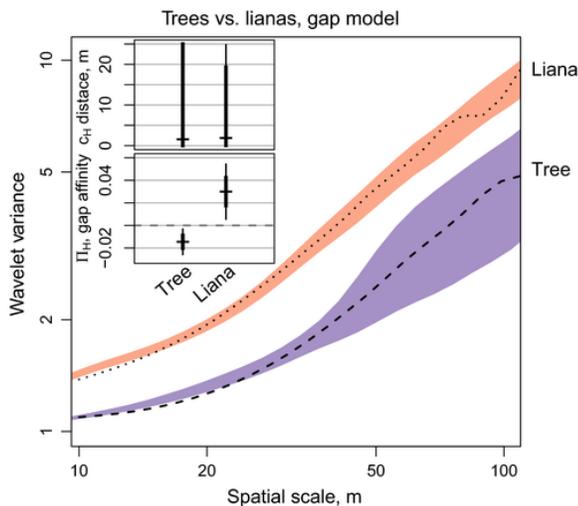


Figure 3 Fitted wavelet variances and parameter values of the model including covariance between species distribution and canopy gaps (Model III). Shaded regions show variability in V among tree and liana species as described in Figure 1a. Lines show fits from the spatial moment Model III that includes influences of canopy gaps on species abundance. Parameter c_H describes the spatial scale of the effects of canopy gaps. Parameter Π_H describes the strength and direction of canopy gap associations with abundance ('gap affinity'), with positive values indicating increased abundance in canopy gaps, and negative values indicating reduced abundance. Intervals show mean \pm SD , and 95% confidence interval. For lianas, other parameters for the gap model are shown in Figure 2 (for trees, there was no improvement in fit for Model III relative to Model II)

3.2 Dispersal syndrome

Dispersal syndrome explained significant variation in aggregation among trees but not among lianas (Figures 1b,c and S4b,c). The best fitting grouping separated tree species into three categories: explosive, wind and zoochoric dispersal, with no significant differences among the animal dispersal vectors. Explosively dispersed trees were significantly more aggregated at all scales than other tree species, zoochory showed intermediate aggregation, and wind-dispersed trees were significantly less aggregated than zoochoric trees at scales of roughly 5–65 m (Figure 1b inset). Based on the fitted spatial moment models, dispersal scale was smallest among explosively dispersed species, intermediate for wind-dispersed species, and largest for zoochoric species (Figure 2b). Conversely, negative density dependence was weakest among explosively dispersed species, intermediate for zoochoric species, and strongest for wind-dispersed species. Spatial scales of density-dependent interactions for zoochoric species were significantly larger than for wind-dispersed species, while estimates for explosively dispersed species included too much uncertainty to detect differences. For liana distributions, we found no significant differences related to dispersal syndrome (Figures 2c and S4c).

3.3 Tree canopy layer and stature

Among trees, shorter-statured species exhibited higher aggregation than taller species (Figure 1d). The best fitting trait-based grouping of canopy layers distinguished three categories: midcanopy and canopy trees combined as a single category, and understory trees and shrubs as separate categories (Figures 1d and S4d). Canopy and midcanopy trees showed the least aggregation, understory trees showed intermediate aggregation, and shrubs showed the most aggregation. Shrub and understory trees showed similar spatial scales for dispersal, while canopy/midcanopy trees had longer-distance dispersal (Figure 2d). Negative density dependence grew stronger for larger-statured trees, with canopy/midcanopy trees showing the most intense negative density dependence, and shrubs the least. Spatial scale for density-dependent interactions was significantly larger for canopy trees than for understory trees, while the estimate for shrubs included too much uncertainty to distinguish differences.

Maximum DBH was significantly related to spatial aggregation in trees (Figure S5a). Consistent with the findings for canopy layer for trees, aggregation decreased with maximum size (Figures 4a and S6a). By contrast, maximum DBH was not significantly related to spatial aggregation in lianas (Figure S5b). Dispersal scale was significantly larger for trees with larger DBH, particularly for DBH >50 cm (Figure 5a). The spatial scale of competitive interactions increased with tree DBH as well, but the change was not significant (Figure 5a). The intensity of negative density dependence increased significantly with maximum DBH up to 100 cm, and then declined rapidly among the few larger tree species.

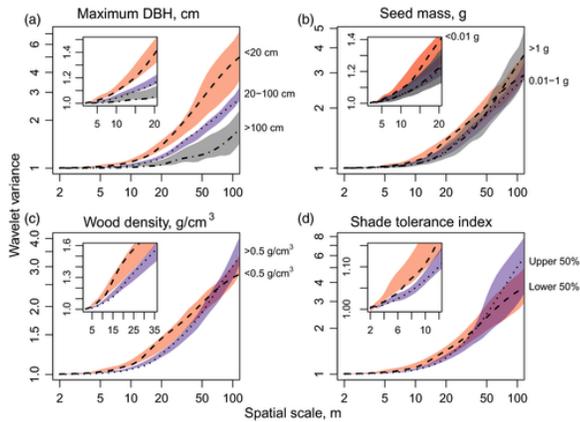


Figure 4 Differences in spatial structure among tree species varying in continuous traits, illustrated here by comparing wavelet variance (V) for discrete groupings of each variable. The groupings are solely for the purpose of easier visualization; likelihood tests and model fitting were conducted in relation to continuous trait variation using the kernel smoothers described in the main text and in Appendix S2, B.1.1 (see Figure S6 for visual renderings of V as a continuous function across traits and scales). Only traits that explained significantly more spatial variability than the null model described in the main text are shown (see Figure S5 for likelihoods of all tests). Shaded regions show mean \pm SD of V for species within each trait-based group, with darker shading indicating overlapping distributions. Lines show model-based estimates \hat{V}_{II} from fitting Model II. Figure insets show subsets of each graph on linear axes

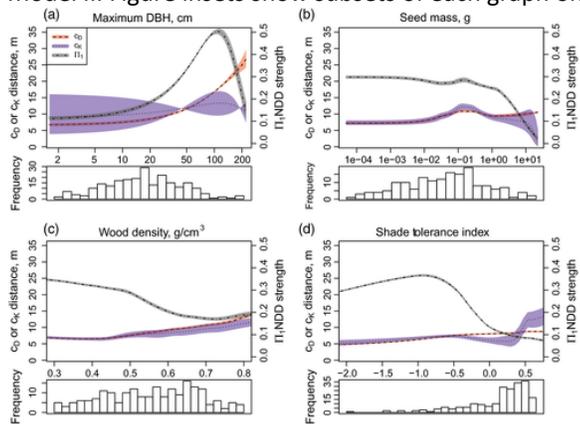


Figure 5 Parameters of the spatial moment models (Model II) as a function of continuous trait values described in Figure 4. Parameters c_d and c_k describe, respectively, the spatial scale of dispersal and conspecific negative density effects. Π_1 describes the intensity of negative density dependence, with larger values indicating more intense negative density dependence. Dashed lines and dotted lines show c_d and c_k , respectively (values on the left vertical axis), while dash-dotted lines show Π_1 (values on the right vertical axis). Histograms below each figure show the frequency distribution of species across trait values. Lines and shaded intervals show mean \pm SD

3.4 Dispersal syndrome by tree stature

For analyses of interactions between dispersal syndrome and tree stature, we divided tree species into two stature groups: canopy/midcanopy trees and shrubs/understorey trees. There were very few explosively dispersed canopy/midcanopy trees or wind-dispersed shrubs/understorey trees, and thus these were omitted

from the analyses. Among canopy and midcanopy trees, we found no significant differences in aggregation between wind-dispersed and animal-dispersed species (Figure 1e), though the fitted models showed that wind-dispersed species exhibited larger-scale dispersal, and less intense negative density dependence (Figure 2e). Among shrubs and understorey trees, explosively dispersed species had higher aggregation, shorter dispersal scale, and less intense negative density-dependence than animal-dispersed species (Figures 1f and 2f).

3.5 Seed mass

Aggregation varied significantly with tree species seed mass (Figure S5c,d); however, differences were small and followed no obvious pattern (Figures 4b and S6b). The spatial scales of dispersal and density dependence in the fitted models varied little, while the strength of negative density dependence declined strongly, particularly for seed mass above 1 g (Figure 5b). For liana species, we found no significant associations with seed mass (Figure S5d).

3.6 Wood density and shade tolerance

For tree species, aggregation declined significantly with wood density and shade-tolerance (Figures 4c,d and S5e,g). For both traits, differences were largest at scales below 10 m (Figure S6c,d). While the direction of associations between traits and aggregation appeared to reverse at spatial scales larger than 50 m, the differences were not significant. In lianas, spatial aggregation was not significantly related to wood density (Figure S5f), and we lacked sufficient data to test for relationships with shade tolerance. Tree wood density and shade tolerance were both significantly and positively correlated with spatial scale of dispersal and density-dependent interactions, though the magnitude of change was small (Figure 5c,d). Intensity of negative density dependence declined significantly with wood density, especially above 0.5 g/cm³ (Figure 5c). There was a similar decline with shade tolerance, but the division was largely binary, with more intense negative density dependence among less shade-tolerant species (Figure 5d).

4 DISCUSSION

Our results confirm that spatial structure of many woody plant species on BCI can be explained in part by associations of functional traits with dispersal and negative density dependence. The spatial moment models that we present are useful approximations of the complex spatial processes that influence species' spatial patterns. Crucially, these models help separate influences of dispersal and density dependence and thereby provide greater insights into the mechanisms underlying spatial patterns. While the differences in how traits relate to patterns of aggregation across scales may be difficult to interpret directly, these differences often correspond to simple changes in spatial moment model parameters—the spatial scale of dispersal, and the spatial scale and intensity of density-dependence. Thus, results from spatial moment models, as well as other process-based models (e.g. Hartig, Calabrese, Reineking, Wiegand, & Huth, 2011), are more easily interpretable than differences in patterns of aggregation alone.

Our results provide new information on interspecific variation in the intensity and scale of negative density dependence. Unlike dispersal, which tended to be associated with monotonic changes in aggregation across scales, density dependence was generally related to the wavelet variance function V in complex ways. For example, smaller seed sizes were consistently associated with more intense negative density dependence in all but our most conservative sensitivity analyses (Figures 5b, S9.4 and S10.4b). This result may be attributable to greater tolerance of larger seeds and seedlings for pests and competitors, which could facilitate establishment near other conspecific individuals (Lebrija-Trejos et al., 2016; Muller-Landau, 2010). Because species that experience similar intensities of negative density dependence, but vary in terms of the spatial scale of interactions, differ greatly in spatial pattern (Figure S1b), differences in tolerance might also explain the inconsistent relationship between seed mass and V . While it might seem that seed mass should be related to

fecundity as well, fecundity in our model relates to the number of 1 cm sapling recruits per adult, which reflects the combined influences of seed production, seedling establishment, growth and survival, which have varying (and largely compensatory) relationships with seed size on BCI (Dalling & Hubbell, [2002](#); Visser et al., [2016](#)).

Similarly, in almost all analyses, larger trees (both in terms of canopy layer and stature) were associated with more intense negative density dependence that acted over larger spatial scales. This result held even when differences in dispersal scale were not significant (e.g. shrubs versus understorey trees). These results are consistent with the mechanisms hypothesized to underlie negative density dependence, as both the abundance of natural enemies and the intensity of resource depletion would be expected to scale with crown size and rooting zone. Density dependence intensity was also predicted to decrease with wood density and shade-tolerance among tree species, consistent with generalized life-history trade-offs between rapid growth strategies, and strategies that enhance competitive ability and tolerance (Kunstler et al., [2015](#); Wright et al., [2010](#)), as well as specific hypotheses regarding physical defence against pathogens provided by denser wood (Augspurger & Kelly, [1984](#); Chave et al., [2009](#)).

Our results indicating significantly less clustering at intermediate spatial scales for wind-dispersed tree species than for zoochoric species is, to our knowledge, a novel finding on BCI. In the fitted spatial moment models, this finding is explained by weaker negative density dependence among zoochoric species. However, in sensitivity analyses with less weight given to rare species, this difference was smaller, though generally still significant. Similarly, our results suggesting increased dispersal scale among wind-dispersed, canopy and midcanopy trees relative to zoochory are not robust to sensitivity analyses with lower weights given to rare species (Figure S10.1 and S10.3). Potentially, these results suggest that our simple models omit important mechanisms (May et al., [2015](#)). For example, an alternate explanation for the differences in spatial patterns could be that zoochory is more effective at long-distance dispersal because of the ability of animal vectors to disperse seeds long distances, but also leads to frequent short-distance dispersal as fruits fall around parent trees, driving aggregation at smaller scales.

An important caveat for our methods is that the ‘mechanistic’ parameters in our spatial moment models are fit to observed data using simple pattern-matching methods. Even though we gain power by testing relationships between model predictions and observations of V across multiple scales, the information provided by the second order statistics is often limited. A likely consequence is that our methods have low power to resolve influences of traits in cases where information is available for only a small number of species and/or censuses. For example, there was high uncertainty in estimates for explosively dispersed species (of which there are relatively few) and lianas (for which we only had data from a single survey), and uncertainty increased in sensitivity analyses where we reduced the weight of rare species or removed species from the analysis. In particular for lianas, it is unclear whether the lack of significant links to traits was a consequence of small sample sizes, or a genuine difference in how liana and tree traits influence spatial structure. For some traits such as maximum DBH, which is less indicative of species strategies in lianas than trees, it is likely that the link with spatial signal is indeed weaker.

Despite these potential limitations, our fitting methods generally worked well across a wide range of parameter values, and neither differences in species abundances and sizes, nor confounding effects of non-equilibrium dynamics appear to have biased our results (Appendix S3). Thus, where sufficient data are available, parameter estimates from our spatial moment models are likely to be reliable indicators of the scale and intensity of spatial interactions. Nevertheless, though our results appear to be well-supported for the groupings of species and the spatial and temporal scales that we consider, this will not necessarily be the case for other species groups or scales. Others applying our methods should therefore utilize similar sensitivity analyses.

4.1 Relation to previous studies

Our results generally accord with existing evidence about relationships between functional traits and spatial structure on BCI. Consistent with previous findings, our results show that most species are spatially aggregated at most spatial scales (Condit, [2000](#); Hubbell, [1979](#)). We also find that dispersal syndrome and stature appear to drive much of the difference in spatial pattern observed across tree species. This finding makes intuitive sense, and is broadly consistent with a non-significant trend in a previous study based on seed trap data (Muller-Landau et al., [2008](#)). Our finding that dispersal scales were lowest for explosively dispersed species, and lower for wind-dispersed trees than zoochoric trees, also matches results from other studies of species spatial structure on BCI (Seidler & Plotkin, [2006](#)), the Guanacaste province of Costa Rica (Hubbell, [1979](#)), and the Pasoh forest in Malaysia (Seidler & Plotkin, [2006](#)). Our quantitative estimates of dispersal scale also match previous results from seed trap studies on BCI, with mean dispersal distances of around 3 m for explosively dispersed species, and around 10 m for zoochory and wind dispersal (compare with Muller-Landau et al., [2008](#)).

Our finding that lianas are substantially more aggregated than trees is also consistent with previous studies using other methods (Ledo & Schnitzer, [2014](#); Schnitzer et al., [2012](#)). Our results suggest that this aggregation is largely due to short-range dispersal: Predicted dispersal scale for lianas ($c_D \approx 3$ m) was similar to that for explosively dispersed trees, which are among the most spatially aggregated tree species on BCI (Muller-Landau et al., [2008](#)). Because our models make no distinction between clonal reproduction and seed dispersal, lower apparent dispersal for lianas may indicate greater vegetative reproduction rather than shorter-distance seed dispersal (Schnitzer et al., [2012](#)). The positive associations between lianas and gaps in our models are also well-supported by existing studies (reviewed by Schnitzer, [2015](#)). Possible drivers of the liana-gap association include relatively higher liana seed arrival in gaps (Puerta-Piñero, Muller-Landau, Calderón, & Wright, [2013](#)), the ability of lianas to survive tree-falls (Dalling et al., [2012](#); Ledo & Schnitzer, [2014](#)), and/or increased gap formation in sites where lianas are common due to liana-induced tree mortality (Ingwell, Joseph Wright, Becklund, Hubbell, & Schnitzer, [2010](#); Putz, [1984](#)). Because canopy gaps by definition have no large trees, but may still support large lianas along the ground, these results could be partially influenced by our definition of canopy gap. Interestingly, accounting for associations with canopy gaps did not change estimates of dispersal scale for lianas, suggesting that our predictions of short dispersal scales among lianas was not a by-product of this association. However, because there was only a single liana census, we could not test assumption that their spatial structure was at equilibrium. Our estimated model parameters for lianas should therefore be regarded with somewhat more scepticism than those for tree species. Furthermore, the spatial resolution of our gap data was substantially lower than that for the tree and liana censuses, which reduces our method's ability to distinguish small differences in scale parameters, and may explain why we could not accurately estimate the spatial scale of gap interactions (c_H , Figure [3](#)).

There are a number of directions in which our approaches and results could be extended to gain additional insights into spatial processes and patterns. Currently, we fit models using only the static spatial pattern information contained in individual species wavelet variance estimators V , treating all individuals of a particular species as identical, and ignoring spatial variation in the environment and in the abundances of other species. Simultaneously utilizing dynamic data on recruitment and mortality, or information about variation in size among individuals and spatial variation in the abiotic and biotic environment could improve our ability to distinguish among competing hypotheses, and to test more complex mechanisms to explain species spatial patterns (Detto & Muller-Landau, [2016](#); Getzin et al., [2014](#); May et al., [2015](#)). For example, information about spatial variation in topography could reveal habitat effects on spatial structuring and thereby enable more complete controls for these effects in fits of models of dispersal and negative density-dependence (Bagchi et al., [2011](#); Condit, [2000](#); Detto et al., [2013](#)). Similarly, utilizing dynamic data from across censuses would enable analysis of how recruitment and mortality events relate to local conspecific spatial and size structure,

and thereby more directly separate influences of dispersal and negative density dependence (Bjørnstad, Ims, & Lambin, [1999](#); Detto & Muller-Landau, [2016](#)). Lastly, jointly modelling multiple species and their interactions would enable investigation of quantitative differences in interaction effects (Comita et al., [2010](#); Ingwell et al., [2010](#); Kunstler et al., [2015](#); May et al., [2015](#)), something that is outside the scope of our simplified models which incorporate heterospecific interactions only implicitly using a non-spatial density dependence term (see Appendix S1, A.2.I in the supplement). All these potential expansions to integrate additional sources of information would require development of substantially more complex spatial moment models and associated methods for linking them to the relevant data.

5 CONCLUSIONS

Our results show that plant functional traits can explain substantial interspecific variation in spatial structure, and demonstrate that traits can be associated with quantitative parameters related to dispersal, negative density dependence and associations with canopy gaps. Our findings accord well with existing evidence and are robust across a wide range of sensitivity analyses. They suggest that simple trait measurements can provide insight about the processes that govern spatial distributions of large numbers of species, which could substantially simplify the process of scaling up current theoretical and empirical understanding of spatial ecology.

Our results also demonstrate the importance of simultaneously considering associations of functional traits with both density dependence and dispersal. For example, while species with shorter-range dispersal mechanisms likely compensate with traits that reduce the intensity of negative density dependence (Harrison et al., [2013](#)), it might be less clear that seed mass could correspond more strongly to density dependence than to dispersal (Lebrija-Trejos et al., [2016](#)). Thus, while functional traits might correspond to characteristics of species that determine spatial structure, they are unlikely to be related through simple linear functions.

The methods that we present here serve as a template showing how to apply spatial moment models to evaluate the role of functional traits and environmental variability in determining the kinds of spatial processes that influence species distributions (see Appendix S4 for a worked example and source code). Spatial moment models have contributed to substantial theoretical advances in the past (Bolker & Pacala, [1999](#)). However, only recently has it become practical to parameterize spatial moment models for real-world systems. As more empirical studies are able to incorporate these tools into their analyses, we expect enormous progress in understanding how spatial structure influences ecological systems, which remains a grand challenge for ecology (Chesson, [2000](#); Levin, [1992](#); Simpson & Baker, [2015](#)).

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AUTHOR CONTRIBUTIONS

M.D. developed the spatial analysis methods and moment models; M.D., H.C.M. and A.T.C. planned the analyses and developed the significance tests; S.J.W. collected the trait data; S.A.S. and S.P.H. collected the liana spatial distribution data; R.C. and S.P.H. collected the tree spatial distribution data; A.T.C. performed the analyses and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

BCI Forest Dynamics Plot tree census data: <https://doi.org/10.5479/data.bci.20130603> (Condit et al., **2012**); BCI Forest Dynamics Plot canopy gap data: <https://doi.org/10.5479/data.bci20140711> (Hubbell et al., **2014**). Source code: Appendix S4 in the Supporting Information, and at https://github.com/adamtclark/FunctionalTrait_WaveletVar.

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