


Counting niches: Abundance-by-trait patterns reveal niche partitioning in a Neotropical forest

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Abstract. Tropical forests challenge us to understand biodiversity, as numerous seemingly similar species persist on only a handful of shared resources. Recent ecological theory posits that biodiversity is sustained by a combination of species differences reducing interspecific competition and species similarities increasing time to competitive exclusion. Together, these mechanisms counterintuitively predict that competing species should cluster by traits, in contrast with traditional expectations of trait overdispersion. Here, we show for the first time that trees in a tropical forest exhibit a clustering pattern. In a 50-ha plot on Barro Colorado Island in Panama, species abundances exhibit clusters in two traits connected to light capture strategy, suggesting that competition for light structures community composition. Notably, we find four clusters by maximum height, quantitatively supporting the classical grouping of Neotropical woody plants into shrubs, understory, midstory, and canopy layers.

Key words: Barro Colorado Island; community structure; competition; emergent neutrality; niche differentiation; self-organized similarity; trait-based clustering; tropical forests.

INTRODUCTION

A basic principle of community ecology is that coexistence requires niche differentiation, that is, species differences that stabilize communities by reducing interspecific competition. However, the high diversity and seemingly continuous phenotypic variation of trees in tropical forests raises questions about the importance of niche differentiation as a contributor to species co-occurrence and patterns of diversity, relative to other community assembly processes such as dispersal and ecological drift (Hubbell 2001, Levine and Murrell 2003, Mouquet and Loreau 2003, Chase and Myers 2011). Indeed, neutral models reflecting chance events provide a good fit to the distribution of species abundances in tropical forests (Hubbell 2001, Volkov et al. 2003), although other studies have found evidence of niche differentiation (Kraft and Ackerly 2010, Götzenberger et al. 2012). One likely reason for these mixed results is a lack of model-validated

quantitative predictions for how niche-based competition shapes community trait structure.

Classical theory posits that only species with trait differences large enough to lower interspecific competition sufficiently will stably coexist. Hence, attempts to find evidence of niche differentiation in nature typically look for greater-than-chance differences in trait values among species (Chase and Leibold 2003, Kraft et al. 2008, Lake and Ostling 2009, Kraft and Ackerly 2010, Götzenberger et al. 2012, D'Andrea and Ostling 2016). However, competition can produce counterintuitive patterns. If two resident species are not distant enough from each other in trait space to allow a third species with an intermediate trait value to invade, the potential invader has higher fitness if it is similar to one of the residents than if it is maximally different from both (MacArthur and Levins 1967). This is because the increase in competition with the close resident is more than compensated by the decrease in competition with the other resident. When this phenomenon is extrapolated to multispecies communities, species are competitively excluded at rates inversely related to trait distance from the nearest trait optimum (D'Andrea and Ostling 2017). As competition

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among species proceeds, a transient pattern arises characterized by distinct clusters of species with similar traits, centered around locally optimal ecological strategies (Scheffer and van Nes 2006). Although competition among species in each cluster eventually leads to exclusion of all but the most competitive species, the similar strategies among the species renders their dynamics near-neutral; indeed, clusters can persist indefinitely under restorative forces such as immigration (D'Andrea et al. 2019), environmental fluctuations (Sakavara et al. 2018), and specialist enemies (Scheffer and van Nes 2006, Barabás et al. 2013).

In other words, although classical literature predicts that niche partitioning will lead to trait overdispersion, more recent literature suggests trait clusters rather than overdispersion as evidence of niche partitioning. We note that the same models that predict overdispersion in stable equilibrium will predict clusters as transients (Scheffer and van Nes 2006, D'Andrea et al. 2019). Furthermore, it has been shown that several ecological forces can maintain the clusters indefinitely as a stationary state. Those forces include immigration (D'Andrea et al. 2019), periodic environments (Sakavara et al. 2018), and “hidden niches”; that is, independent niche axes providing extra intraspecific regulation, such as specialist enemies (Scheffer and van Nes 2006, Barabás et al. 2013). Given the widespread influence of these forces in nature, we expect clusters to be a more general signature of niche differentiation than the stricter circumstances under which overdispersion might arise.

Clustering by organismal size has been reported in animal (Scheffer and van Nes 2006) and phytoplankton communities (Sakavara et al. 2018), but is not known to occur in tropical forests—a focal point for the development and tests of coexistence theory. Furthermore, previous efforts to detect species clusters have typically ignored species abundances and/or relied on arbitrary binning of trait space (Scheffer and van Nes 2006, Yan et al. 2012) or temporal data to distinguish between occasional and permanent species (Vergnon et al. 2009). However, recent work has proposed a parameter-free method that uses trait and abundance data to identify and count the clusters, which was validated using population dynamic models of competition with immigration (D'Andrea et al. 2019).

Here we use this approach to test whether high abundance values tend to be clustered with respect to trait values in the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama (Condit 1998, Hubbell et al. 1999, Condit et al. 2012a) We use four morphological traits: seed mass, maximum tree height, wood density, and leaf mass per area (LMA). Seed mass is thought to reflect strategies along a tolerance–fecundity trade-off axis (Muller-Landau 2010), whereby large-seeded species specialize in surviving stressful environmental conditions at the cost of low fecundity and vice versa. Maximum tree height, wood density, and LMA are associated with competition for light (Kunstler et al. 2016), and as such

may reflect plant strategies related to partitioning light-availability gradients both vertically (i.e., among forest canopy layers) and horizontally (i.e., across forest patches at different stages of succession). Such partitioning of light access is central to the forest architecture hypothesis (Kohyama 1993) and the related successional niche hypothesis (Grime 1979, Tilman 1988).

Trait pattern indicative of a niche mechanism will likely only become evident at a spatial scale above that of any spatial heterogeneity involved in the mechanisms (Kraft and Ackerly 2010, D'Andrea and Ostling 2016). Therefore, we look for signatures of niche partitioning at the whole-plot (50 ha) scale, large enough to encompass the spatial heterogeneity in patch-age since disturbance involved in these niche mechanisms (Hubbell et al. 1999). Because immigration can reinforce local clustering if surrounding forests have species clustered around the same trait-based niche optima, or mask local clustering if surrounding forests have species clustered around different trait-based niche optima, we compare results at the plot scale with results from a combined pool of 40 census plots within 30 km of BCI (Condit et al. 2013, 2016; Fig. 1).

METHODS

The Barro Colorado Island Forest Dynamics Plot is a 1,000 × 500 m tract of tropical forest on Barro Colorado Island in Panama (Hubbell et al. 1999, Condit et al. 2012b; Fig. 1). The plot has been censused for stems above 1-cm diameter at breast height (dbh) in 1982, 1985, and every 5 yr through 2015. The plot contains approximately 210,000 stems with dbh ≥ 1 cm, and about 300 tree species. Results shown in the main text pertain to the 2000 census; however, results are consistent across all available censuses (Appendix S1: Table S1, Figs. S3–S6).

We used four traits related to plant architecture, leaf structure, and seed size. Trait data, drawn from Wright et al. (2010), were based on the following protocols: (1) Maximum height was estimated as the mean height of the six largest (by dbh) individuals, measured using a range-finder. (2) Wood density (g/cm^3) was measured after drying at 60°C. (3) Leaf mass per area (g/m^2) was measured on leaf laminae, excluding petioles and petiolules, averaged across six individuals. For species that reach the canopy we used leaves exposed to direct sunlight—that is, sun leaves. For all others we used shade leaves collected from the crowns of the tallest individuals in the 50-ha plot. (4) Seed mass (g) refers to endosperm plus embryo only and was measured after drying at 60°C. Traits with skewed distributions (LMA and seed mass) were log-transformed to reduce the skew. Palms were excluded from wood and leaf trait analyses, because of their substantial differences in physiology from dicots.

We restricted our analysis to reproductive individuals (adults), because population dynamic models producing emergent clusters do not consider population structure. We consider individuals to be reproductive when their

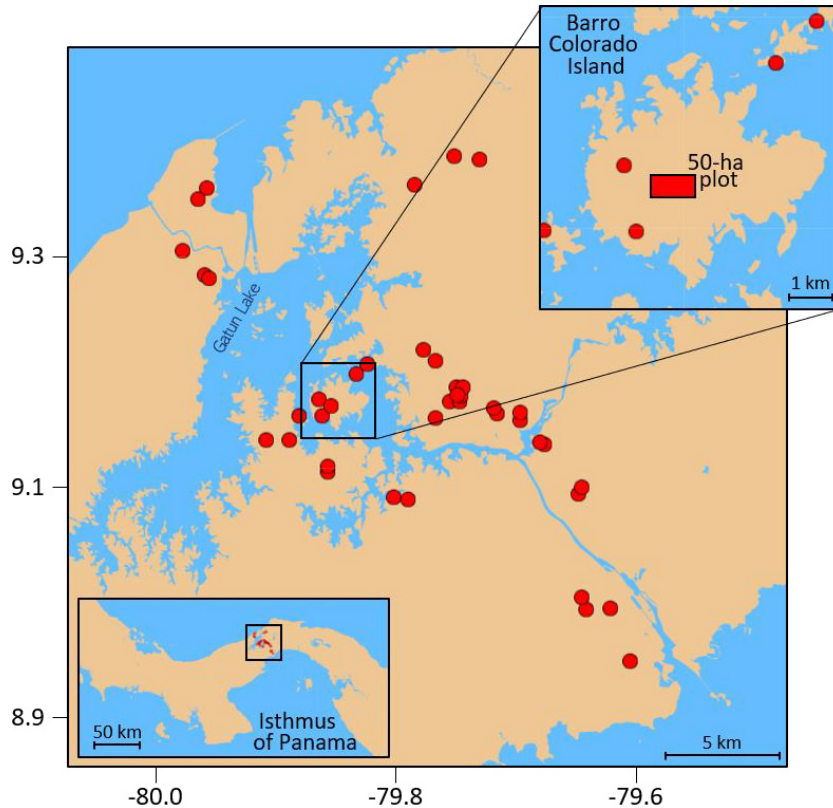


FIG. 1. Field site. Intact tropical forest covers 20% of Panama. Our regional pool is an aggregate of 40 sampling sites within 30 km of BCI. Combined, these sites comprise approximately 850 species, of which trait data were available for 242 species (maximum height), 219 (wood density), 234 (leaf mass per area), 177 (seed mass), comprising between 9,528 and 13,743 adult trees. Barro Colorado Island, spanning roughly 16 km², sits in an artificial lake in the Panama Canal. The 50-ha Forest Dynamics Plot, located near its center, is a 1,000 × 500 m patch of forest containing 300 tree species and 21,000 adult trees.

dbh exceeds half the maximum dbh observed for its species, a relationship that explains over 80% of interspecific variation in reproductive size thresholds (see Visser et al. 2016:Fig. S9). Maximum dbh was estimated as the average of the six largest individuals in the BCI plot in 2005, and an additional 150 ha of mapped tree plots located within 30 km and mostly within 10 km of BCI (Visser et al. 2016).

The regional pool consists of 40 1-ha sampling sites within 30 km of BCI (Condit et al. 2013, 2016). In 38 of these sites, individuals with maximum dbh > 1 cm were censused in 40 × 40 m internal subplots, and individuals with dbh > 10 cm were censused in the entire plot. In the remaining two plots, all individuals with maximum dbh > 10 cm were censused in the entire plot. Hence, we standardized the counts by the respective sampling area to estimate densities in these sites. Of the circa 850 species contained in these sites, trait data were available for those also found on BCI (see Table 1, caption to Fig. 1). Although lack of pattern among this subset of species in the regional pool does not rule out clustering among all species, it shows that the pattern on BCI is not simply mirroring regional-scale pattern inherited via immigration.

Our clustering metric has two foundations: the k-means clustering algorithm (MacQueen 1967), an optimization procedure which assigns species to clusters by minimizing the average trait distance between individuals in the same cluster, and the gap method (Tibshirani et al. 2001), which compares the observed data against null distributions, and selects the number of clusters that maximizes the difference between within-cluster trait dispersion in the observed and null communities. Specifically, given a candidate number of clusters k , the k-means algorithm finds the arrangement of species into k clusters that minimizes within-cluster trait dispersion:

$$D_k = \frac{1}{k} \sum_C \sum_{i,j \in C} n_i n_j d_{ij}^2,$$

where C refers to a cluster ($1 \leq C \leq k$), n_i is the abundance of species i , and d_{ij} is the trait distance between species i and j . The algorithm starts with randomly chosen trait values in the local community as possible cluster centers, then puts species into the cluster whose center is the closest to them, then recalculates cluster centers, and so on until the algorithm converges or

TABLE 1. Clustering results for the 50-ha plot and regional pool.

	Species		Individuals		Clusters (K)		z score (Z)		P value (P)	
	50 ha	Region	50 ha	Region	50 ha	Region	50 ha	Region	50 ha	Region
Maximum height	259	242	20,620	13,743	4*	1*	2.3*	3.4*	0.01*	0.02*
Wood density	229	219	17,139	9,273	5*	20	2.1*	1.6	0.02*	0.06
Leaf mass/area	250	234	18,368	9,528	3	3	0.2	1.5	0.40	0.07
Dry seed mass	185	177	18,259	10,667	15	3	0.2	1.0	0.38	0.16

Notes: For each header, the left column refers to the 50-ha BCI plot (50 ha), and the right column refers to the regional pool (Region). The total number of species for which trait data were available is listed under Species, and the total number of individuals represented is listed under Individuals. The number of clusters K is the value at which the gap index peaks. z scores and P -values were obtained by comparing the gap statistic against 1,000 null communities. In the case of maximum height, in addition to the peak at $K = 1$ listed, the regional pool also had a significant subpeak at $K = 4$ ($Z = 2.0$, $P = 0.03$). Significant results ($P < 0.05$) are marked with an asterisk.

changes in D_k fall below a specified threshold. Because the result can depend on the starting set of cluster centers, the procedure is repeated with different starting sets, and the final cluster arrangement with the lowest D_k across all sets is selected (note that the clusters need not be equally spaced). We use enough starting sets that larger numbers do not lower within-cluster dispersion further (typically between 1,000 and 10,000).

We then apply this k-means algorithm to 1,000 null communities, and define the gap index for k clusters as

$$G_k = \frac{1}{1000} \sum_{\text{nulls}} \log(D_k^*) - \log(D_k),$$

where D_k^* is the cluster dispersion in a given null community. This index measures the degree to which trait dispersion D_k in the observed community differs from its null expectation for k clusters (see Tibshirani et al. 2001, D'Andrea et al. 2019 for details). Notice that tighter-than-expected clustering in the data for k clusters will lead to a positive gap G_k , and vice versa. Finally, we find the number of clusters that maximizes the gap index. We call this maximal value—corresponding to the peak in the gap curves in Figs. 2 and 3—the gap statistic, $G = \max(G_k)$, and the value of k at which it occurs is the estimated number of clusters K . We note that Tibshirani et al. (2001) refer to the gap index G_k as the gap statistic, and estimate the number of clusters using a slightly different approach. Later studies found deficiencies with that approach (Dudoit and Fridlyand 2002, Sugar and James 2003), and modifications have since been proposed (Yan and Ye 2007). Our method, designed to find whether high abundances tend to cluster with respect to trait values, was benchmarked using simulation tests where the number of clusters is known a priori (see D'Andrea et al. 2019).

We obtain a null distribution of gap statistics by performing the above routine on each of the null communities, and from this distribution we extract significance (P value) and standardized effect size (z score). The z score is $Z = (G - \mu)/\sigma$, where

$$\mu = \frac{1}{1000} \sum_{\text{nulls}} G_{\text{null}},$$

is the mean of the null gap statistics and

$$\sigma^2 = \frac{1}{1000} \sum_{\text{nulls}} (G_{\text{null}} - \mu)^2,$$

is the variance. The P value is the proportion of null communities with a higher gap statistic than the observed community:

$$P = \frac{1}{1000} \sum_{\text{nulls}} I(G_{\text{null}} > G),$$

where the indicator function I is 1 if its argument is true, and zero otherwise.

Our null communities contain the same set of observed trait values and abundances, with abundances randomized across the traits. We therefore test for a nonrandom association between traits and abundances, as opposed to a nonrandom set of traits or abundances. Although a nonrandom trait distribution has interest in its own merit, it could be arguably caused by forces beyond local competitive interactions. Local abundances reflect the outcome of local competitive interactions and environmental filtering to a higher degree than a presence-absence list of locally occurring species, as the latter is strongly influenced by dispersal from the regional species pool. Therefore, trait clustering among local species without regard for abundance could simply reflect the clustered trait distribution of the regional pool, leaving it unclear whether local competition is the cause rather than evolutionary history.

RESULTS

We found significant clustering of species abundances by trait values on BCI based on species maximum height (Fig. 2A, E), with the gap statistic exceeding null expectations by 2.3 standard deviations (Table 1). There were four height-based clusters, falling at approximately 8-m

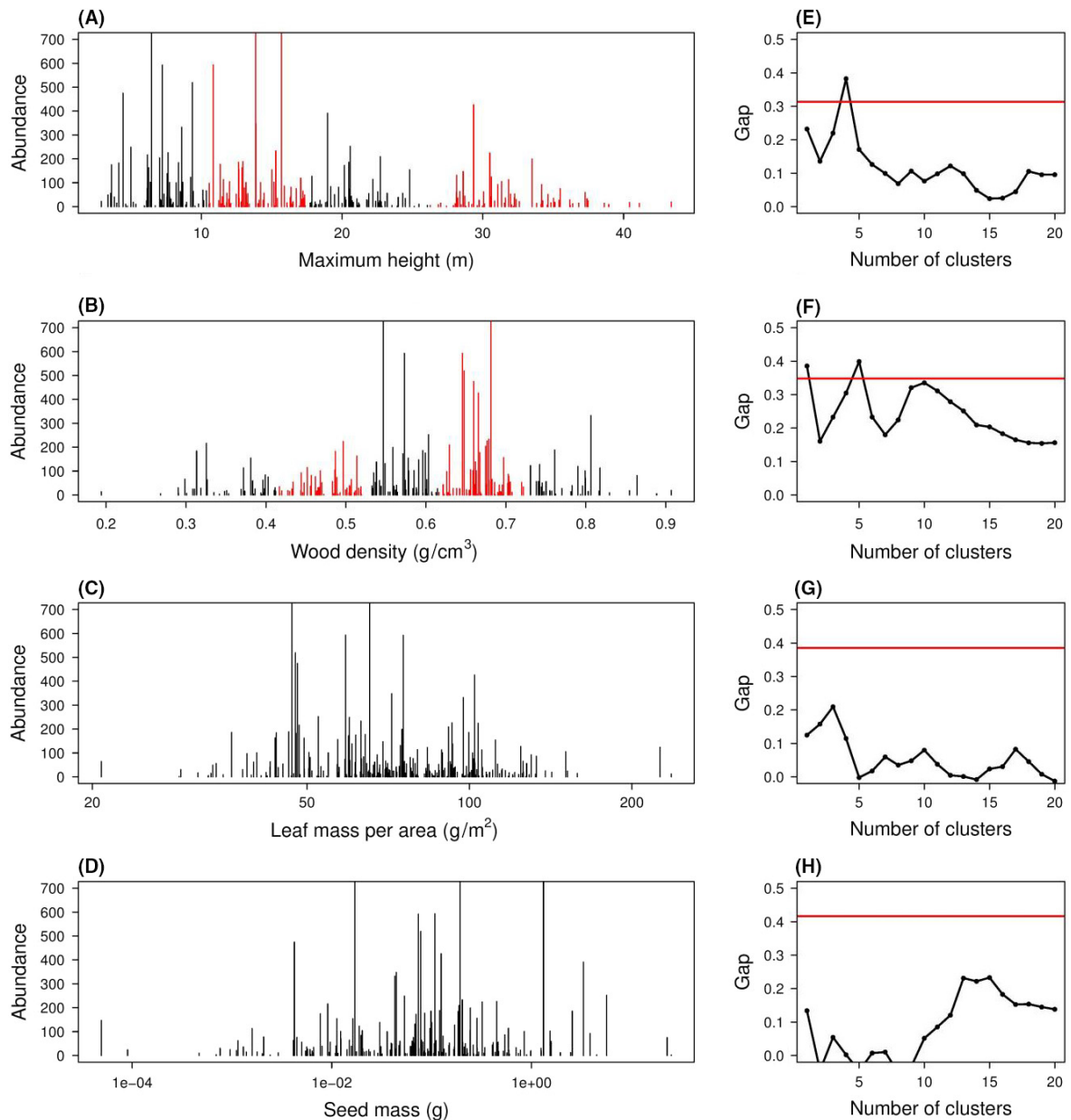


FIG. 2. Results. Stem plots show trait distribution in the 50-ha plot on BCI for (A) maximum height, (B) wood density, (C) leaf mass per area, and (D) seed mass. Each stem represents a species, with its trait value plotted on the abscissa and abundance on the ordinate. Data shown for the 2000 census. The corresponding gap curves (E–H) plot the gap index against the potential number of clusters. The gap statistic is the highest point on the curve, with the red line indicating the 95th quantile of the expected gap statistic under no pattern, obtained from 1,000 null sets. The peaks above the red line in (E) and (F) reveal clustering by maximum height, with four clusters, and wood density, with five. The alternating colors in the respective stem plots show cluster membership of each species.

intervals. Intriguingly, the pattern aligns well with the historical division of humid Neotropical forests into four strata of about 10 m each: shrubs, understory, midstory, and canopy (Richards 1952, Terborgh 1985, Condit et al. 1995; Fig. 3, Appendix S1: Fig S1). We also found a significant pattern of five abundance-by-trait clusters based on wood density on BCI (Fig. 2F), exceeding null expectations by 2.1 standard deviations (Table 1). Notably, all species on BCI were also significantly clustered around a

single wood density optimum. This occurred because species with intermediate wood densities were more common than those with extremely low or high wood densities (Fig. 2B), potentially indicating physiological costs or environmental filters against extreme trait values. We found no evidence for clustering based on LMA or seed mass.

The similar number of clusters by maximum height and wood density led us to ask if the two trait-based patterns reflected the same underlying niche axis. Even

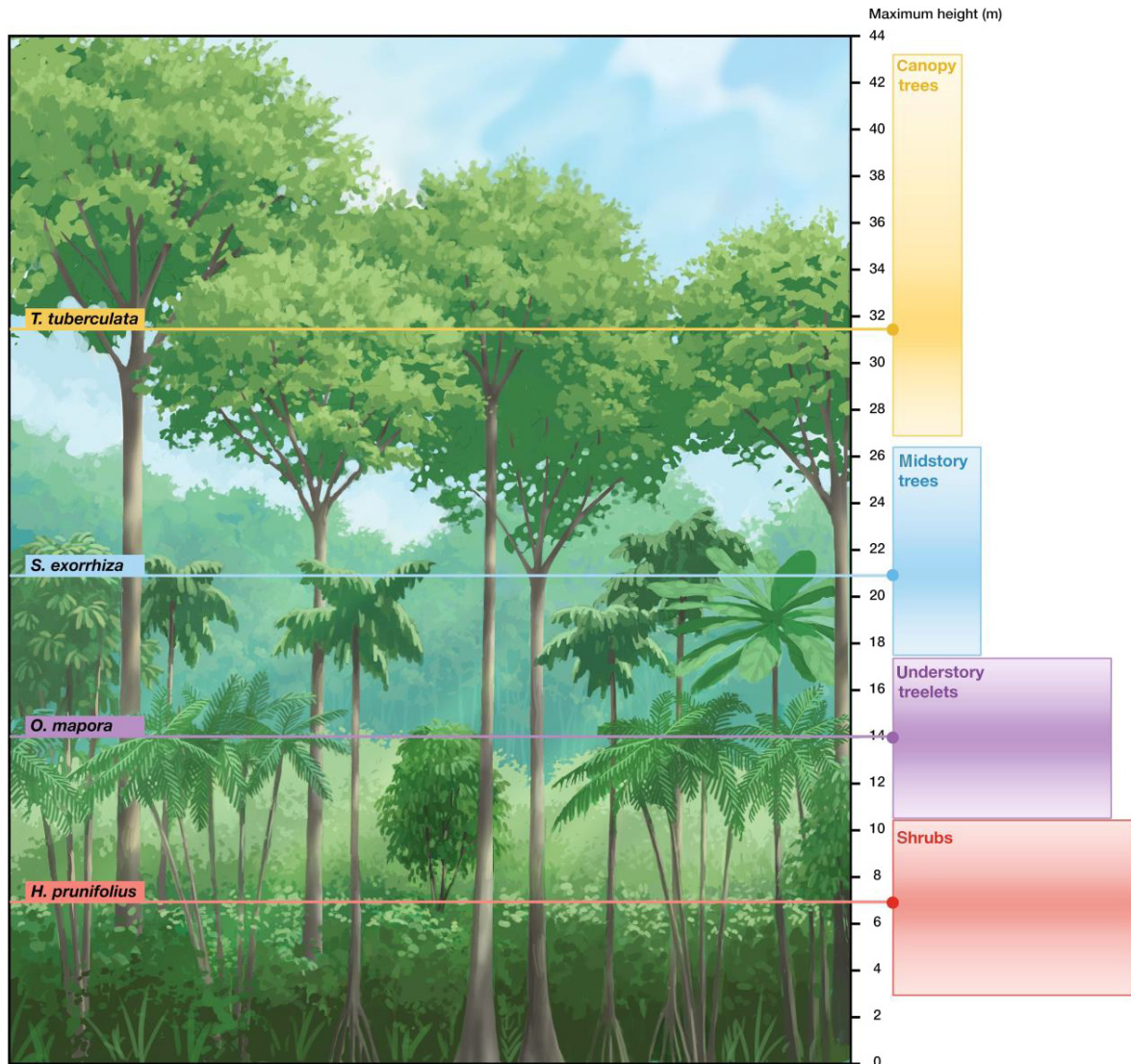


FIG. 3. Height layers. Visual representation of the forest on Barro Colorado Island, highlighting the four height-based groups identified by our metric: shrubs (61 ± 2 species; $8,071 \pm 712$ adult individuals), understory treelets (71 ± 3 ; $7,308 \pm 165$), midstory trees (61 ± 1 ; $2,957 \pm 114$), and canopy trees (64 ± 1 ; $2,836 \pm 82$), where the numbers represent mean and standard deviation across the seven censuses. Horizontal lines show maximum height of the dominant (most abundant) species in each group.

though maximum height and wood density did not correlate significantly (Pearson's $\rho = -0.10$, P value = 0.06), maximum height clusters correlated with wood density clusters (χ^2 -test P value = 0.02, Cramér's $V = 0.20$), supporting this tentative hypothesis.

We found significant abundance-by-trait clustering by maximum height at the regional scale, with the highest gap index occurring at $K = 1$ cluster, and a secondary but still significant peak at $K = 4$ clusters (Appendix S1: Fig. S2A, B). The existence of four height-based clusters at both local and regional scales suggests a consistent organization of species into the same four niches across many tropical forest communities. However, a key difference between local and regional height-based patterns is

the presence of a significant single cluster at the regional scale. This single regional peak reflects a unimodal abundance trend along the maximum height axis, with trees in the second height cluster being consistently the most abundant in their communities. This abundance trend may result from an interplay of higher light incidence at larger heights and the potential for a larger number of smaller-sized trees in a given area.

As for lack of clustering by wood density in the regional pool, we hypothesize that differences in environmental or ecological conditions across the region may have created different trait optima (cluster centroid values) in different communities, leading to the erosion of cluster structure when the communities are combined.

DISCUSSION

Our results underscore competitive partitioning of light as a major driver of tropical forest community structure. Specifically, we found cluster-based evidence for niche partitioning by maximum height, a trait associated with light capture, and wood density, a trait associated with shade tolerance (Wright et al. 2010). Conventional descriptions of tropical forest structure have long included references to different strata (sub-canopy, canopy, etc.), but to our knowledge there has never been any quantitative empirical support for their existence.

Testing for trait-based clustering is an appealing approach for the detection of niche partitioning because it conceptually unites the notions of stable species coexistence via differences and transient species coexistence via similarity (Holt 2006). Perhaps counterintuitively, it is precisely because species with similar strategies compete more strongly, and experience similar competitive effects from the rest of the community, that clusters emerge (D'Andrea et al. 2018). In other words, clusters reflect the simultaneous advantages of differing from others while being similar to those favored strategies.

We note there are special cases where competition could allow for coexistence of species with any trait value (Leimar et al. 2013). Specifically, the function specifying the relationship between competition and species traits (often referred to as the competition kernel) must have a strictly positive Fourier transform, which is not a general property of competition based on trait differences. For example, in the family of exponential kernels, only those with exponent ≤ 2 will satisfy the condition, and small perturbations of these kernels will break the property and lead to cluster formation. However, in the absence of empirical evidence that the competition kernels on BCI possess those special properties, a more general expectation is for cluster formation rather than a continuum of traits.

The mechanistic origin of clustering may involve environmental selection favoring certain traits over others. For example, according to Terborgh's sunfleck model (Terborgh 1985), light availability below the canopy may peak at various vertical strata because of intersection of light cones originating from gaps in the canopy. Latitudinal parameters that affect the angle of incidence, combined with the shape of tree canopies in tropical forests, predict three such strata below the canopy, for a total of four optimal tree heights based on light availability. Alternatively, the height-based clusters we identified may arise through trade-offs between the light-related advantages of being tall and shading others, and the budgetary constraints that investment in height impinges on reproductive growth, such as through losses in recruitment or shade tolerance (Kohyama 1993, Kohyama and Takada 2009). These trade-offs may result in an effective relationship between interspecific competition and height similarity. In such a case, the number

of clusters would relate to how quickly competition drops with increasing separation in maximum height. Regardless of the mechanism, the height-based clusters reflect the existence of multiple light-related niches, as well as stabilization via light-related niche partitioning.

The existence of four clusters by height suggests that only four species can coexist on BCI based on differences in height alone, but it does not mean that only four species can stably coexist on BCI. Additional niche axes may support higher coexistence, and in fact may be responsible for the maintenance of the observed clusters. Barabás et al. (2013) pointed out that additional niche axes, such as susceptibility to different herbivores and pathogens, are required for the permanence of clusters in a closed community subject to no temporal variation in the environment. Though recent empirical studies report a good deal of overlap in enemy host use, models suggest that small differences in susceptibility to enemies between tree species may still contribute significantly to diversity maintenance (Sedio and Ostling 2013). Hence, they likely also contribute to the permanence of clusters along the trait axes we report in our study. Another example additional niche axis is the successional niche (Tilman 1988): trees sharing the same height niche may niche-differentiate by shade tolerance. This could be reflected in the distribution of wood density values and/or other traits related to successional strategy.

Wood density in Barro Colorado Island tree species has been found to be a good predictor of species niche strategies along a trade-off axis between survival under stressful conditions and rapid growth under optimal conditions (Wright et al. 2010). Therefore, the clustering we found in wood density suggests niche partitioning along a growth–mortality trade-off axis, that is, the successional niche (Tilman 1988). The precise positions of the clusters could have many interacting causes: the available pool of traits, external filtering from the environment, resource availability, and the shape of the competition kernel. In the case of wood density, given its connection to the successional niche, the distribution of light gaps in the forest may possibly determine the positions of the niches. The number of clusters may also be influenced by the rate at which competition drops between species of disparate wood density: the faster the drop, the more niches are allowed.

The wood density results are not fully independent from our maximum height results, as indicated by the correlation between height and wood density clusters. To delineate the niche space driving pattern on BCI fully, a multivariate trait treatment would be required. However, such an approach raises questions of how to best convert trait values along different trait axes into a good predictor of competition. Moreover, traits could combine in different ways to form multidimensional niche space (D'Andrea et al. 2018); for example, Euclidean distance may be a poor predictor of competition, and therefore not be useful for detecting clustering. Determining how competition maps to multivariate trait space requires

mechanistic niche models going beyond the existing theoretical literature, which typically focuses on contributions of individual traits.

The absence of clustering in LMA and seed mass does not preclude a role for these traits in niche partitioning on BCI. D'Andrea et al. (2019) showed that a loose connection between trait value and niche strategy can mask clustering along the relevant niche axis. Seed mass is linked to dispersal and recruitment ability (Muller-Landau et al. 2008), and is therefore a candidate for clustering along a niche axis characterizing a competition–colonization trade-off—hence its inclusion in our study. However, seed mass alone may be a poor predictor of a species' strategy along this niche axis, for example, because of the effects of other traits such as drought tolerance and dispersal mode. LMA is theoretically connected to niche strategies (Wright et al. 2010), but there is substantial ontogenetic variation in its predictive ability of growth, with the relationship being stronger in the seedling stage. Eventually, other aspects of physiology become limiting as the plant grows. Hence, LMA may be a noisy predictor of the niche strategy (Wright et al. 2010). We conclude that the lack of clustering in these traits may be due to their loose connection to niche strategies rather than no involvement in niche partitioning.

Our study provides a new line of evidence that niche differentiation shapes tropical forests, notwithstanding neutral theory's success at fitting species abundance distributions (Rosindell et al. 2012). Yet, our results go further by identifying specific numbers of niches and their associated trait optima. Future extensions of clustering analysis could look at other traits related to defense chemistry or abiotic preferences, further delineating the niches contributing to coexistence in tropical forests.

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LITERATURE CITED

- Barabás, G., R. D'Andrea, R. Rael, G. Meszéna, and A. M. Ostling. 2013. Emergent neutrality or hidden niches? *Oikos* 122:1565–1572.
- Chase, J. M., and M. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. The University of Chicago Press, Chicago, Illinois, USA.
- Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B* 366:2351–2363.
- Condit, R. 1998. *Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots*. Berlin, Germany: Springer Science & Business Media.
- Condit, R., R. A. Chisholm, and M. O. Hunter. 2012a. Thirty years of forest census at Barro Colorado and the importance of immigration in maintaining diversity. *PLoS ONE* 7:1–6.
- Condit, R., B. M. J. Engelbrecht, D. Pino, R. Pérez, and B. L. Turner. 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America* 110:5064–5068.
- Condit, R., S. Lao, R. Perez, S. B. Dolins, R. Foster, and S. Hubbell. 2012b. *Barro Colorado Forest Census Plot Data (Version 2012)*. <http://dx.doi.org/10.5479/data.bci.20130603>
- Condit, R. S., S. P. Hubbell, and R. B. Foster. 1995. Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419–439.
- Condit, R. S., R. Pérez, S. Aguilar, and S. Lao. 2016. Data from tree censuses and inventories in Panama. repository.si.edu/handle/10088/28866.
- D'Andrea, R., and A. M. Ostling. 2016. Challenges in linking trait patterns to niche differentiation. *Oikos* 125:1369–1385.
- D'Andrea, R., and A. Ostling. 2017. Biodiversity maintenance may be lower under partial niche differentiation than under neutrality. *Ecology* 98:3211–3218.
- D'Andrea, R., A. Ostling, and J. P. O'Dwyer. 2018. Translucent windows: How uncertainty in competitive interactions impacts detection of community pattern. *Ecology Letters* 21:826–835.
- D'Andrea, R., M. Riolo, and A. M. Ostling. 2019. Generalizing clusters of similar species as a signature of coexistence under competition. *PLoS Computational Biology* 15:1–19.
- Dudoit, S., and J. Fridlyand. 2002. A prediction-based resampling method for estimating the number of clusters in a dataset. *Genome Biology* 3:1–21.
- Götzenberger, L., et al. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews* 87:111–127.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Page plant strategies and vegetation processes. Hoboken, NJ: John Wiley and Sons.
- Holt, R. D. 2006. Emergent neutrality. *Trends in Ecology & Evolution* 21:531–533.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Page monographs in population biology. Princeton University Press, Princeton, New Jersey, USA.
- Hubbell, S. P., et al. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283:554–557.
- Kohyama, T. 1993. Size-structured tree populations in gap-dynamic forest—the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology* 81:131–143.
- Kohyama, T., and T. Takada. 2009. The stratification theory for plant coexistence promoted by one-sided competition. *Journal of Ecology* 97:463–471.
- Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community assembly across spatial

- scales in an Amazonian forest. *Ecological Monographs* 80:401–422.
- Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322(5901):580–582.
- Kunstler, G., et al. 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529:1–15.
- Lake, J. K., and A. M. Ostling. 2009. Comment on “Functional traits and niche-based tree community assembly in an Amazonian forest.” *Science* 324:1015; author reply 1015.
- Leimar, O., A. Sasaki, M. Doebeli, and U. Dieckmann. 2013. Limiting similarity, species packing, and the shape of competition kernels. *Journal of Theoretical Biology* 339:3–13.
- Levine, J. M., and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics* 34:549–574.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- MacQueen, J. B. 1967. Some methods for classification and analysis of multivariate observations. 5th Berkeley Symposium on Mathematical Statistics and Probability 1:281–297.
- Mouquet, N., and M. Loreau. 2003. Community patterns in source–sink metacommunities. *American Naturalist* 162:544–557.
- Muller-Landau, H. C. 2010. The tolerance–fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences of the United States of America* 107:4242–4247.
- Muller-Landau, H. C., S. J. Wright, O. Calderón, R. Condit, and M. O. Hunter. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* 96:653–667.
- Richards, P. W. 1952. *The tropical rain forest*. University Press, Cambridge, UK.
- Rosindell, J., S. P. Hubbell, F. He, L. J. Harmon, and R. S. Etienne. 2012. The case for ecological neutral theory. *Trends in Ecology & Evolution* 27:204–209.
- Sakavara, A., G. Tsirtsis, D. L. Roelke, R. Mancy, and S. Spatharis. 2018. Lumpy species coexistence arises robustly in fluctuating resource environments. *Proceedings of the National Academy of Sciences of the United States of America* 115:738–743.
- Scheffer, M., and E. H. van Nes. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences of the United States of America* 103:6230–6235.
- Sedio, B. E., and A. M. Ostling. 2013. How specialised must natural enemies be to facilitate coexistence among plants? *Ecology Letters* 16:995–1003.
- Sugar, C. A., and G. M. James. 2003. Finding the number of clusters in a dataset: an information-theoretic approach. *Journal of the American Statistical Association* 98:750–763.
- Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. *American Naturalist* 126:760–776.
- Tibshirani, R., G. Walther, and T. Hastie. 2001. Estimating the number of clusters in a data set via the gap statistic. *Journal of the Royal Statistical Society B* 63:411–423.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey, USA.
- Vergnon, R., N. K. Dulvy, and R. P. Freckleton. 2009. Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecology Letters* 12:1079–1090.
- Visser, M. D., M. Bruijning, S. J. Wright, H. C. Muller-Landau, E. Jongejans, L. S. Comita, and H. de Kroon. 2016. Functional traits as predictors of vital rates across the life cycle of tropical trees. *Functional Ecology* 30:168–180.
- Volkov, I., J. R. Banavar, M. O. Hunter, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424:1035–1037.
- Wright, S. J., et al. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91:3664–3674.
- Yan, B., J. Zhang, Y. Liu, Z. Li, X. Huang, W. Yang, and A. Prinzing. 2012. Trait assembly of woody plants in communities across sub-alpine gradients: Identifying the role of limiting similarity. *Journal of Vegetation Science* 23:698–708.
- Yan, M., and K. Ye. 2007. Determining the number of clusters using the weighted gap statistic. *Biometrics* 63:1031–1037.

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