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Higher β-diversity observed for herbs over woody plants is driven by stronger habitat filtering in a tropical understory

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Abstract. Herbaceous plants are a key component of tropical forests. Previous work indicates that herbs contribute substantially to the species richness of tropical plant communities. However, the processes structuring tropical herb diversity, and how they contrast with woody communities, have been underexplored. Within the understory of a 50-ha forest dynamics plot in central Panama, we compared the diversity, distribution, and abundance of vascular herbaceous plants with woody seedlings (i.e., tree and lianas <1 cm DBH and ≥20 cm tall). Beta-diversity was calculated for each community using a null model approach. We then assessed the similarity in alpha and beta-diversity among herbs, tree seedlings, and liana seedlings. Strengths of habitat associations were measured using permutational ANOVA among topographic habitat-types. Variance partitioning was then used to quantify the amount of variation in species richness and composition explained by spatial and environmental variables (i.e., topography, soils, and shade) for each growth form. Species richness and diversity were highest for tree seedlings, followed by liana seedlings and then herbs. In contrast, beta-diversity was 16–127% higher for herbs compared to woody seedlings, indicating higher spatial variation in this stratum. We observed no correlation between local richness or compositional uniqueness of herbs and woody seedlings across sites, indicating that different processes control the spatial patterns of woody and herbaceous diversity and composition. Habitat associations were strongest for herbs, as indicated by greater compositional dissimilarity among habitat types. Likewise, environmental variables explained a larger proportion of the variation in species richness and composition for herbs than for woody seedlings (richness = 25%, 14%, 12%; composition = 25%, 9%, 6%, for herbs, trees, and lianas, respectively). These differences between strata did not appear to be due to differences in lifespan alone, based on data from adult trees. Our results point to contrasting assembly mechanisms for herbaceous and woody communities, with herbs showing stronger niche-derived structure. Future research on tropical herbaceous communities is likely to yield new insights into the many processes structuring diverse plant communities.

Key words: Barro Colorado Island; community assembly; environmental filtering; habitat association; lianas; null model; species richness; variance partitioning.

Introduction

The majority of the world's terrestrial biodiversity is housed in tropical forests (von Humboldt 1807, Wallace 1878), with plant richness in some cases exceeding 650 tree and shrub species/ha (Valencia et al. 2004). The high local diversity of tropical forests poses a daunting challenge to ecologists, who have long sought to explain how so many species coexist without one superior competitor becoming dominant (Gause 1934, Wright 2002). Despite the attention given to tropical plant diversity, the vast majority of research on the subject has focused exclusively on woody individuals (i.e., trees, shrubs, and lianas). These studies have greatly improved our understanding of both patterns of woody plant diversity, as well as the underlying processes generating them (Wright 2002). However, in contrast to the large number of studies conducted on woody plants, studies on tropical herbaceous plant diversity and composition remain rare, particularly at local scales (Royo and Carson 2005). This places our knowledge of tropical herbaceous communities well behind that for trees and lianas, and severely limits our ability to recognize and understand the full extent of tropical plant diversity as a whole.

Surprisingly, the lack of studies on the herbaceous layer in the tropics lies in stark contrast to temperate forests, where the herbaceous groundflora has received much attention over the past decades (Whigham 2004,

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Gilliam 2007, and Gilliam 2014 for reviews). This focus on temperate forest herbs has been driven largely by the recognition that they contribute significantly to forest community diversity, comprising 80% of total plant species richness on average (Gilliam 2007). In addition, studies have shown that temperate forest herbs influence tree seedling regeneration (Royo and Carson 2006), provide evidence of niche partitioning (Gilbert et al. 2004), and mediate many important ecosystem processes such as nutrient cycling (Muller 2014). Herbs have similarly been shown to contribute substantially to the diversity of tropical forests, representing 50% of the species richness in some cases (Gentry and Dodson 1987, Linares-Palomino et al. 2009). However, in comparison to temperate forests, research on tropical herbaceous communities, beyond their contributions to total species counts, is severely lacking.

Similarly, research on the beta-diversity of tropical herbs is also scant compared to the large body of literature on both tropical woody plant and temperate herb beta-diversity. Of the few studies that have looked at spatial variation in tropical herb communities, most have either focused only on the most common species (Svenning et al. 2004), have restricted sampling to specific taxa such as palms or ferns (Vormisto et al. 2000, Tuomisto and Ruokolainen 2003, Tuomisto et al. 2003, Zuquim et al. 2012), have only sampled flowering or fruiting individuals (Gentry and Emmons 1987), or do not include abundance data (Svenning et al. 2004). Furthermore, all of these studies have focused on large spatial scales (i.e., landscape to regional).

One area where information is particularly lacking is in our understanding of how environmental resource gradients shape herb distribution patterns (i.e., local habitat filtering). Tropical woody species have been shown to associate with both topographic (Webb and Peart 2000, Harms et al. 2001, Kanagaraj et al. 2011, De Cáceres et al. 2012) and soil nutrient gradients (John et al. 2007, Dalling et al. 2012). Furthermore, the strength and type of habitat filtering have been shown to differ among life stages (e.g., between seedlings, saplings and adult trees) (Webb and Peart 2000, Comita et al. 2007*b*, Kanagaraj et al. 2011, Dalling et al. 2012) and among growth forms (e.g., lianas vs. trees; Dalling et al. 2012) in tropical forests, suggesting that patterns found for adult trees are not necessarily generalizable. There are good reasons to expect that herbs may respond differently to resource gradients than do woody species. For example, herbs are often more sensitive to drought due to their lower rooting depth and lack of secondary tissue (Costa 2006). Herbs may also be more sensitive to pathogen and herbivore loads (Royo and Carson 2005), which have themselves been shown to correlate strongly with environmental variables such as light and moisture (Augspurger 1984). Furthermore, herbs are highly dispersal limited, which also leads to aggregated patterns (Leigh et al. 2004).

To help fill these gaps, we present results from a census of the herbaceous groundlayer of an intensively studied 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama. We compare spatial patterns of diversity and composition between the understory herbaceous and woody plant communities (i.e., tree, shrub and liana seedlings), focusing on three questions: (1) How do alpha- and beta-diversity differ between herbaceous and woody seedlings in a tropical forest understory community? We expected herbs to contribute significantly to overall community richness, but herb richness to be lower than total woody richness (Croat 1978). However, we expected herbs to exhibit stronger spatial aggregation (i.e., higher beta-diversity) than woody individuals due to greater resource sensitivity and dispersal limitation. (2) Do herbs and woody seedlings show similar spatial patterns in alpha and beta-diversity? In other words, are sites with high woody richness also home to high herb richness, and are sites with unique woody communities also home to unique herb communities? If woody and herbaceous communities respond similarly to environmental resource gradients, we would expect to see strong correlations in local alpha- and beta-diversity between them. Alternatively, if different processes regulate these growth forms, or if competition between them is strong, we may expect to see weak or even negative correlations. To explore this question further, we asked (3) Do the actual processes generating observed spatial patterns of alpha and beta-diversity differ between herbs and woody seedlings? We hypothesized that habitat filtering would be strongest for herbs, resulting in greater habitat associations and stronger correlations with environmental variables.

Materials and Methods

Study site

The study was conducted in the 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama (9°10′ N, 79°51′ W) (Condit 1998, Hubbell et al. 1999, 2005). The vegetation is seasonal tropical moist forest, and the island receives ~2600 mm of precipitation per year, with a distinct dry season from January to April (Windsor 1990). All stems ≥1 cm diameter at breast height (DBH) in the BCI 50-ha plot are tagged, mapped, and measured at five year intervals.

Woody seedlings census

Since 2001, tree, shrub and free-standing liana seedlings ≥20 cm tall and <1 cm DBH have been tagged, mapped and measured every 1–2 years in ~20,000 1 × 1 m seedling plots that are spaced at 5-m intervals throughout the 50-ha BCI plot (Comita et al. 2007*a*, 2010, Comita and Hubbell 2009). For all analyses, we considered liana seedlings separately from tree and shrub seedlings (hereafter referred to simply as tree seedlings) because of their distinct growth form and ecological strategy (Putz 1984, Dalling et al. 2012).

Herb census

In 2012, we conducted a census of the herbaceous understory community in a subset of the 20,000 seedling plots (Salpeter 2013). We employed a stratified random sampling design based on topographic habitat types defined by Harms et al. (2001). The four primary habitat types were "high-plateau," "low-plateau," "slope," and "swamp," and within each of these habitat types, thirty 20 × 20 m quadrats were randomly selected for herb sampling. Only 26 quadrats were sampled in the swamp habitat and 29 in the slope habitat to avoid existing trails, resulting in 115 total 20 × 20 m quadrats and 1840 1 × 1 m plots (Appendix S1: Fig. S1). For this study, we defined herbs as all non-woody rooted vascular plants that were not twining around or climbing another individual at the time of the census. Herbaceous climbers were not included in the census due to their differences in life-history strategy, as well as to avoid problems with sampling. In particular, sampling of climbers was made difficult due to the fact that they were often rooted outside of the plot, and measuring percent cover was difficult for very tall individuals. In nearly all cases, unidentified species were readily distinguishable from one another and were thus retained in all analyses as morphospecies.

Measuring abundance

For woody seedlings, we used data on the total number of individuals and the height of each individual from the 2012 seedling census, using only the 1 × 1 m seedling plots that were also used in the herb census. For herbs, we measured the total percent cover and maximum height attained in each 1 × 1 m plot. For all growth forms (i.e., trees/shrubs, lianas, and herbs), we also calculated the proportion of 1 × 1 m plots in which each species was found within each of the larger 20 × 20 m quadrats (out of 16 total), which we refer to hereafter as frequency. Comparisons among herbs, tree, and liana seedlings were then made using relative importance values (RIVs), calculated as:

$$\mathrm{RIV}_{\mathrm{herb}} = [\mathrm{COVER}_{\mathrm{rel}} + \mathrm{FREQ}_{\mathrm{rel}} + \mathrm{HEIGHT}_{\mathrm{rel}}]/3$$

$$\mathrm{RIV}_{\mathrm{woody}} = [\mathrm{DEN}_{\mathrm{rel}} + \mathrm{FREQ}_{\mathrm{rel}} + \mathrm{HEIGHT}_{\mathrm{rel}}]/3$$

In all analyses, RIVs were first square-root transformed to reduce the impacts of highly abundant species. Furthermore, to ensure that the particular RIV metric used did not greatly influence our results, we reran all analyses using several different combinations of abundance metrics, and found that our results were highly consistent and did not change any conclusions (Appendix S2).

Environmental data

Topographic variables included mean elevation, aspect, slope steepness, and convexity of each 20 × 20 m quadrat. A topographic wetness index (TWI) was also calculated from a 5-m scale resolution digital elevation map (Hengl 2009). Aspect data were sin- and cos-transformed to avoid problems with circularity, and both variables were used in all subsequent analyses (Legendre et al. 2009). Data on soil chemistry (i.e., pH, Al, B, Ca, Cu, Fe, K, Mg, Mn, Zn, NH_4+ and NO_3) in the BCI 50-ha plot were also used (Dalling et al. 2014). These data were sampled at a 50-m resolution and then kriged for use at the 20 × 20 m scale (Dalling et al. 2014). Because of the large numbers of individual soil variables used, they were first reduced using principal components analysis, and the first axis was used to describe overall soil fertility (John et al. 2007).

Understory light availability was estimated using canopy height survey data collected in 2012 (Hubbell et al. 2014). For every 5 × 5 m subsection of the 50-ha plot, the presence/absence of vegetation at incremental heights above ground level was recorded (i.e., 0–1 m, 1–2 m, 2–5 m, 5–10 m, 10–20 m, 20–30 m, and above 30 m). These data were then used to calculate a shade index for each 5 × 5 m quadrats, and averaged for each 20 × 20 m quadrat used here.

Species richness and diversity

For each growth form and each habitat type, we calculated species richness, the Chao-1 richness estimator (to correct for undersampling; Appendix S1: Fig. S2; Chao 1984), the exponentiated Shannon-Wiener diversity index, and the undersampling-corrected Chao-Shen index (Chao and Shen 2003).

Beta-diversity

Following the advice of Anderson et al. (2011), we used several methods for quantifying beta-diversity: (1) Whittaker's multiplicative estimate (β_{Whit}), (2) the mean Morisita-Horn distance ($\bar{d}$), and (3) and the total variance of the site-by-species matrix [SS(**Y**)]. SS(**Y**), which was calculated using the Hellinger-transformed site-by-species matrix (Legendre and Gallagher 2001), is useful because it allows for the partitioning of beta-diversity into individual site and species contributions (Legendre et al. 2005, Legendre and De Cáceres 2013). Here, we use the local site contribution to beta-diversity (LCBD) to test whether the sites contributing the most to beta-diversity differed among growth forms (i.e., question 2 in *Introduction*). We used a null model to control for differences in total species pools among the three growth forms by randomly shuffling the identities of species within plots a total of 999 times and calculating the mean and standard deviations of each null-derived beta-metric (Chase et al. 2011, Kraft et al. 2011). Because the null model requires true count data, only frequency values were used when calculating beta-diversity.

Habitat filtering

For each growth form, we examined species composition among the four topographic habitat types using nonmetric multidimensional scaling ordination (NMDS)

with Morisita-Horn dissimilarities, and tested for significant differences using permutational multivariate ANOVA (PERMANOVA; Anderson 2001). We also used indicator species analysis to determine which species from each strata were positively associated with each of the four habitat types (Dufrêne and Legendre 1997). We next used variance partitioning using the continuous environmental variables measured. We partitioned the variation in richness and composition into individual fractions explained by both environment (i.e., topographic variables, soil fertility, and shade) and spatial descriptors. Principal coordinates of neighbor matrices (PCNMs) were used as spatial descriptors (Dray et al. 2006). PCNMs that were significantly correlated with richness and composition were identified using forward selection, and fractions of explained variation were measured using adjusted R-squared values (Borcard et al. 1992). All analyses were done in the R statistical programming language (R Core Team 2015) using the "vegan" package (Oksanen 2011) for community analyses and the "packfor" package (Dray et al. 2011) for forward selection.

Results

Alpha- and beta-diversity of the herbaceous vs. woody community

Richness and diversity of herbs was substantially lower than tree and liana seedling diversity for all indices (Table 1). A total of 54 herb species from 19 plant families were recorded in the herb census, compared to 166 tree and shrub species from 45 families and 75 liana species from 23 families. Nonetheless, herbs increased the total species richness of the understory by 22%. The herbaceous layer was dominated by a few common species (i.e., *Selaginella arthritica*, *Pharus latifolius*, *Tectaria incisa*, and *Adiantum lucidum*), which made up over 60% of the total herb community (Appendix S1: Table S1, Fig. S3). Three of these species are ferns (*S. arthritica, T. incisa* and *A. lucidum*), and all are widely distributed in the New World tropics (Croat and Busey 1975, Croat 1978). In contrast to alpha diversity, beta-diversity (i.e., deviation from the null expectation) was highest for herbs, ranging from 16 to 127% higher than woody seedlings, depending on which index was used (Table 1).

Correlations in local diversity and composition among sites

Herbs and woody seedlings differed in their spatial patterns of alpha diversity. Among habitat types, herb species richness was highest in the swamp, while for tree and liana seedlings, slopes generally contained the most species (Table 1). Over the entire plot, there was no correlation between the number of herb and tree seedling species per 20 × 20 m quadrat ($r = -0.10$, $P = 0.27$; Fig. 1a), nor between herb and liana richness ($r = 0.06$, $P = 0.53$). In contrast, there was a strong positive correlation between tree seedling and liana seedling richness ($r = 0.44$, $P < 0.01$; Fig. 1a). These results were similar when using the Shannon-Wiener index (herbs:tree seedlings: $r = -0.11$, $P = 0.22$; herbs:liana seedlings: $r = 0.07$, $P = 0.46$; tree seedlings:liana seedlings: $r = 0.41$, $P < 0.01$). Likewise, individual sites with unique species compositions were not the same for herbaceous and woody communities (Fig. 1b). Local site contributions to beta-diversity (LCBD) were uncorrelated between herbs and tree seedlings ($r = 0.15$, $P = 0.11$), as well as between

Table 1. Alpha- and beta-diversity estimates for herbs, tree, and liana seedlings within the BCI 50-ha plot. For the species richness and Shannon estimates, values are given for the community as a whole, as well as for each individual habitat type.

		Alpha-diversity				Beta-diversity				
	Habitat	Richness	Chao1	exp(H')	exp(H'_{Chao})	β_W	β_{WC}	$\bar{d}$	SS(**Y**)	n
Herbs	All	54	68 ± 10	18.83	19.28	24.03	24.14	14.83	10.59	115
	Hi Plateau	24	30 ± 6	11.77	13.02	–	–	–	–	30
	Low Plateau	29	45 ± 16	14.09	14.93	–	–	–	–	30
	Slope	28	35 ± 6	12.55	13.44	–	–	–	–	29
	Swamp	41	61 ± 14	23.84	26.60	–	–	–	–	26
Tree seedlings	All	166	204 ± 16	60.77	66.05	19.25	20.08	11.20	9.06	115
	Hi Plateau	87	114 ± 13	44.50	50.28	–	–	–	–	30
	Low Plateau	98	164 ± 31	52.06	59.27	–	–	–	–	30
	Slope	107	155 ± 20	57.67	66.97	–	–	–	–	29
	Swamp	98	206 ± 49	50.21	61.06	–	–	–	–	26
Liana seedlings	All	73	91 ± 11	34.54	37.58	15.68	15.00	6.53	5.54	115
	Hi Plateau	43	55 ± 8	24.63	29.70	–	–	–	–	30
	Low Plateau	45	54 ± 7	29.71	34.06	–	–	–	–	30
	Slope	52	95 ± 26	31.39	37.81	–	–	–	–	29
	Swamp	44	57 ± 8	27.54	35.26	–	–	–	–	26

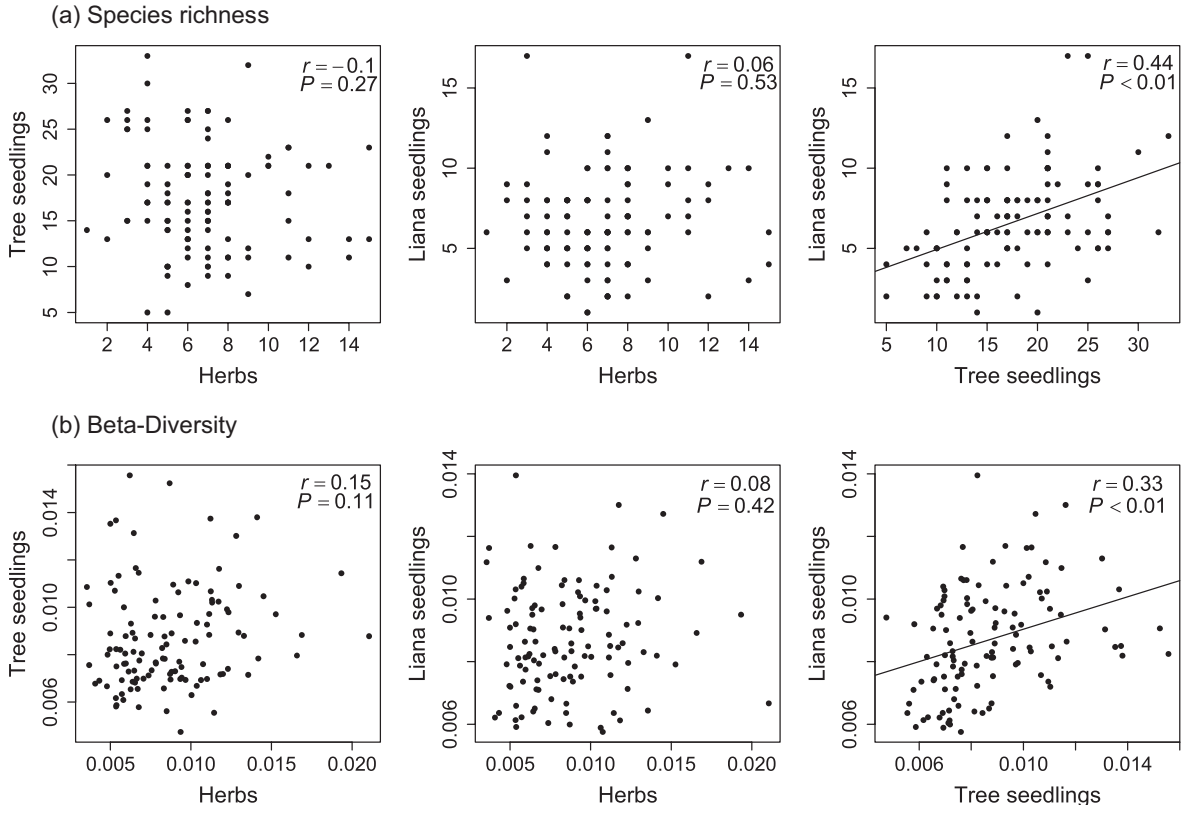

FIG. 1. Scatter plots and correlations between herbaceous plants, tree seedlings, and liana seedlings for local species richness and local site contributions to beta-diversity (LCBD). Each point represents a 20 × 20 m quadrat. LCBD values are the sums of squared deviations from the community-wide mean for individual quadrats. Best-fit line shown for significant correlations.

herbs and liana seedlings (r = 0.08, P = 0.42). As with alpha diversity, tree seedling and liana seedling LCBD values were significantly correlated (r = 0.33, P < 0.01).

Habitat associations and response to resource gradients

Habitat filtering was much stronger for the herbaceous community than for the woody understory communities. Separation in multivariate species-space was greatest for herbs (Fig. 2), and the PERMANOVA results revealed that habitat type explained more than twice the amount of variation in composition for herbs than for woody seedlings (F = 13.28, R^2 = 0.29 for herbs vs. F = 5.40, R^2 = 0.13 for tree seedlings), and more than three times the amount for liana seedlings (F = 2.65, R^2 = 0.07). For all three communities, the swamp habitat contributed the most to variation in species composition, but this was strongest for herbs and weakest for lianas.

Variance partitioning models explained the highest amount of total variation for herb richness and species composition (Fig. 3). Environment alone explained little of both herb and tree seedling richness, but the shared fraction and spatial fractions were highest for herbs (Fig. 3a). For species composition, all three communities had similar fractions explained only by the environment, but the shared and spatial fractions were again much higher for herbs (Fig. 3b). The three growth forms varied widely in their correlations with individual environmental variables, but the variation explained by each was nearly always highest for herbs (Appendix S1: Fig. S5). For species composition, elevation and TWI were important environmental variables for all three growth forms, and shade index was only important for herb richness.

DISCUSSION

We found that the herbaceous groundlayer of a well-studied neotropical forest contributes substantially to overall understory diversity. Including non-scandent herbaceous plants increased total understory plant species richness by 22% compared to estimates based solely on woody seedlings. Individual herb species were more highly aggregated than their woody neighbors, resulting in higher overall beta-diversity, which our results suggest is due to stronger habitat associations and dispersal limitation. Interestingly, across site correlations in diversity between herbaceous and woody communities were not significant, likely driven by the differential responses of growth forms to environmental resource gradients. Our results suggest that contrasting mechanisms structure

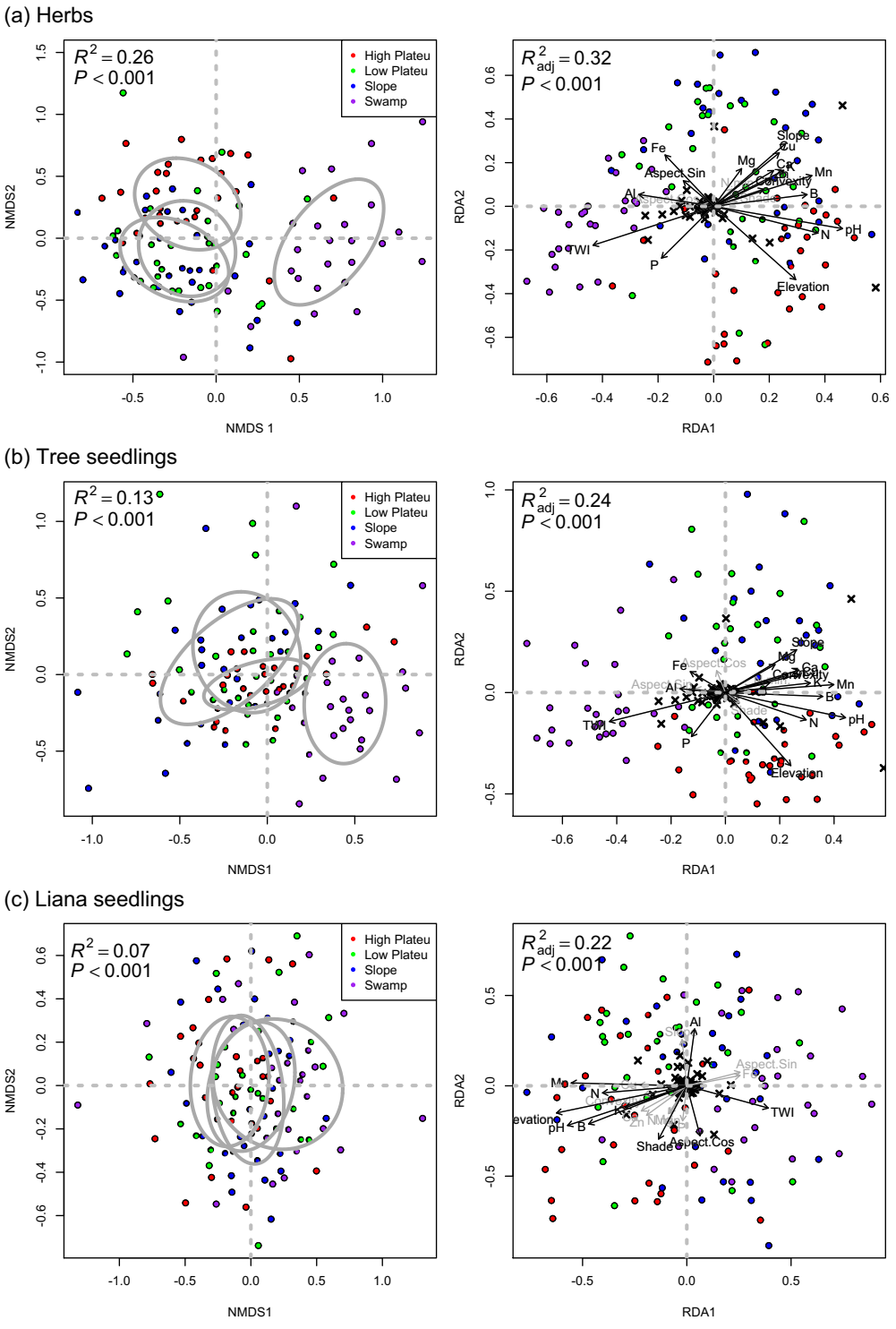

FIG. 2. Non-metric multidimensional scaling (NMDS) ordination (left panels) showing the locations of 115 sampling quadrats in species-space. Points are color-coded according to habitat type, and 95% confidence ellipses are overlain. An outlier that severely influenced the results of the NMDS for liana seedlings was removed from the analysis. Permutational multivariate ANOVA (PERMANOVA) results (Pseudo *R*-squared statistic and associated *P*-value) are shown in the top left corner. Redundancy analysis (RDA; right panels) showing the relationship between community composition and individual measured environmental variables. Adjusted *R*-squared values and *P*-values are shown in the top left corner. In all panels, the *x*-axis represents ordination axis 1, and the *y*-axis represents axis 2.

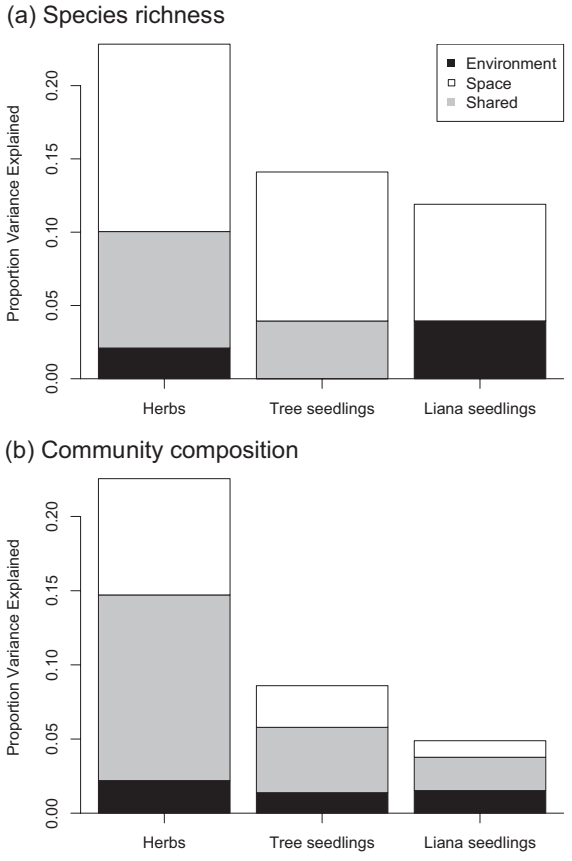

FIG. 3. Variance partitioning models showing individual fractions of variation explained by environmental and spatial descriptor variables (PCNMs). The top panel shows results for species richness (a), and the bottom panel for species composition (b). Environment (black) and space (white) fractions indicate unique contributions towards the overall amount of variance explained, and the gray fraction indicates the redundant portion co-explained by each.

herbaceous and woody communities, which helps further our understanding of tropical forest community assembly and diversity.

Understory alpha- and beta-diversity

The contribution of herbs to total species richness reported here (18% of all understory species sampled) was lower than that recorded in Croat (35.4%; 1978). However, the Croat census was conducted across the entire 15.6-km^2 island and included clearings, trails, shorelines, and successional areas where herbs are more highly abundant. The relatively low overall percent coverage values for the herbaceous community recorded within the 50-ha plot explains, in part, why herb species richness was lower than for woody seedlings. Despite this observation, the 54 herb species recorded indicate that herbs are capable of coexisting with each other, as well as with woody species in the BCI community, albeit at low abundances. Furthermore, our estimate of herbaceous richness is certainly an underestimate due to the fact that climbing vines and epiphytes were not included in our census.

In contrast to alpha-diversity, beta-diversity was highest for herbs, suggesting three possible scenarios: (1) herbs are more sensitive to environmental resource gradients or habitat-type than woody seedlings; (2) interspecific variation in response to resources or habitats is highest in herbs; and/or (3) herbs are more dispersal limited than woody individuals. Previous work on temperate herbs indicates that herbaceous plants are highly sensitive to fine-scale variation in soil moisture and light gradients (Gilliam 2007, Neufeld and Young 2014). Specifically, the shallow and rhizomatous rooting nature of forest herbs, as well as their lack of secondary tissue, greatly increases wilting risk (Weatherley and Slatyer 1957, Kennedy and Booth 1958, Poulsen 1996, Whigham 2004, Costa et al. 2005). Similarly, the fact that ground herbs occupy the lowest canopy strata in forests makes them highly dependent on spatially variable and transient solar events such as sun flecks (Chazdon and Pearcy 1991). If herbs partition light gradients more strongly than woody seedlings, we would expect to see higher aggregation such as observed here. In general, interspecific variation in functional traits and life-history strategy may be greater for herbs than for woody seedlings (Whigham 2004). Germination requirements in particular are highly specific and vary among herbaceous species (Bierzychudek 1982, Whigham 2004). Likewise, herbs are highly dispersal limited due to their short stature and small fruit size that limits animal dispersal, leading to greater aggregation.

For both liana and tree seedlings, it is worth pointing out that the lower beta-diversity observed could be due to the fact that these communities have not yet experienced a long enough time interval for environmental filtering effects to become evident. The average lifespans of these growth forms are much longer than for herbs, and it is possible for habitat associations of trees and shrubs to change in strength through time (i.e., from seedling to saplings to adults; Webb and Peart 2000). Indeed, environmental filtering has been shown to strengthen topographic habitat associations over time for both shrubs and trees at our study site (Comita et al. 2007*b*, Kanagaraj et al. 2011). To explore this idea further, we conducted an additional post-hoc analysis on the habitat associations of adult trees found within the same 20 × 20 m quadrats where herbs were sampled. We found that the strength of habitat partitioning was still greatest for herbs, although adult trees did show stronger correlations with both the habitat categories (PERMANOVA results: $F = 7.17$, $R^2 = 0.16$) and to the continuous gradients (Variance partitioning results: adj-$R^2 = 0.15$) than did tree seedlings. This was despite the fact that adult trees were sampled continuously over the 20 × 20 quadrats, while herbs were sampled within much smaller 1 × 1 m subquadrats. Thus, these data suggest that the herbaceous community likely

does sort more strongly along abiotic gradients than do woody seedlings and trees, and that this effect is not simply due to differences in ontogeny. Likewise, Dalling et al. (2012) reported relatively weak habitat associations for adult lianas on BCI. Strong negative distance- and/or density-dependence can also alter spatial distributions by reducing clumping and thereby reducing local scale turnover in species composition. Studies have found strong negative density dependence at early life stages for woody species in the BCI forest (Harms et al. 2001, Comita et al. 2010). However, the role of density dependence in shaping spatial distributions and diversity of herbaceous plants has received much less attention (Comita et al. 2014) and should be a focus in future studies.

Correlations in local diversity among communities

The concept of a linkage between strata (e.g., herbs and trees) is well developed in the temperate literature (see Gilliam 2007 for review), but little to no work on this topic has been conducted in the tropics. Within the BCI plot, sampled quadrats that had high or low levels of richness/diversity, as well as quadrats that had unique species compositions, were not the same for herbaceous and woody communities. At larger spatial scales, positive correlations in richness/diversity between plant habit have been observed in many studies (Gentry and Emmons 1987, Wright 1992, Gilliam 2007). This has been attributed to landscape- to geographic-scale variation in climate and soil fertility that impacts both herbaceous and woody communities in similar ways. This does not seem to be true, however, at the local community scale, suggesting that herbs either respond to resource conditions differently than do woody individuals, and/or that competitive interactions between growth forms limit the ability of each to persist in tandem. A similar result was reported from a subtropical forest in China by Both et al. (2011), although their results come from a much larger study area, and used adult canopy trees (Both et al. 2011). In contrast to herbaceous vs. woody diversity, the positive correlation between tree and liana seedlings suggests that similar processes control their distribution and abundance at these scales. Dalling et al. (2012) showed that for adult trees and lianas, the number of species significantly associated with specific habitat types was strongly positively correlated, likely due to similar light and soil moisture requirements. Our results indicate that these findings hold for juvenile tree and liana seedlings, but not for herbs.

Response to environmental resource and spatial gradients

The strong correlations of herb diversity and composition with habitat type, measured environmental variables, and spatial gradients provide insight into the mechanisms driving high beta-diversity of tropical herbs in the BCI plot. Our results are in contrast to Svenning et al. (2004), who found similar levels of explainable variation in herbs and tree seedling composition on BCI. However, their study focused on a larger spatial scale (the entire 15.6 km^2 island) and they only sampled the presence/absence of the most common herbaceous species. At the local 50-ha scale analyzed here, herbs were found to be more sensitive to variation in both habitat type and measured environmental variables. In particular, the swamp habitat was a more important driver of herbaceous beta-diversity than woody beta-diversity, which we attribute primarily to reduced adult tree densities and higher light levels in the swamp (Harms et al. 2001). Furthermore, the herbaceous community is likely better adapted to the waterlogging and flooding that occurs in the swamp than are woody individuals. Thirteen herb species (19%) were found exclusively within the swamp (in contrast to 6% and 5% for tree and liana seedlings), suggesting that many herb species might be incapable of surviving the dry season in other areas of the plot (see Data S1). Lastly, herbs in the swamp habitat may benefit from reduced intra-guild competition from highly abundant herb species such as *Selaginella arthritica*, which had a 9-fold reduction in cover within the swamp compared to other areas of the plot (Appendix S1: Table S1). The absence of this otherwise dominant species likely relieves competitive pressure for swamp specialists such as *Aechmea magdalenae* and *Commelina erecta*. Herbs also responded more strongly to soil fertility than did lianas and tree seedlings. This was also likely driven by the swamp habitat, which had the lowest soil fertility among the four habitats. In addition to the benefits of the swamp described above, these nutrient poor soils may promote diversity by decreasing overall productivity and thus exclusionary interactions among competing species (Grime 1973). In general, however, the use of soil resources by tropical herbaceous plants is not well known (Lu et al. 2010), and much more research needs to be conducted on this topic.

For all three communities, the amount of variation in the variance partitioning models explained solely by the spatial descriptors can be attributed either to stochastic aggregative processes (e.g., dispersal limitation), or by additional spatially structured environmental variables that were not measured in this study (Legendre et al. 2009, Anderson et al. 2011). For example, explained variation attributed to spatial descriptors may be a result of responses to finer light or soil gradients that were not captured in our dataset (Chang et al. 2013). More detailed light/canopy measurements such as red/far-red wavelengths or sunfleck dynamics may increase the amount of variation attributed to this component (Chazdon and Pearcy 1991). Regardless, it is clear that such deterministic niche processes shape herb assembly at BCI, and that these processes are likely stronger than for woody seedlings. At the same time, we expected dispersal limitation to be strongest in the herb layer. While correlations with spatial descriptors alone do not

necessarily indicate dispersal-assembly (Anderson et al. 2011), the high fraction of herb variation explained by space alone, combined with the fact that understory herbs tend to be weak dispersers, suggests this is likely. However, the dispersal dynamics of tropical understory herbs is not well understood, and future studies of seed dispersal patterns are needed to better quantify the contribution of this mechanism to beta-diversity. Such data could also be compared to existing long-term data on seed dispersal for woody plants on BCI (Muller-Landau et al. 2008).

Conclusions

Our results point to important differences in the structure and assembly of tropical herbaceous vs. woody understory communities. Notably, these findings suggest that different management and conservation strategies may be required for different plant growth forms, even within the same community. For example, management strategies directed at canopy tree diversity and complexity could have important (whether positive or negative) consequences for understory communities. These consequences should be assessed and taken into account in decision-making. It is also unknown what role tropical herbs play in regulating important ecosystem processes such as nutrient cycling and tree regeneration, which is well-documented for temperate forests (George and Bazzaz 1999, Lu et al. 2011). Additional research on this topic would help inform conservation and management decisions.

Lastly, we suggest that herbs are a unique system for elucidating pattern and process at local scales in tropical forests. Despite contributing less to overall biomass and diversity than in temperate regions, tropical herbs still account for a large proportion of total species richness. Life-history strategies among herbs are also more diverse than for trees, so studying trait diversity of tropical herbaceous systems would be highly informative (Bierzychudek 1982, Both et al. 2011). Also, many of the well-known problems of studying tropical tree populations (e.g., long generation times and large size) are much less of an issue with herbs. Thus, important ecological questions such as the role of niche vs. neutral assembly, dispersal limitation, environmental stochasticity, and physiological tolerance, etc., may be better addressed using tropical herbaceous species than trees. Therefore, we suggest that an increased focus on tropical herbaceous communities in plant ecology research be promoted. This could be achieved by integrating the monitoring of herbaceous plants into already existing networks of forest dynamics plots that currently focus on woody plants (e.g., the Center for Tropical Forest Science-ForestGEO network). Inclusion of herbaceous plant studies into existing plot networks would undoubtedly yield new insights into the processes structuring both woody and herbaceous plant communities in diverse forests around the globe.

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