

Woody Plant Species' Habitat-
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Barro Colorado Island and the
Contributing Roles Played by
Biological, Historical, and Random
Processes

Harms

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Woody Plant Species' Habitat-Association Patterns in the Forest on Barro Colorado Island and the Contributing Roles Played by Biological, Historical, and Random Processes

Kyle E. Harms

ABSTRACT. Spatial patterns of species' distributions are often biased with respect to environmental variables, including discrete habitats. Patterns alone, however, cannot uniquely identify the combinations of processes that produced them. Many alternative processes could give rise to positive and negative habitat associations, including a population's history of dispersal limitation and niche-based interactions with the abiotic or biotic environment, possibly owing to habitat specialization. Because of the research infrastructure and detailed species' distributional and dynamic data provided by the 50-ha Forest Dynamics Plot, Barro Colorado Island has been a hub and catalyst for research into patterns of local-scale habitat associations and their underlying causes. Further research into the mechanisms that generate habitat-association patterns will continue to improve our understanding of tropical community assembly, the origins and maintenance of tropical diversity, and the likely future conditions of tropical plant assemblages.

Keywords: community assembly; distribution pattern; habitat association; habitat specialization; niche; pattern; process; spatial autocorrelation; spatial distribution; torus-translation test

When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this!

—Charles Darwin ([1859] 1985: 125)

A great deal of basic science is the description of patterns in the natural world and the pursuit of evidence for the underlying processes that cause, maintain, or modify them. One obvious and intriguing type of pattern is the heterogeneous distribution of individuals from a single population among habitats.

At a given focal scale and moment in time, a plant species' pattern of distribution is biased with respect to a defined habitat if more (or fewer) of its individuals occur in that habitat than expected from a specified null hypothesis. As an example, consider the small tree *Annona glabra* (Annonaceae), which is abundant along portions of the lakeshore of Barro Colorado Island (BCI), but not in the island's interior (Croat, 1978; Einzmann and Zotz, 2024). Divide the 1,560-ha island into 1,000 contiguous, equal-area grid cells; dichotomize those grid cells into "shoreline" versus "island-interior" habitats; and A.

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glabra's distribution of stems would be highly nonrandomly positively associated with the shoreline habitat and negatively associated with the island-interior habitat.

Many alternative processes or combinations of processes—operating on a variety of spatial and temporal scales (Levin, 1992)—could have produced an observed pattern of habitat associations (Harms et al., 2001). For instance, a species' realized habitat associations do not necessarily reflect its fundamental niche, defined as the abiotic and biotic environmental characteristics that would allow a population to remain viable (Hutchinson, 1957).

Ammonia glabra may be restricted to BCI's shoreline by virtue of ecophysiological (habitat) specialization—for example, individuals only survive and reproduce in shoreline-habitat conditions. Yet alternative causes and histories of pattern assembly are also possible. A species that was previously distributed throughout the island might later have suffered a population decline, possibly driven by a fatal, host-specific disease that emanated from a mid-island infection but that has not reached the shoreline individuals. A population that established from seeds that floated to BCI from a previously off-island species might be temporarily present only along the island's margins. Although the latter two narratives are unlikely explanations for *A. glabra*'s distribution, they do exemplify alternative, testable, process-based explanations for a biased distribution pattern of habitat association.

Based on their population-dynamic properties, McPeck (2017:10) described four means by which a species could cooccur with heterospecifics in a given community (or habitat): “coexisting, neutral, sink, and walking dead” (to which we could add “transiently passing through,” especially for mobile taxa). To coexist with other species requires persistence, but the other possibilities do not assume this threshold level of habitat suitability. A useful complement to mechanisms for presence in a given habitat consists of the mechanisms for absence, such as dispersal limitation, establishment limitation, and their components (Muller-Landau et al., 2002). The species clothing Darwin's entangled-bank habitat are present, whereas other species are absent, because of the deterministic, niche-based, selective influences that Darwin probably primarily imagined, as well as various historical influences of chance and dispersal, as Hubbell (1979, 2001) and others have suggested (Connell, 1978; Velend, 2016).

In this chapter, I review research on habitat associations of woody plants on BCI, and the mechanisms that underlie these associations. I begin with early research describing plant distributions among habitats, followed by the development and application of the torus-translation test for nonrandom associations with discrete habitat types. I then selectively summarize subsequent research on habitat associations involving additional types of tests, continuous environmental variables, and other research sites. Finally, I describe research on the processes underlying observed habitat associations. I close with a discussion of directions for future research.

EARLY RESEARCH ON HABITAT-ASSOCIATION PATTERNS OF TREES AND SHRUBS ON BCI

A great deal of botanical, ecological, and evolutionary interest in BCI's plants and vegetation patterns have blossomed since biologists first began visiting the island. Standley (1927) published the first BCI flora; Kenoyer (1929) carried out the first phytosociological study of the island; and Enders (1935) produced BCI's first vegetation map. Knight (1975) calculated the first ordination for some of BCI's woody taxa and interpreted the phytosociological patterns with respect to habitats defined by forest age (young versus older), soil type (Frijoles clay versus gley), and underlying bedrock (four categories from Woodring, 1958; Yavitt, 2024; Yavitt et al., 2024).

The establishment of the BCI 50-ha Forest Dynamics Plot (FDP) in the 1980s created an unprecedented resource for documenting and analyzing spatial distributions of individual plant species (Detto, 2024; Hubbell et al., 2024). The resulting data include the location (to 0.1 m) and species identity of every stem with a diameter at breast height (dbh) of 1 cm or larger in the entire 1,000 × 500 m area. During the nascent development of the FDP, Hubbell and Foster (1983:28) drew “qualitative conclusions” (i.e., without applying statistics) about edaphic and topographic habitat associations from the initial census of large stems (>20 cm dbh). Most species had patchy distribution patterns, several of which appeared to be biased with respect to three “major habitats”: steep slopes, uplands of the plateau, and flats. Hubbell and Foster (1986b) followed up with chi-squared tests of association for species with ≥10 stems ≥1 cm dbh distributed among slope, plateau, streamside/ravine, and swamp habitats.

In their milestone perspective on the biological, historical, and random processes that pattern and maintain diversity in the forest on BCI, Hubbell and Foster (1986a) inferred habitat specialization from patterns of habitat association. They specifically mentioned guilds of “pioneers” and “edaphic and topographical specialists.” Other chapters in these BCI centennial volumes concern potential gap specialists or pioneers and their associations with canopy gaps (Brokaw, 2024; Dalling, 2024; Dent and Ely, 2024).

DEVELOPMENT AND APPLICATION OF THE TORUS-TRANSLATION TEST OF HABITAT ASSOCIATIONS

When I began my graduate research on BCI in the early 1990s, all assessments of associations between plants and environmental features that had been done for BCI were either non-statistical descriptions or relied on statistical tests that assumed each stem could be treated as an independent entity (e.g., chi-squared tests). These approaches are useful for some purposes—for example, to describe where fruits are available to frugivores. The locations of different stems of the same species, however, are generally not independent. More generally, to understand

why plants are distributed the way they are, or to predict their occurrences (e.g., Caillaud et al., 2010), it is useful to recognize that processes other than niche-based habitat sorting may contribute to an aggregated population pattern, to consider how multiple processes combine to assemble distribution patterns, and to employ tests that potentially partition the influences of those processes.

Seed dispersal distributes plants' seeds away from the mother plant (Augspurger, 2024; Beckman et al., 2024; Howe, 2024), but dispersal in tropical woody species is generally limited, such that conspecific stems are aggregated, and density (number of individuals per unit area) is spatially autocorrelated (Condit et al., 1992, 2000; Hubbell et al., 1999; Muller-Landau et al., 2004, 2008). Habitat variables are also generally spatially autocorrelated (Bell et al., 1993). In habitat-association analyses that aim to help us understand why plants are distributed as they are, we would like to know whether a statistical cross-correlation or association between the two spatially autocorrelated patterns (the spatial patterns of density and habitats) results from habitat-specific effects on species performance, or for other, potentially spurious, reasons. Yet cross-correlation of two spatially autocorrelated patterns elevates the type 1 error rate; in other words, false significant associations are likely to appear (Clifford et al., 1989).

To factor the spatial aggregation of stems into habitat-association assessments, I developed the torus-translation test (Harms, 1997). While on BCI, I often worked in the evenings in the Center for Tropical Forest Science (CTFS) office on the third floor of Yellow House (a building long since demolished). One evening, I was thinking about habitat associations and better ways to test for them, while looking at printed maps of species' distributions on the FDP. As I held a printed map in my hands, I noticed that by rolling the paper map into a tube and thereby bringing the northern edge of the map to abut the southern edge, I could continuously translate the intact habitats of the plot north or south within plot boundaries that remained fixed in space. I could also bend the tube-map into a donut shape, thereby uniting the eastern and western boundaries, which allowed me to translate the intact habitats east or west. Without knowing it at the time, I had discovered for myself the torus and realized it would be a useful device for generating expected patterns for habitat-association analyses. My torus-translation test evaluates whether the spatial pattern of a species' population is distributed with respect to habitats as expected by chance, and not whether the individuals are distributed entirely at random among habitats. This is a bit like matching a paw to a track in the mud on a BCI trail to identify the track's maker—when the shapes match, a causal relationship is more likely.

We divided the BCI FDP into seven discrete habitat types, defined by a combination of topography, hydrology, and forest age (Harms et al., 2001; Fig. 1). We translated the habitat map many times about a torus, while keeping the tree map fixed in space. Decoupling the habitat map from the tree map allowed us to generate many values for our metrics of habitat

association (density or relative density per habitat) under the null hypothesis of random associations between the two. We then compared observed values of the metrics with the frequency distributions from the torus randomizations to test whether observed values were extreme relative to expectations. Out of 171 species, each with ≥ 65 stems ≥ 1 cm dbh in the 1990 census, 64% had one or more significant habitat associations (Harms et al., 2001; Fig. 2).

One means by which to judge whether 64% surpasses random expectations employs false habitat maps. I inverted, reversed, and inverted-plus-reversed the BCI FDP habitat map to generate the three false maps that nevertheless perfectly maintain habitat shapes, sizes, and contiguities (Fig. 1). I overlaid the true tree map on each of these false habitat maps, and reran the entire set of torus-translation tests for species' habitat-associations to generate an expected overall level of habitat association between the observed trees and the false habitat maps. For the 171 species, the three false maps resulted in 73 (41%, inverted map), 53 (30%, reversed map), and 72 (41%, inverted-plus-reversed map) species with significant habitat associations. The false-map average was 37%—more than 40% fewer than for the true habitat map (64%). Chance alone cannot account for patterns of habitat association on the BCI FDP.

FURTHER RESEARCH DOCUMENTING HABITAT-ASSOCIATION PATTERNS ON BCI AND BEYOND

Subsequent research has expanded on the initial torus-translation analyses of trees on the BCI 50-ha FDP in multiple ways, involving application to more plots, incorporation of continuous environmental data, and development of additional testing methods.

Two additional types of false-map habitat-association tests generate their null hypotheses by simulating many iterations of either false population maps or false habitat maps without torus translations. Plotkin et al. (2000, 2002) developed Poisson cluster modeling methods to simulate false populations with true populations' patterns of contagion. Zuleta et al. (2020) used an iterative amplitude-adjusted Fourier transform method to generate false habitat maps that nevertheless preserved key aspects of habitat spatial structure. Harms et al. (2001) also developed a randomized-habitat-generation technique.

Other habitat-association tests take spatial aggregation into account through autologistic regression that incorporates an autocorrelation term into the statistical model (He et al., 2003), or wavelet analyses to disentangle spatial structure at different scales (e.g., potentially interpreted as small-scale seed-dispersal limitation versus larger-scale niche-based sorting; Clark et al., 2018). Three especially good book-length resources for further details and methods to statistically test habitat association patterns for plants treated as points on landscape maps are Illian et al. (2008), Legendre and Legendre (2012), and Wiegand and Moloney (2014).

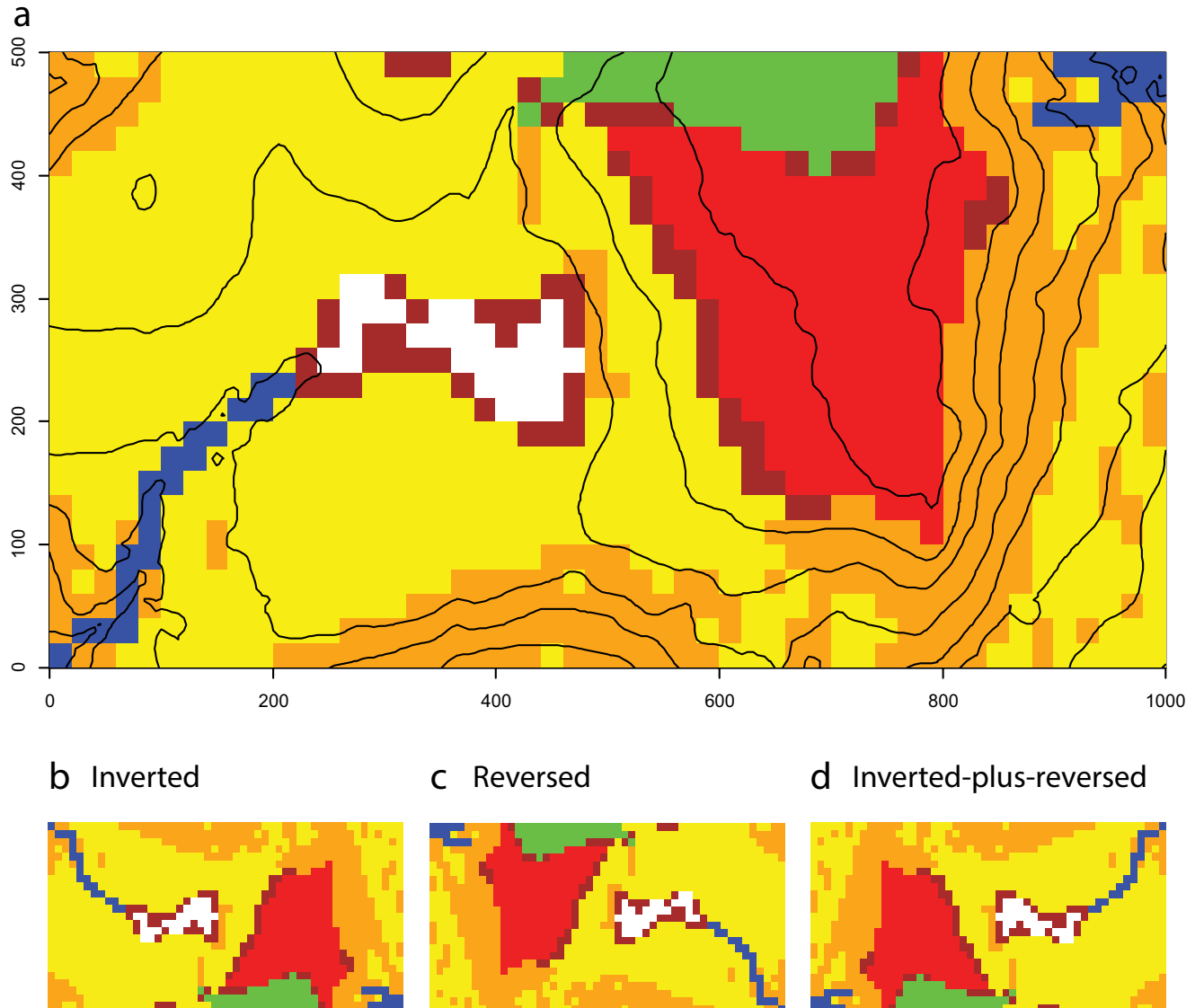


FIGURE 1. Habitats of the Barro Colorado Island (BCI) 50-ha Forest Dynamics Plot, as defined in Harms et al. (2001). Contour lines mark 5-m increments in elevation. The horizontal axis is easting (m); the vertical axis is northing (m). Red = High Plateau; orange = Slope; yellow = Low Plateau; green = Young Forest; blue = Stream; white = Swamp; brown = Mixed. (a) The true BCI seven-habitat map; (b) the false inverted map; (c) the false reversed map; and (d) the false inverted and reversed map.

Several assessments of patterns of habitat association, using the aforementioned techniques with discrete habitat categories, have since been done for other large-scale forest dynamics datasets. This includes an analysis of lianas on BCI (Dalling et al., 2012) as well as multiple studies of trees in other plots in the Smithsonian ForestGEO network, formerly the Center for Tropical Forest Science (e.g., Valencia et al., 2004; Gunatilleke et al., 2006; Yamada et al., 2006; Chuyong et al., 2011). These additional assessments were, in many cases, facilitated

by the availability of my torus-translation test in R packages, previously the CTFS R package (<http://ctfs.si.edu/ctfsdev/CTFSRPackageNew/>) and now as a function (*tt_test*) in the *fgeo* R package (<https://forestgeo.si.edu/explore-data/r-package>).

Research groups have sampled edaphic and hydrologic environmental properties in FDPs, providing continuous variables for comparison with plant distributions. For example, John et al. (2007) sampled soils and used geostatistical kriging to map available elements and other edaphic properties (e.g., pH) of

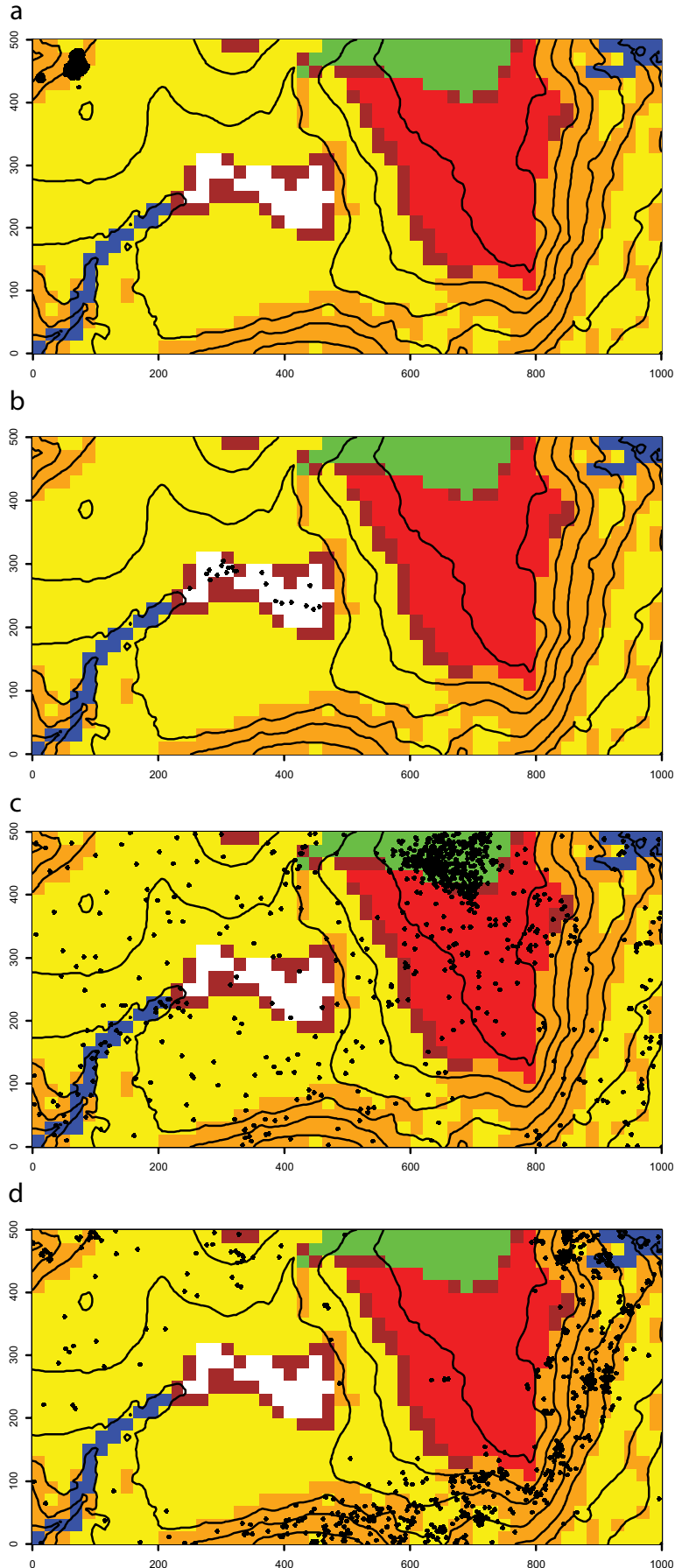


FIGURE 2. Four selected species' distributions with respect to habitats of the Barro Colorado Island (BCI) 50-ha Forest Dynamics Plot (as in Fig. 1). Habitat-association results are from Harms et al. (2001); accordingly, individual tree locations are from the 1990 BCI FDP census. Both axes indicate distance in meters. (a) *Anaxagorea panamensis* (Annonaceae) was positively associated with the Slope habitat according to the chi-squared test, but not according to the torus-translation test; all 589 stems occurred in the northwestern-most hectare (each individual stem is a black point on the map). (b) Although 21 stems of *Elaeis oleifera* (Arecaceae) were too few to conduct the tests using criteria in Harms et al. (2001), all individuals occurred within the Swamp or immediately adjacent Mixed habitat. (c) *Gustavia superba* (Lecythidaceae) was positively associated with the High Plateau and Stream habitats according to the chi-squared tests, but not according to the torus-translation test; and was positively associated with the Young Forest by both the chi-squared and the torus-translation tests—Young Forest results are from the same set of tests, but were not reported in Harms et al. (2001). (d) *Ocotea whitei* (Lauraceae) was positively associated with the Slope habitat by both the chi-squared and the torus-translation tests.

the BCI, La Planada (Colombia), and Yasuni (Ecuador) FDPs. Baldeck et al. (2013b) extended those analyses to community-level patterns, in which we found tree-assemblage species-compositional structure significantly related to soil properties.

In addition to assessments of static patterns of habitat associations, research groups have noted significant changes in FDP habitat associations through ontogeny (e.g., Comita et al., 2007; Kanagaraj et al., 2011; Baldeck et al., 2013a). From habitat-specific temporal floristic changes, Legendre and Condit (2019) suggested that the BCI FDP swamp is drying and being invaded by species previously excluded by seasonal inundation. A variety of larger-scale patterns of habitat association also occur among several BCI taxa throughout the entire island (Garzon-Lopez et al., 2014) and across the Isthmus of Panama (Condit et al., 2013; Condit, 2024).

The take-home message from all of these assessments of habitat association is that an intermediate, but larger than expected, fraction of species have distributional biases (habitat associations). The consistency emerges even though results of these types of analyses depend to some degree on details of the statistical tests (e.g., Harms et al., 2001), user-defined habitat definitions (e.g., Itoh et al., 2010; Zuleta et al., 2020), placement of an FDP with respect to landscape-level heterogeneity, and other factors.

PROCESSES BEHIND THE PATTERNS: POTENTIAL CAUSES OF HABITAT ASSOCIATIONS ON BCI

Insofar as species exhibit nonrandom habitat associations, the obvious next question is: which mechanisms underlie these associations? To the extent that species' distributions are biased because of environmentally determined variation in postdispersal performance, which physiological trade-offs and environmental axes (e.g., water, nutrients) underlie these performance differences? Plant ecophysiology and other endeavors that relate environmental influences to plant traits, physiological or demographic performance, and various trade-offs have grown into an enormous enterprise on BCI. Here, I briefly discuss a few key studies specifically related to woody plant habitat-association patterns. Other chapters in these BCI centennial volumes provide additional examples: for rooting depth, see Andrade and Jackson (2024); for deciduousness, see Bohlman (2024); for drought resistance, see Engelbrecht (2024); for wood traits, see Hietz (2024); for leaf traits, see Santiago (2024); for lianas, see Schnitzer and Carson (2024); and for plant hydraulics, see Wolfe (2024).

Hydrologic-niche differences and variation in water availability appear to shape several relatively common species' distributional patterns on BCI. For 48 native Panamanian tree and shrub species, Engelbrecht et al. (2007) found consistent relationships between experimentally determined estimates of drought sensitivity and habitat association patterns both within the BCI FDP (in which slopes tend to have moister soils) and across the Isthmus of Panama rainfall/seasonality gradient. At both spatial scales, species with lower drought sensitivity were associated with drier habitats, and species with higher drought sensitivity were associated with wetter habitats. Kupers et al. (2019c) generated a detailed hydrologic map for BCI's FDP and found that naturally regenerating seedlings' drought sensitivities were related to species' hydrologic habitat-association patterns (Kupers et al., 2019a, 2019b). Similarly, among selected evergreen tree species on the BCI FDP and across the Isthmus of Panama, plants with lower wilting points were associated with drier habitats (Kunert et al., 2021). Lopez and Kursar (1999) subjected four common BCI trees to experimental flooding and concluded that positive associations with flood-prone habitats (e.g., the BCI FDP swamp) in seasonal forests were associated with tolerance to flooding followed by drought.

Edaphic-niche differences and variation in soil conditions also appear to shape species' distributional patterns on BCI. For 15 pioneer species, seedling growth responses to phosphorus treatments matched expectations based on large-tree distributions with respect to soil-phosphorus across the Isthmus of Panama (Zalamea et al., 2016). Silvera et al. (2003) hypothesized that the two cooccurring morphotypes of *Trema micrantha* (Cannabaceae) partition the soil-nutrient differences between the poorer soils of landslides (exposed mineral soils) and the richer soils of island-interior gaps (Pizano, 2024).

Patterns of phylogenetic or trait dispersion among habitats are often interpreted in terms of habitat filtering and competitive

displacement among taxa (Webb et al., 2002; Cavender-Bares et al., 2004). Several research groups have uncovered significant nonrandom patterns of phylogenetic structure among the FDPs' discrete habitats and continuous-variable environmental conditions (Kembel and Hubbell, 2006; Schreeg et al., 2010; Baldeck et al., 2013c, 2016; Pearse et al., 2013). Just as they do for a plant's interactions with the abiotic environment, traits mediate a plant's interactions with other organisms (competitors, herbivores, mutualists; e.g., Pizano et al., 2011; Kembel et al., 2014; Coley, 2024a, 2024b). These biotic interactions can also shape habitat-specific plant performance and the emergent patterns of species' habitat associations (e.g., Fine et al., 2004, 2006; Endara et al., 2022).

Using a combination of traits and relative abundance changes among habitats through time, Rubio and Swenson (2022) suggested that species within the BCI FDP cluster into functional-group categories, within which ecological drift may be more influential than among those groups. This forest-dynamics narrative echoes Hubbell and Foster (1986a). It is also consistent with an island-wide assessment of the relative roles played by deterministic and neutral processes (Svenning et al., 2004, 2006), from which evidence supported important roles for both niche-based determinism and chance. Even so, a degree of nonrandom within-habitat partitioning is suggested by some negative relationships between trait similarity and spatial associations between pairs of taxa at small, 5-m neighborhood scales within the BCI FDP (Velázquez et al., 2015).

Just as a population's distributional biases among habitats could result from environmental influences on postdispersal performance, seed dispersal could also give rise to habitat associations. Through seed-addition experiments on BCI, Svenning and Wright (2005) found widespread, consequential seed-dispersal limitation among BCI's woody plant taxa, so the potential exists for differential dispersal to cause abundance differences among habitats that run counter to patterns that would otherwise occur under unlimited dispersal. Habitat selection and habitat-related movement patterns of animal seed-dispersers could bias seed deposition (e.g., Schupp et al., 2002; Russo and Augspurger, 2004; Hirsch et al., 2012). In addition, the third trophic level could have an indirect influence on habitat-related seed dispersal. For example, if the landscape of fear generated by ocelot predators (Gálvez and Hernández, 2022) varies among habitats, habitat-specific variation in secondary seed dispersal or predation by agoutis could occur.

FUTURE DIRECTIONS

Many open questions remain concerning the causes and consequences of habitat associations in tropical forests. (1) To what extent do nonrandom patterns of habitat association result from species' niche requirements as expressed through phenotypic traits? For the majority of tropical plant species (especially rare taxa) on BCI and throughout the tropics, we remain ignorant

of the underlying causes of their patterns of distribution, their niche differences and similarities, and how their traits mediate the interplay between environment and demographic performance. (2) How important is habitat specialization to patterns of relative abundance? Futuyma and Moreno (1988) convincingly argued that specialization should be gauged comparatively, and Hubbell (2001: 10) claimed that “no other general attribute of ecological communities besides species richness has commanded more theoretical and empirical attention than relative species abundance,” yet we have almost no idea whether any particular species has the relative abundance value that it does (at any spatial scale) for niche-based (e.g., habitat specialization), mostly chance-based, or other nonniche historical reasons. (3) How important are niche differences (e.g., habitat specialization) for the origins and maintenance of BCI's and the entire planet's species diversity? We speculate repeatedly that they matter (e.g., Chesson, 2000; Wright, 2002), but we do not know with quantitative objectivity how important they are relative to other drivers (e.g., Janzen–Connell effects; Milici and Comita, 2024). (4) How will species' distributions, relative abundances, and persistence respond to anthropogenic global change (e.g., climate, nutrient deposition, land use)? Better understanding of the mechanisms that underpin current patterns of species' distributions would help predict the nature of changes to come.

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