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Research article

Variation of tropical forest assembly processes across regional environmental gradients

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ABSTRACT

Determining how the relative strength of community assembly processes varies along resource gradients is critical for understanding community responses to environmental change. A key challenge for addressing this issue at regional scales is that environmental gradients typically encompass multiple coupled resource gradients (*e.g.* water, light, soils), which can complicate hypotheses about the drivers of community variation. We used data on functional traits and phylogenetic relatedness to infer assembly processes of tree communities across regional environmental gradients in Puerto Rico.

We censused trees in 24, 0.25-ha mature plots located along a precipitation gradient and on soils derived from two parent materials (limestone and volcanic). In each plot, we quantified abiotic conditions in terms of mean annual precipitation, canopy openness, and soil nutrients. We used three functional traits with relevance for drought tolerance and resource acquisition strategies (wood density [WD], leaf mass per area [LMA], and maximum height [H_{max}]), and a molecular phylogeny, to characterize tree community composition in terms of (i) community-weighted mean trait values (i.e., plot average trait values, weighted by relative basal area), (ii) functional diversity, and (iii) phylogenetic diversity.

Mean annual precipitation was negatively correlated with understory light availability (for plots on both soil types), and soil fertility (among plots on limestone soils). Soil fertility varied substantially between plots on each parent material, and was generally higher among plots on limestone-derived soils. Among the limestone soil plots, which occur on the drier half of the precipitation gradient, increasing mean annual precipitation was associated with lower community-weighted mean WD and LMA, and taller H_{max}. Additionally, functional diversity (of WD and H_{max}) and phylogenetic diversity increased with precipitation among limestone soil plots, suggesting an important role for abiotic filtering in driving functional and phylogenetic convergence in arid conditions. In contrast, we did not find significant relationships between environmental conditions and community-weighted mean traits or diversity metrics among plots on volcanic-derived soils, which occur along the wetter half of the precipitation gradient.

Together, our results suggest that drought tolerance is the dominant assembly mechanism controlling tree composition in dry forests. In wetter forests, functional diversity appears to be maintained by a combination of hierarchical competition for light and niche partitioning. Overall, our results exhibit geographic variation in the mechanisms governing composition of tropical forests across regional environmental gradients, and highlight the importance of considering complex environmental gradients at large spatial scales.

1. Introduction

Determining how the relative strengths of community assembly processes vary along resource gradients is a central goal in ecology (Weiher et al., 2011; Whittaker, 1967). Addressing this

Abbreviations: CWM, community-weighed mean; $SES.MPD_{FUN}$, standardized effect size of mean pairwise functional distance; $SES.MPD_{PHY}$, standardized effect size of mean pairwise phylogenetic distance; WD, wood density; LMA, leaf dry mass per area; H_{max}, maximum height; PIC, phylogenetic independent contrasts.

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issue across regional scales in natural systems is critical for understanding how environmental change will alter the composition of ecological communities. One major challenge, however, is that broad scale environmental gradients typically encompass multiple coupled resources (e.g. water, light, soils), which can complicate hypotheses about the drivers of community variation.

Plant functional traits can provide insight to the physiological mechanisms that link assembly processes with patterns of community composition (Bernard-Verdier et al., 2012; Mason et al., 2012; McGill et al., 2006). An important step for interpreting functional patterns as evidence for community assembly processes, however, is to identify the physiological mechanisms that link various functional traits to particular assembly processes. For instance, the concept of abiotic (or 'environmental') filtering implies a selective pressure for traits that confer conservative resource-use strategies under low resource conditions because species with acquisitive life history strategies are unable to persist (Reich, 2014; Weiher and Keddy, 1995). In drought-prone environments, high wood density (WD, $g\,cm^{-3}$) confers a survival advantage for trees because it is associated with greater resistance to drought-induced xylem cavitation (Chave et al., 2009; Hacke et al., 2001). Leaf traits associated with low water loss through transpiration (e.g., high leaf dry mass per area, LMA = 1/SLA, $g\,m^{-2}$) also reflect tolerance to limited water availability (Poorter et al., 2009; Wright et al., 2001). In wetter conditions, traits that confer 'acquisitive' strategies associated with rapid resource acquisition and exploitation may be favored via competitive dominance hierarchies (Kunstler et al., 2016). For instance, rapid growth and tall stature can confer competitive dominance for light capture that may become a stronger determinant of community composition as water availability (and productivity) increases.

Interactions among resource gradients can, however, complicate these relatively straightforward predictions (Fig. 1). For example, higher annual precipitation is generally associated with higher net primary productivity (NPP; Chapin et al., 2002; Zhao and Running, 2010) and a concomitant reduction of understory light availability (Bazzaz, 1979; Bazzaz and Pickett, 1980). Because plants' water and carbon economies are inextricably linked, a negative relationship between water and understory light availability may lead to different hypotheses about functional strategies that should be favored at opposite ends of the gradient (i.e., drought tolerance vs. shade tolerance). Meanwhile, precipitation can also influence soil nutrient availability: higher precipitation is related to higher rates of soil leaching (Austin and Vitousek, 1998; Radulovich and Sollins, 1991; Schuur and Matson, 2001) but higher NPP can also be related to greater nutrient inputs via rapid litter recycling. Moreover, soil nutrient availability has been shown to interact with light availability to mediate plant performance (Russo et al., 2005). Disentangling the joint influences of such coupled gradients is essential for understanding the drivers of community composition at large spatial scales.

To date, the most prominent hypothesis in functional (and phylogenetic) community ecology is that relatively strong competitive interactions in areas of high resource availability should lead to high local diversity as a result of niche partitioning (Kraft and Ackerly, 2010; Mason et al., 2013; Muscarella et al., 2014; Swenson et al., 2006). In terms of coexistence theory (Chesson, 2000), this hypothesis emphasizes the role of interspecific niche differences in maintaining local diversity. In contrast, however, competitive dominance hierarchies can also constrain the local diversity of traits that mediate fitness differences among species (Grime, 2006; Kunstler et al., 2016, 2012; Lasky et al., 2014; Mayfield and Levine, 2010; Navas and Violle, 2009). This scenario can result in the opposite pattern whereby functional (and potentially phylogenetic) diversity declines with increasing resource availability. In fact, Navas and Violle (2009) proposed that local functional diversity should

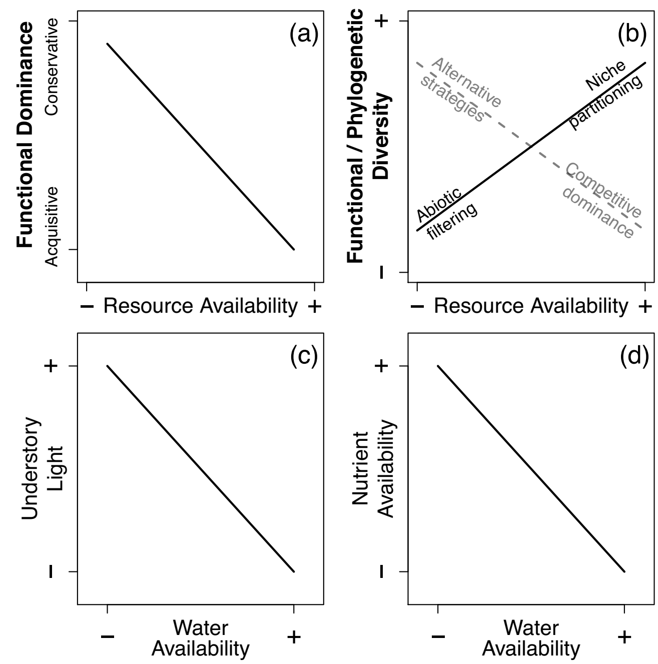

Fig. 1. (a) Theory and empirical results suggest that under low resource conditions, communities should be dominated by species with traits associated with conservative strategies (e.g., high WD, LMA and low H_{max}). Under high resource conditions, in contrast, species with traits associated with acquisitive strategies (e.g., low WD, LMA and high H_{max}) should dominate. (b) An often hypothesized shift in the relative importance of abiotic filtering to niche partitioning as the dominant assembly mechanism leads to the prediction that functional diversity should increase along a gradient of resource availability (solid line in (b)). However, competitive dominance hierarchies and alternative strategies to cope with abiotic stress can lead to the opposite pattern (dashed line in (b)). Note that panel (b) assumes that relevant functional traits are phylogenetically conserved (see Introduction). Complicating these hypotheses about plant functional responses is the fact that, particularly at broad spatial scales, environmental gradients often comprise multiple axes of variation. For instance, we expect both (c) understory light availability and (d) nutrient availability to be negatively correlated with mean annual precipitation.

be highest in sites where the importance of resource competition for structuring communities is intermediate because traits that convey both stress tolerance and competitive dominance would represent viable life history strategies. According to this hypothesis, communities that are very strongly influenced by either abiotic stress or competitive interactions are expected to display relatively low functional diversity (Grime, 2006; Mayfield and Levine, 2010).

Contemporary patterns of functional community composition reflect the combined effects of the assembly processes described above (i.e., abiotic filtering and niche partitioning) as well as biogeographic history. Analysis of the phylogenetic diversity in local communities can help clarify the degree to which functional patterns observed today result from shared ancestry versus convergent evolution to similar environmental conditions (Cavender-Bares et al., 2009; Muscarella et al., 2016). Combining metrics of functional and phylogenetic community composition can offer under-exploited insight to the links between resource availability and (contemporary and historical) assembly process across environmental gradients (Fig. 1a; Bernard-Verdier et al., 2012; Cornwell and Ackerly, 2009; Mason et al., 2012; Muscarella et al., 2016; Spasojevic and Suding, 2012; Weeks et al., 2016).

We quantified functional and phylogenetic aspects of forest composition across regional environmental gradients on the island of Puerto Rico defined by precipitation, soil fertility, and understory light availability. To disentangle the processes structuring tree