



## Evidence for trait-based community assembly patterns in hardwood hammock forests

SURESH C. SUBEDI <sup>1,2,†</sup> J. AARON HOGAN <sup>3</sup> MICHAEL S. ROSS,<sup>1,4</sup>  
JAY P. SAH,<sup>4</sup> AND CHRISTOPHER BARALOTO<sup>3</sup>

<sup>1</sup>Department of Earth and Environment, Florida International University, Miami, Florida, USA

<sup>2</sup>Wetland and Aquatic Center, USGS, Gainesville, Florida, USA

<sup>3</sup>International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, Florida, USA

<sup>4</sup>Southeast Environmental Research Center, Florida International University, Miami, Florida, USA

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**Abstract.** The hardwood forests of south Florida, commonly referred to as hammocks, persist as well-drained patches of broadleaf forest, embedded in a matrix of brackish water swamp, freshwater marsh, or pineland. Little is known about the patterns of community assembly of these subtropical forest communities in the landscape mosaic of south Florida. We used a functional trait approach to understand the composition of these communities and their responses to environmental variation across four areas of south Florida: the pine rocklands and freshwater marshes in Everglades National Park, and the lower and upper Florida Keys, where the hammocks are surrounded by halophytic swamp communities. These sites represent an environmental gradient from less-productive, more xeric sites in the lower Florida Keys, to more-productive, wetter sites in the Everglades marshes. We examined the patterns of trait variation at three levels (individual, population, and community) to examine the underlying processes driving assembly in these hammock communities. To understand processes governing community composition in each site, we used methods that partition variance in six traits (maximum tree height, specific leaf area, wood specific gravity, leaf nitrogen, leaf phosphorus, and leaf stable carbon isotope ratios) into internal and external filtering components. Community-weighted mean trait values for three traits (specific leaf area, height, and leaf phosphorus) increased significantly from dry, less-productive coastal sites in the Florida Keys to the moist, more-productive areas on the mainland, while wood specific gravity and leaf  $\delta^{13}\text{C}$  showed the opposite pattern. For one or more traits per site, standardized effect sizes differed significantly from null expectation. Processes such as competition for resources (e.g., water, nutrients, light) and species sorting across microhabitats (i.e., within site) operate to increase local functional trait variation within communities and among species across sites. External filtering on individuals for height and leaf phosphorus differed significantly from null expectations across sites, while external filtering on species was only observed for specific leaf area, maximum tree height, and leaf phosphorus. These results are consistent with strong environmental filtering across the region, among local communities differing in freshwater accessibility or that occupy different positions along strong edaphic gradients. Our results confirm the importance of intraspecific variation among species and reflect a high degree of trait plasticity across the environmental gradient.

**Key words:** community assembly; environmental filtering; hardwood hammock; internal filtering; south Florida; *T*-statistics.

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† **E-mail:** subedi.suresh@gmail.com

## INTRODUCTION

Functional trait variations among species have been used to quantify plant community assembly processes across broad environmental ranges, including hemisphere-wide (Swenson et al. 2012), latitudinal (LaManna et al. 2014, Lawson and Weir 2014), or elevational (Enquist et al. 2015, Umaña and Swenson 2019) gradients. Interspecific trait variability may also be driven by local factors, such as gradients in light intensity (Marques et al. 2000), soil water availability (Chaturvedi et al. 2011a,b), species interaction and heterogeneity in resource availability (Moreira et al. 2012), and disturbances (Subedi et al. 2019). Despite the recognition that intraspecific trait variation is the key in explaining a population's resilience to environmental change and an individual's ability to coexist and compete with its neighbors (Albert et al. 2010, Jung et al. 2010, Violle et al. 2012, Siefert et al. 2015), only a few studies have examined the relationship between interspecific and intraspecific trait variability in explaining diversity patterns across local and regional spatial scales (Paine et al. 2011, Hulshof et al. 2013, Le Bagousse-Pinguet et al. 2014). Employing both interspecific and intraspecific variations in community assembly processes has the promise of separating local- and regional-scale drivers of plant community assembly patterns.

If plant functional traits are indicative of environmental filtering processes that shape communities, then their variation across landscape may reflect how they are positioned along a hierarchy of successively finer-scale environmental filters from the regional to local scale (Sommer et al. 2014, Gillison 2016). Identifying the spatial scale and environmental factor that most strongly shapes each functional trait can help to disentangle processes that are most critical to community assembly (McGill 2008). The primary factors that drive trait variation at regional scales include climate, topography, disturbance, (Keddy 1992, Grime 2006, Paine et al. 2011), and dispersal factors (de Bello et al. 2013). In contrast, the main drivers of trait variation at the local scale are competition (Grime 2006) and microenvironmental heterogeneity (Cavender-Bares et al. 2006). Community trait similarity increases with increasing sample size at the

regional scale (Willis et al. 2010) and with increasing size of the regional pool considered (Swenson et al. 2006). Therefore, as the sampling of plant functional traits increases from small to larger spatial scales, we expect communities to exhibit more similar trait values. Conversely, we expect intraspecific variation to increase with increasing environmental variation at the regional scale.

Processes that lead to trait differentiation (e.g., competition) are believed to be most strong at small spatial scales where individuals interact directly. A high degree of trait differentiation due to competition is also expected in highly diverse plant communities, such as in tropical rainforests (Paine et al. 2011, LaManna et al. 2017). In such communities, trait variation is larger among species relative to intraspecific variation, especially at the seedling stage, with similar capacities to capture light, water, and nutrients (Cornelissen et al. 2003). Since inter- and intraspecific trait variability is a product of environmental variation and an interaction between genetic variation or phenotypic plasticity that play major roles in community assembly (Xavier Jordani et al. 2019), traits may also differ in their responsiveness to singular environmental stressors (Lavorel and Garnier 2002). Several studies have shown that communities in regularly disturbed habitats were sorted according to their abilities to tolerate disturbance (de Bello et al. 2005). For example, in water-limited systems, species lacking traits associated with the ability to reduce or avoid water losses, such as specific leaf area and height, are filtered out along gradients of moisture and soil resource availability (Fonseca et al. 2000, Cornell and Ackerly 2009).

Here, we assess the relative importance of local vs. regional environmental filters in community assembly processes in the tropical dry forests of south Florida. These forests, locally referred to as hardwood hammocks, represent a northern edge of the Caribbean biodiversity hot spot (Franklin et al. 2018), and as such may be influenced by the same processes (e.g., environmental filtering, habitat heterogeneity, competition) to shape the distribution of plant species and communities throughout the Caribbean Basin. The hardwood hammock forests of south Florida persist today as patches in broadleaf evergreen forest within a landscape mosaic of urban areas, brackish water

wetlands, freshwater marshes, and pine rockland forests. On the basis of physical, edaphic, climatic, and hydrological conditions, south Florida hardwood communities can be divided into four main areas: pine rockland hammocks in eastern Everglades (pine hammocks), marsh tree island hammocks in central Everglades (marsh hammocks), upper Florida Keys hammocks, and lower Florida Keys hammocks (Ross et al. 2016). These areas differ and are arranged along soil moisture-, nutrient-, salinity-, and storm-related environmental gradients (Appendix S1: Table S1). Trees may become drought-stressed when freshwater is exhausted, and thus, community assembly processes in this environment may be strongly affected by the ability of different species to tolerate/compete for scarce water and nutrients. Trees may feature traits related to fast growth and competitive superiority in marsh hammocks, while trees in stressful environment may be characterized by ability to survive under extreme conditions, that is, stress tolerance. For example, trees may be relatively tall and characterized by high specific leaf area in marsh hammocks, while trees are expected to be shorter, low specific leaf area, high wood specific gravity, and high  $\delta^{13}\text{C}$  in drought environment in lower Florida Keys (Westoby et al. 2002, Poorter et al. 2006, Kraft et al. 2008). Similarly, in nutrient-limited environments, leaf nutrients (such as P and N) are expected to be low, as the nutrients in the leaves generally reflect soil nutrient availability and photosynthesis ability of the species (Subedi et al. 2012).

While studies have examined compositional variation among south Florida hardwood hammocks (Armentano et al. 2002, Ross et al. 2016), no study has addressed trait variation in relation to local- and landscape-scale drivers (Appendix S1: Table S1). To assess the relative strength of local- and landscape-scale processes in patterns of community assembly from the Florida Keys to the Florida mainland, we examined the patterns of trait variation at local and regional scales and considered the underlying processes driving those patterns in south Florida hardwood hammock communities. We questioned whether the filtering process varied at local and regional scales along moisture and nutrient gradients. Considering the strong environmental variation across the study area, we

hypothesized that the local environmental conditions associated with each region would provide a unique filter evident in the trait values of the resident species. Moreover, we expected that local-scale filtering would be outweighed by regional-scale assembly processes (i.e., metacommunity differences) in unproductive sites in the Florida Keys and pine rocklands, while local filtering would be a stronger driver in less-stressful environments in the central Everglades. If local-scale filtering dominates patterns of assembly, then trait values will be more different in plots within a region than among regions. However, if regional filtering is strong relative to local-scale filtering, we anticipate a higher trait similarity within regions than between regions.

## MATERIALS AND METHODS

### Study site

The study took place in the Florida Keys and Everglades National Park in the southeastern portion of peninsular Florida. Hardwood hammocks are widely distributed throughout the region, including the coastal barrier islands and Everglades National Park and adjacent areas on the south Florida mainland. In general, these hammocks occupy shallow soil above well-drained limestone substrates and are rarely flooded. Numerous hammocks are embedded in several habitat matrices, including pinelands, freshwater marshes, and coastal wetlands (Fig. 1). In the Everglades, hardwood hammock patches occur as either individual forest fragments surrounded by marsh or as part of a larger forested tree patch, in combination with a range of swamp forest types (Ross et al. 2006). In the latter case, hardwood hammocks usually occupy <1000 m<sup>2</sup> in the heads of the tree islands, while the entire tree island may encompass ten hectares or more. Hardwood hammocks are also a common feature in pine forests dominated by slash pine (*Pinus elliotti* var *densa*), which once occupied uplands throughout the Atlantic Coastal Ridge, but today are most common on Long Pine Key in Everglades National Park. Hardwood hammock forests are common in the Florida Keys, a chain of limestone islands that begins in Biscayne National Park and arcs west–southwest to Key West (Ross et al. 2003). On the Florida peninsula, pine hammocks are typically found

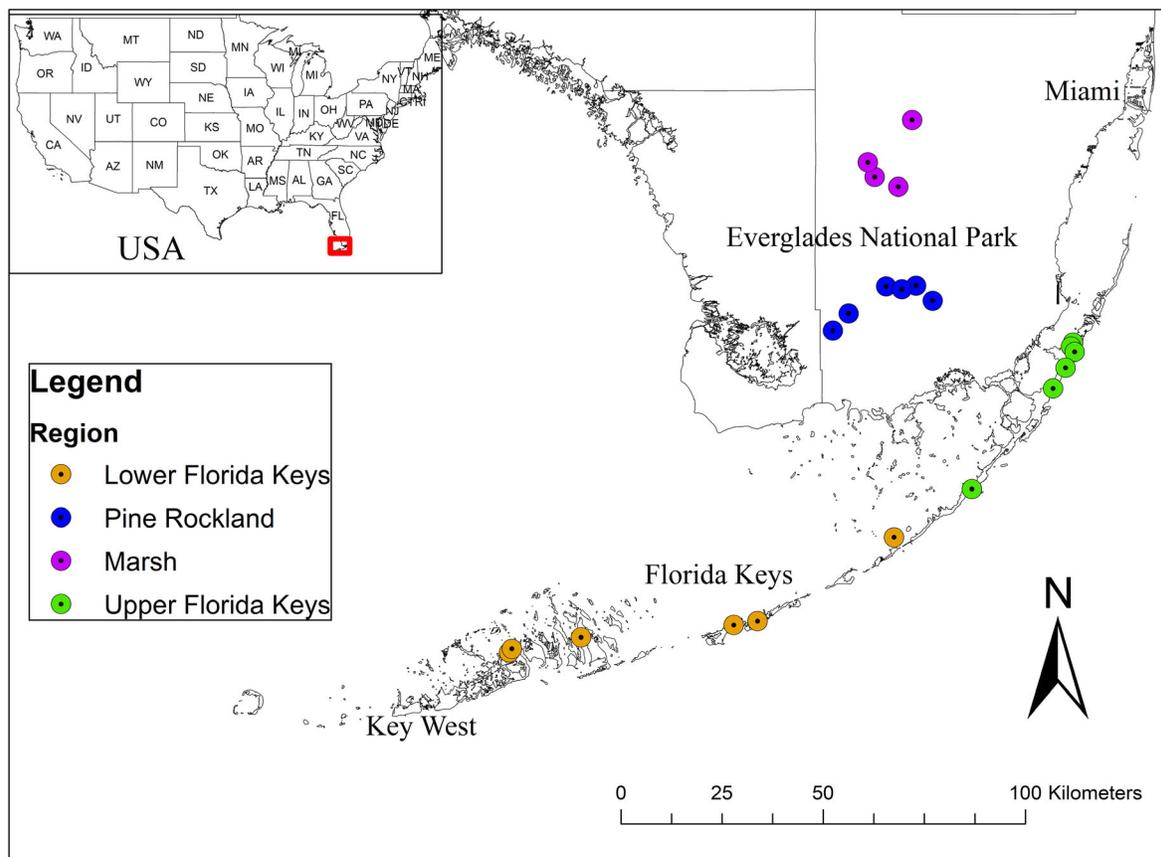


Fig. 1. Study site distribution across four regions (Everglades marsh hammock, pineland, upper Florida Keys, and lower Florida Keys).

on shallow organic soils above well-drained limestone substrates (Ross et al. 2016). Hammocks in the Florida Keys (lower Florida Keys and upper Florida Keys) are found on shallow soils 1–2 m above sea level and on limestone outcroppings. The organic soil layer is typically thin, causing trees to depend in varying degree on groundwater as their water source in Florida Keys and pine rocklands (Subedi 2017). In the Florida Keys, even the water closest to the surface can be brackish, because the porous limestone that forms these islands is extremely permeable, allowing groundwater to mix freely with surrounding seawater (Ross et al. 2003). The marsh hammocks are embedded in the Everglades peatland itself in central Everglades. Such hammocks are rarely flooded, but are rooted in deep mineral soils. For example, soil nutrient availability, particularly phosphorus, is

exceptionally high in Everglades marsh hammocks (Ross et al. 2006, Wetzel et al. 2009) compared with hammock patches in the Florida Keys, whereas elevated groundwater salinity is a stressor for coastal forests in the Florida Keys that is absent in the interior Everglades (Subedi 2017). The Florida Keys are drier than the rest of south Florida, and the variable proximity of marine waters, warmed by passage of the Gulf Stream, adds further climatic heterogeneity across the south Florida region (Moses et al. 2013).

#### *Trait selection*

The study of functional traits has incorporated numerous traits thought to be important in plant performance and which represent relatively independent aspects of plant ecological strategy (Fonseca et al. 2000). We selected six traits based on previous studies in south Florida and the

Florida Keys (Redwine 2007, Subedi 2017) that had identified physiological and morphological characters strongly associated with plant growth and survival in hardwood hammock forest. These traits were as follows: specific leaf area (SLA), wood specific gravity (WSG), maximum canopy height at maturity (height, HT), leaf total nitrogen (N), leaf total phosphorus (P), and leaf stable carbon isotope ratio ( $\delta^{13}\text{C}$  is used as proxy to drought stress in plants). As a group, these traits encompass many of the aspects of woody plant strategy (Westoby et al. 2002, Kraft et al. 2008; Table 1).

### Study design and trait measurement

Twenty-two permanent plots ( $20 \times 20 \text{ m}^2$ ) were established representing four regions of south Florida (Fig. 1). Data from five of these plots, those located in upper Florida Keys, had also been incorporated in an earlier study (Subedi et al. 2019). All trees  $>1 \text{ cm}$  diameter at breast height (dbh) were used to calculate species abundance in the community, but trait

measurements were performed only on mature trees ( $>7.5 \text{ cm dbh}$ ). Tree heights were measured with a telescoping height pole that determined the shortest distance between the upper boundary of the main photosynthetic tissues on the plant and ground level (Pérez-Harguindeguy et al. 2013). Leaf characteristics (SLA, N, P, and  $\delta^{13}\text{C}$ ) and WSG were determined for three individual trees of each species present in each plot, comprising five replicates per tree. Recently expanded sun leaves were sampled when possible, but in cases of understory species, the most illuminated leaves on the plant were selected (Cornwell and Ackerly 2009). Specific leaf area was calculated using freshly collected leaves without petioles (entire leaf for species with simple leaves, leaflets for species with compound leaves); area was measured with a leaf area meter (LI-3000C), followed by oven-drying at  $70^\circ\text{C}$  for 72 h before weighing. Using branch samples, we determined wood specific gravity as the ratio of the oven-dried (at  $100^\circ\text{C}$ ) mass of the bark-removed wood sample (30 cm long) divided by the mass of water displaced by its fresh (green) volume. Carbon isotope ratio ( $\delta^{13}\text{C}$ ), leaf phosphorus content, and leaf nitrogen content were obtained for each leaf measured for SLA. Sample processing for the leaf stable carbon isotope ratios and nutrient analysis was done by drying at  $65^\circ\text{C}$  to constant weight, grinding to a fine powder, and combusting 2–3 mg subsamples in an elemental analyzer (Carlo Erba Reagents, Le Vaudreuil, France) coupled to an isotope ratio mass spectrometer (IRMS Delta Plus; Finnigan MAT, San Jose, California, USA) operating in the continuous flow mode at the mass spectrometer facility at the University of Miami, USA.

### Environmental variables

Extensive environmental data have been collected in our sampling sites over the last 30 yr in South Florida Ecosystem Lab (SOFTTEL; <http://softtel.fiu.edu>; e.g., Ross et al. 2003, Ross and Sah 2011, and Ogurcak 2016). Groundwater salinity, groundwater depth relative to the land surface (relative elevation), total soil depth, soil nitrogen, soil phosphorus, soil pH, and soil organic matter have all been measured. As the systems of south Florida vary little in total topographic relief, these variables constitute a group most likely to vary across the landscape. Among

Table 1. Measured traits and their functional importance

Trait	Functional importance
Height (HT)	Key determinant of competition for resources
Specific leaf area (SLA), leaf area/dry wt	Fast-growing species with cheap leaf construction costs (high SLA) against slow-growing and stress-tolerant species with expensive leaf construction costs (low SLA)
Wood specific gravity (WSG, dry wt/volume)	Fast-growing species with low wood specific gravity against slow-growing but stress-tolerant, that is, high-survival, species with high wood specific gravity
Leaf total phosphorus (P), $\mu\text{g/g}$ dry matter	Important for water and P-limited system such as Florida Keys dry tropical forest
Leaf nitrogen (N), $\text{mg/g}$ dry matter	A significant impact on primary productivity and nutrient cycling in any ecosystem
Leaf carbon stable isotope ratios ( $\delta^{13}\text{C}$ )	An indicator of the set point for leaf gas exchange regulation and reflects leaf-level water use efficiency (WUE) and the overall trade-off between carbon gain and water loss during transpiration

Note: Sources are Westoby et al. (2002), Poorter et al. (2006), Wright et al. (2007); Kraft et al. (2008).

these, soil depth was measured at 20 equidistant locations along a 20-m transect laid out through the middle of the permanent plot by probing to bedrock with a metal rod for all the plots. We acquired ground elevation, soil organic matter, soil nitrogen, soil phosphorus, soil pH, and groundwater salinity data from our earlier studies (Ross et al. 2003, Ross and Sah 2011, Ogurcak 2016), as our permanent plots were established adjacent to transects for earlier studies. Unfortunately, for a few sites (three in the Florida Keys and two in Long Pine Key), similar environmental data were not available. Thus, those sites were excluded from trait–environment relationship analysis. Altogether, 17 sites (four in lower Florida Keys, five in upper Florida Keys, four in pineland, and four in marsh hammocks) were used to represent the environmental gradient across the region. To reduce the dimensionality of the seven environmental variables among the 17 sites and limit collinearity among variables, we used a principal component analysis (PCA) applied to the environmental data matrix.

#### Statistical analysis

We calculated and compared community-weighted means (CWM) for functional traits across sites. Community-weighted mean weight individual trait values by species abundances, thus allowing for the comparison of among sites (Violle et al. 2012, Hulshof et al. 2013). The CWM for a site is calculated as  $CWM_p = \sum_s \mu_i f_i$  where  $p$  is plot,  $s$  is species, and  $\mu_i$  and  $f_i$  are the mean trait value and relative abundance of the species  $i$  as a proportion of total tree density. To calculate CWM per plot, we used relative abundance of the species based on all trees > 1 cm dbh. We used a low diameter limit for calculation of relative abundance because of the widespread importance of small trees in the south Florida hardwood hammock forests, where most tree species rarely exceed 10 cm dbh (Ross et al. 2010). The CWM trait values were then compared among regions, and linear regression analyses were performed to relate CWM trait values to environmental variables.

We used Taudiere and Violle's (2016) trait statistics ( $T$ -statistics), which are based on variance ratios that account for intraspecific variation relative to interspecific variation (Lepš et al. 2011). Since the relative importance of intra- and

interspecific trait variation is a key parameter of species coexistence, these variance ratios can test for internal and external filtering in a given community at different spatial and organizational scales (e.g., individual, species, whole community). In this method, three statistics were calculated for each site: individual-to-community trait variance (individual–community), individual-to-regional trait variance (individual–regional), and community-to-regional trait variance (community–regional, which corresponds to  $T$ -statistics explained by Violle et al. 2012; Table 2). Individual–community trait variance is the ratio of trait variance within a single local population to the total variance across all species in the plot. Individual–regional trait variance is the ratio of trait variance of all individuals in a community to the total variance in the regional pool. Community–regional trait variance, a measure of interspecific trait variance, is the ratio of community-wide species variance to total variance in the regional species pool. Individual–community trait variance measures the strength of internal filters; that is, how strongly local processes such as microenvironmental heterogeneity or density-dependent processes such as competition act on community assembly. In contrast, individual–regional and community–regional trait variance ratios measure the strength of external filters at the individual and species levels, respectively. The individual–community trait variance ratio considers the trait values of all individuals in the community and in the regional pool at the individual level, regardless of species identity, whereas the community–regional trait variance ratios consider species (population) means within communities and the regional pool. When community variance is high in comparison with the total variance, relatively little external filtering (e.g., climatic constraint) is indicated. Conversely, when community trait variances are low, community collectively is strongly filtered by either abiotic stress or environmental filtering.

To determine the statistical significance of each statistic (individual–community, individual–regional, and community–regional trait variances), results from our four geographical regions were compared to null expectations, generated by randomly re-sampled data, and then, the standardized effect sizes (SES) were calculated as

Table 2. Description of the null models used to calculate significance for *T*-statistics (adapted from Taudiere and Violle 2016)

Terminology	Violle <i>T</i> -statistics	Null hypothesis	Randomization	Statistical definition	Statistical explanation
Individual–community	T_IP.IC	No internal filtering: Trait value distribution of all the individuals within a given community does not depend on species identity	Individuals trait values are randomized within the community	$\sigma_{IP}^2/\sigma_{IC}^2$	The ratio of within-population variation (intraspecific trait variation) to within-community variation (intra-site trait variation)
Individual–regional	T_IC.IR	No external filtering acting on individuals: Individual trait value distribution is drawn randomly from the regional pool	Individual trait values are randomized within the regional pool, keeping the number of individuals in each community constant	$\sigma_{IC}^2/\sigma_{IR}^2$	The ratio of within-community-wide (intra-site) trait variation to total (regional) trait variation.
Community–regional	T_PC.PR	No external filtering: Species mean trait value distribution is drawn randomly from the regional pool	Species trait mean values are randomized within the regional pool, keeping the number of individuals in each community constant	$\sigma_{PC}^2/\sigma_{PR}^2$	The ratio of community-wide (intra-site) trait variation to the fixed regional trait means

$$SES = (I_{obs} - I_{sim})/\sigma_{sim},$$

where  $I_{obs}$  is the observed CWM trait value,  $I_{sim}$  is the mean of simulated CWM trait values from randomized data, and  $\sigma_{sim}$  is the standard deviation of these simulated values (Table 2). In our randomizations, we used 999 bootstrap replicates. Statistical analyses were conducted using the *cati* package version 0.99 (Taudiere and Violle 2016), in R version 3.5.3 (R Core Team 2019)

## RESULTS

### *Variation in species and functional diversity along the gradient*

Almost half (44.2%) of the variation in environment among sites was explained by the first principal component (Fig. 2), which had strong correlations with soil depth, soil phosphorus, soil organic carbon, and soil pH (Appendix S1: Table S2). The lower and upper Florida Keys, and pineland sites load on the left side of the axis 1 (Fig. 2), due to lower soil depth and soil phosphorus contents, but higher soil organic carbon. The second principal component explained about 21.1% of the variation in environmental gradient (Fig. 2), with strong contributions from groundwater salinity and soil nitrogen content (Appendix S1: Table S2). The lower and upper Florida Keys sites load on the lower side of the axis 2, that is, *y*-axis (Fig. 2), due to higher

groundwater salinity and lower nitrogen content in the soil than marsh and pine sites. These low-elevation Florida Keys forests may experience water stress because of the proximity of brackish groundwater. The pineland hammocks are distinguished from other sites along axis 2, due to high soil nitrogen, low phosphorus, and fresher groundwater salinity (Fig. 2). In general, the ordination illustrates two main environmental gradients represented by two principal components: one mainly represented by phosphorus, soil organic matter, and soil depth, and second by groundwater salinity and soil nitrogen.

Community-weighted mean trait values showed significant trends along the environmental gradient represented by first principal component of PCA for five of the six tested traits; the exception was only leaf nitrogen (Fig. 3). The CWM of SLA, tree height, and leaf phosphorus increased, while that of WSG and  $\delta^{13}C$  decreased significantly from the dry and low-resource sites in the Florida Keys to the higher resource sites in the marsh hammocks. Community-weighted mean trait values showed significant trends along the environmental gradient represented by second principal component of PCA for only one trait, that is, wood specific gravity (Appendix S1: Fig. S1). The CWM of wood specific gravity decreased significantly from coastal sites in the Florida Keys to the freshwater sites on the Florida mainland.

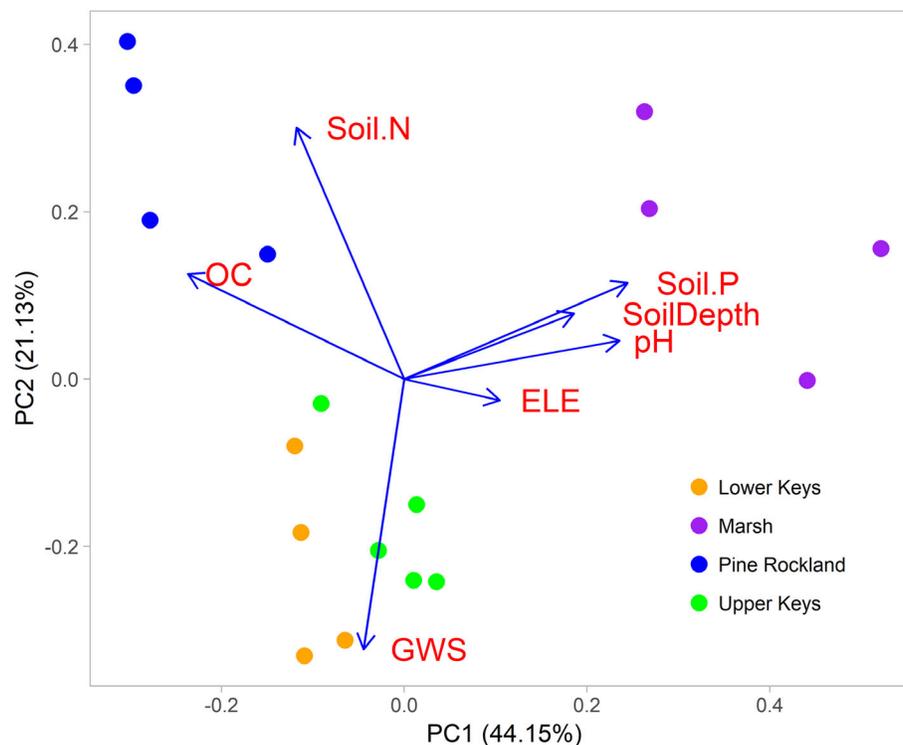


Fig. 2. Site variation across south Florida hammocks. Environmental variables used for PCA are groundwater salinity (GWS), soil depth, soil nitrogen (Soil.N), soil phosphorus (Soil.P), soil pH, soil organic carbon (OC), relative elevation, that is, elevation relative to groundwater (ELE). Each point represents the sites, and colors represent the different regions: Everglades marsh (Marsh), pine rocklands (Pine), lower Florida Keys (LFK), and upper Florida Keys (UFK).

The four regions varied in their CWM trait values (Fig. 4). Community-weighted mean trait values of five of the six measured traits, that is, SLA, height, wood specific gravity, leaf phosphorus, and leaf  $\delta^{13}\text{C}$ , differed across regions. Specific leaf area in lower Florida Keys hammocks was lower than in the other three regions (Fig. 4). Concurrently, marsh hammocks in tree islands of the interior Everglades exhibited low wood specific gravity and high leaf phosphorus (Fig. 4). The very high leaf phosphorus observed in marsh hammocks parallels the exceptionally high soil phosphorus in the tree islands of this region. Leaf  $\delta^{13}\text{C}$  was highest in the lower Florida Keys and most negative in marsh hammocks.

#### Community assembly patterns

The standardized effect sizes of measured CWM functional trait values, in relation to their simulated null expectation, are plotted (Fig. 5).

For all traits, the individual–community trait variance ratios, which reflect within-plot intraspecific-to-interspecific variation, differed significantly from null expectation that signifies the importance of local processes in hardwood hammock community assembly across the gradient. The tests of relative strength of external filtering, both individual–regional and community–regional trait variances, also showed significant differences from null expectations; that is, trees were filtered across regions based on their trait values at both individual and species levels.

The strength of internal filtering decreased toward the very productive marsh hammock sites. In the very stressful sites in the lower Florida Keys, individual–community trait variance was significantly lower than null expectation for all six traits (Fig. 5; Appendix S1: Fig. S2), indicating strong competition among trees within a community. Individual–community trait variance for the

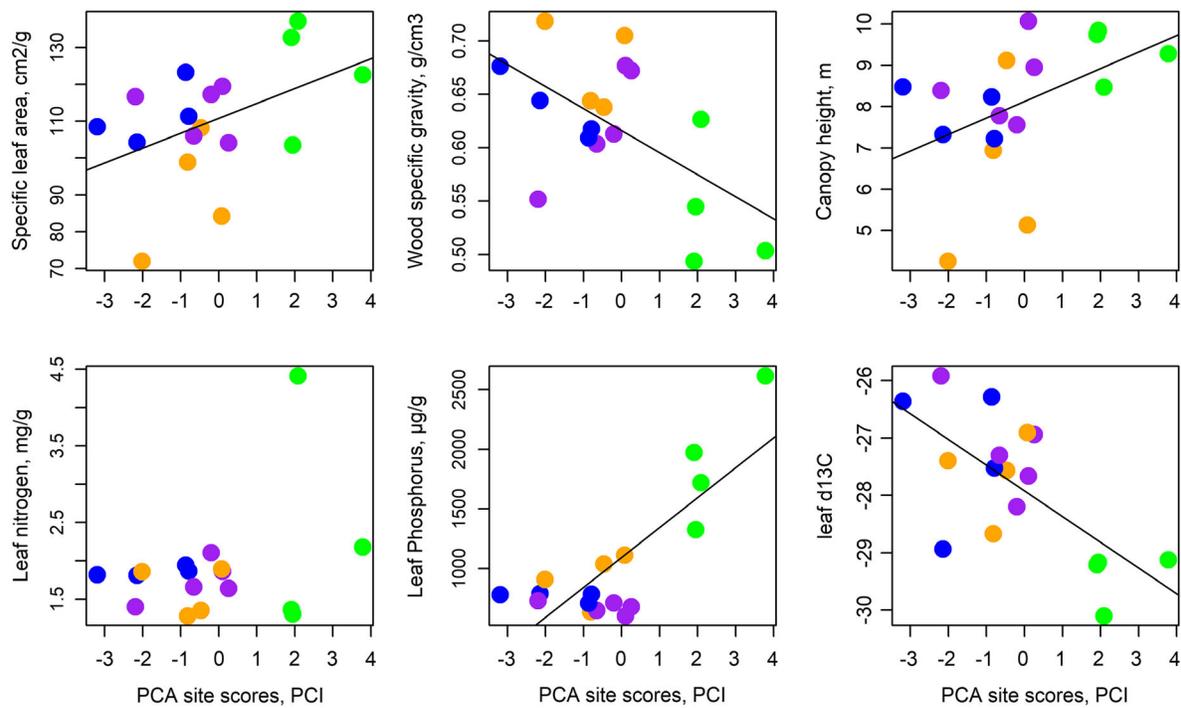


Fig. 3. Patterns of community-weighted mean (CWM) trait values across the environmental gradient represented by PCA loadings (first principal component). Linear regression line is shown only for relationships significant at  $P = <0.05$ . Each point represents the hammock site, and the assigned color for region is the same as in Fig. 2.

other three areas (upper Florida Keys, pine, and marsh) showed significant differences from null expectations for only three traits, that is, SLA, wood specific gravity, and height (Appendix S1: Fig. S2), which indicates that a strength of local processes in community assembly may be decreasing from stressful sites to more-productive sites.

With respect to external filtering, in the lower Florida Keys, individual–regional trait variance differed significantly from the null expectation for three traits (height, SLA, and phosphorus), while the species-level metric (community–regional trait variance) differed significantly only for SLA. It indicates a strong environmental filtering in this region is related to water and nutrient availability. In the upper Florida Keys, significant differences in individual–regional trait covariation metrics from the null expectations were observed for one trait, that is, leaf phosphorus (Fig. 5; Appendix S1: Fig. S2), indicating that environmental filtering in this region is related to phosphorus availability. Similarly,

external filtering in pine hammocks is also related to nutrient and/or moisture availability as individual–regional trait variances differed significantly from the null expectation for two traits (height and leaf phosphorus; Fig. 5). In marsh hammocks, external filtering is indicated by significant difference in individual–regional and community–regional trait variances from null expectations for leaf  $\delta^{13}\text{C}$  (Appendix S1: Fig. S2).

## DISCUSSION

Our analysis of trait variance indicates the importance of local and regional effects of environmental gradients on the functional composition of plant communities in southern Florida. Water and nutrient availability act as environmental filters to select for hardwood hammock assemblages with functional strategies adapted to survive in stressful environments in coastal and pine rockland environments. In contrast, local processes appear to be more important in

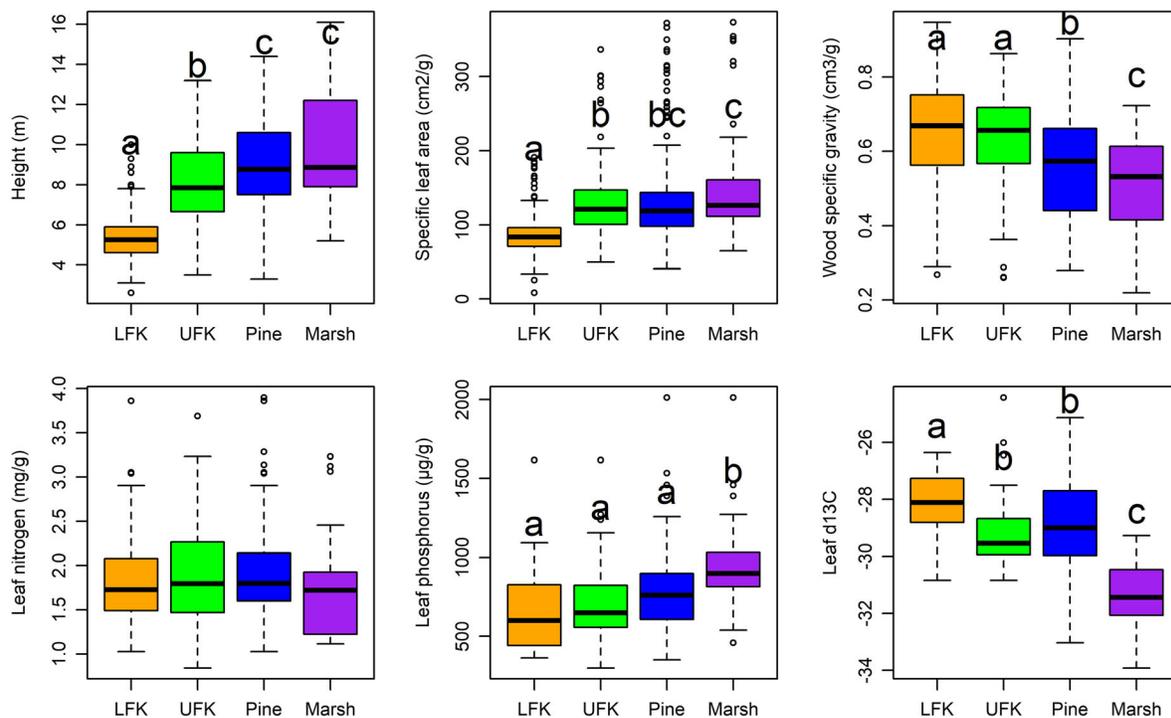


Fig. 4. Trait variation within and across four regions: Everglades marsh (Marsh), pine rocklands (Pine), lower Florida Keys (LFK), and upper Florida Keys (UFK). Labels include the same letter do not differ ( $p < 0.05$ ).

the Everglades marsh sites, where water and nutrients are less limiting.

Generally, abiotic filtering of species occurs along large-scale environmental gradients, while trait dissimilarity is responsible for species coexistence at local scale by competition (Grime 2006). We observed evidence of environment filtering across the broad environmental gradient from more-stressful environments in the coastal Keys and pine rockland communities to resource-rich deep-soil marsh hammocks. For instance, tall species with high SLA and low WSG were selected at resource-rich sites, while short species with low SLA were more abundant at stressful sites (Fig. 3). Furthermore, we found external filtering to act at both species and individual levels, indicating that intraspecific trait variability is important for species functional trait responses to the environment at a regional scale. Moreover, a wide distribution of few species (e.g., *Bursera simaruba*, *Sideroxylon salicifolia*, *Eugenia foetida*, *E. axillaris*) across the whole region provides evidence of a nested metacommunity pattern (Ross et al. 2016), coupled with

high intraspecific trait variation in these species (Appendix S1: Fig. S3). Likely, individuals occurring in resource-rich environments represent a subset of the greater species pool that is otherwise well adapted to survive on the stressful end of the gradient (Ross et al. 2016). Potentially, species may be able to span the gradient because of plasticity in physiological and morphological traits that can provide greater access to resources when they become limiting. For example, some common species that are present throughout the gradients studied here were found to have very high intraspecific variation (Appendix S1: Fig. S3). Their populations likely benefit from intraspecific trait variation because they can adjust to tolerate low-resource environments where plant growth is strongly limited by water and nutrient or light availability. Species that adjust their physiological or morphological traits to take advantage of spatially variable light availability or temporally variable water and nutrient availability in low-resource systems may outperform less plastic neighboring species (Funk 2008, Poorter et al. 2019). Thus, our results confirm the

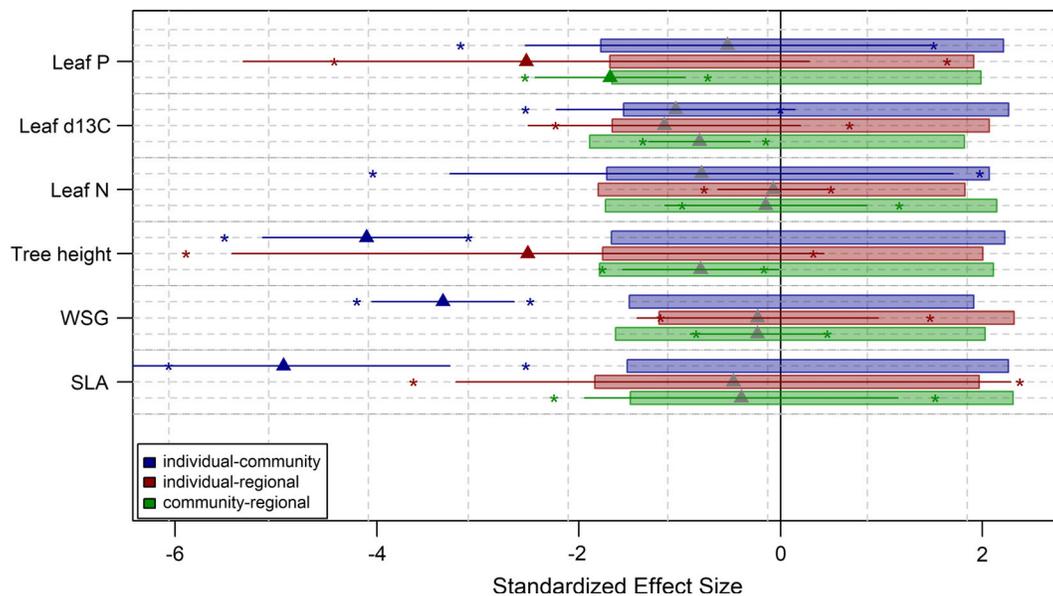


Fig. 5. Standardized effect size (SES) of  $T$ -statistics of six traits: (1) specific leaf area (SLA); (2) wood specific gravity (WSG); (3) maximum tree height (HT); (4) leaf nitrogen (N); (5) stable carbon isotope ratio ( $\delta^{13}\text{C}$ ); and (6) leaf phosphorus (P) across four regions: lower Florida Keys, upper Florida Keys, pine rockland, and Everglades marsh. Each star represents the SES value for one region. The triangles and the segments represent the mean and the standard deviation of the SES values for a given  $T$ -statistic (i.e., mean and standard deviation of regional values), respectively. Boxes delimit the confidence interval of the null model for the whole gradient; thus, for a given statistic, the mean of the SES (star) is significantly different from the null distribution if it is not embedded within the box. Individual–community represents as the ratio of within-population variance to total within-community variance, individual–community represents as the community-wide variance relative to the total variance in the regional pool, and community–regional trait variance represents as the ratio of within-community variance relative to the total variance in the regional pool (see Table 2 for detail).

importance of intraspecific variation especially for species of wider distributions across steep environmental gradients.

Environmental filters may exclude species with combinations of functional traits that are unsuitable at any given site. In the Florida Keys dry tropical forest, community assembly is expected to be driven mainly by freshwater availability (Subedi et al. 2019). As a functional group, the low SLA, high WSG, high leaf  $\delta^{13}\text{C}$ , and short stature of Keys forests suggest that trees in this region are better adapted to drought stress more than trees in other areas. However, studies in dry tropical forest have shown that hurricane winds might filter the species pool for shorter statured taxa, whereas soil moisture and nutrients may only play a secondary role in selecting trees (Van Bloem et al. 2006). Trees are more susceptible to occasional salt water brought

by storm, tide, and wave activities in coastal environments, and salt deposition in soil may occur in hurricane-prone areas such as the Florida Keys. The effect of salt stress is even more pronounced where water availability is limited such as in the Florida Keys forests (Ogurcak 2016, Subedi et al. 2018). Therefore, the ability of trees to survive under salinity exposure, drought, and hurricanes clearly contributes to environmental filtering in the Florida Keys.

Our findings also showed that intraspecific variation was more important than interspecific trait variation in the lower Florida Keys (three traits at the individual level, only one trait at the species level), especially for traits implicated in tolerance of drought, nutrient, and wind disturbances. In the upper Keys, external filtering was based on only one trait, that is, leaf phosphorus at the individual level, indicating that strategies

to survive in this phosphorus-limited environment remain important regardless of species. Resource availability for trees in this region is greater than in the lower Florida Keys hammocks. For instance, our results suggest that trees have more access to nutrients and water with deeper soil, and thus are more productive in this region than in the lower Florida Keys (Ross et al. 1992). However, trees in the upper Florida Keys are clearly phosphorus-limited (Redwine 2007), and the ability to tolerate limited phosphorus availability may determine their persistence in this region. Similarly, in pineland habitats, very shallow calcitic soil (<10 cm depth) might cause trees to suffer drought and nutrient stress. Our observation of strong external filtering on height and leaf phosphorus and evidence of significantly low soil/leaf nutrients and height (Fig. 5) compared to resource-rich sites supports that trees are filtered to these environments on the basis of their strategy to survive in limiting environments. In resource-rich sites, however, external filtering is less important; instead, we found evidence of resource competition among trees, as reflected by internal filtering. Species in this region had very low intrinsic water use efficiency as indicated by very low leaf  $\delta^{13}\text{C}$  (Ellsworth 1999), with trees in marsh hammocks less than half compared to other sites (mean intrinsic water use efficiency 40.72  $\mu\text{mol/mol}$  for marsh hammocks compared to 82.98  $\mu\text{mol/mol}$  for lower Florida Keys; Appendix S1: Fig. S4). Significantly higher water use efficiency in higher groundwater salinity and nutrient-limited environments in lower Florida Keys, and decreasing toward upper Florida Keys and pine rockland and lowest in moist and nutrient-rich freshwater environments in marsh hammocks support that tolerance of drought stress represents an important regional environmental filter for community assembly.

At a local scale, the observed evidence of resource competition among trees within each region was reflected by internal filtering. According to the stress-gradient hypothesis (Maestre et al. 2009), competition would be more intense when abiotic stress is low due to increased resource uptake rates by dominant individuals or species relative to inferior ones. However, our results suggest that internal filtering in the most stressful sites (lower Florida Keys) remains

stronger than in other regions, indicating competition for limiting resources among trees at the plot scale. Competition appears then to have an important role in structuring hardwood hammock communities at the local scale at both ends of the resource gradient. Some resources (e.g., water, nutrients) associated with stressful environments may actually be heterogeneous at the plot scale. In contrast, populations at resource-rich sites outcompete inferior competitors for resources such as light and space. Therefore, biological factors such as neighbor effects in which tree experiences different microenvironments are likely to come into play at this level (Silvertown 2004), resulting in increased functional variation.

In southern Florida, within-site variability in plant traits may result from microtopographic differences produced by physical and chemical erosion, resulting in a rough karst surface characterized by peaks and valleys that can vary by decimeters to meters over very short distances. This variation in microtopography affects access to groundwater and nutrient sources. In addition, treefall accompanying the frequent south Florida windstorms and hurricanes create microenvironmental heterogeneity within a community. On well-drained sites in the lower Florida Keys, where some islands maintain a freshwater lens (Ogurcak 2016), trees at lower elevations may be favored by better access to fresh groundwater than those on higher ground. The observed internal filtering in all six traits demonstrates the strong competition among species at the stressful end of the gradient. Consistent with the lower Florida Keys communities, significant internal filtering was also observed in upper Florida Keys coastal and pine rockland communities but only in three traits (SLA, wood specific gravity, and height), indicating more moderate levels of competition relative to the lower Florida Keys. Nevertheless, it further supports the importance of competition within dry and resource-limited environments such as in Florida Keys hammocks.

The observed internal filtering for a few traits in resource-rich sites may be due to competition; as communities become taller, increased partitioning of light can occur. In high-resource sites such as in marsh hammocks, where moisture and nutrients are more abundant, trees exhibit traits that allow them to grow rapidly in height

(high SLA and low wood specific gravity), supporting earlier observations describing early successional species (Ross et al. 2016, Subedi et al. 2019). Species in Everglades marsh hammocks also have relatively high stomatal conductance (Lin and Sternberg 1992), which likely contributes to their high growth rates. High SLA and low WSG are also associated with fast return on investment in assimilation (Wright et al. 2007, Chave et al. 2009). However, canopy cover in marsh hammocks is relatively high, so light availability at the ground level is relatively limited (S. C. Subedi, *personal observation*). Resource availability is therefore more akin to moist closed-canopy tropical forests (Poorter et al. 2006), where competition for light has been shown to be an important determinant of species coexistence. Therefore, the observed internal filtering through competition in marsh hammocks could relate to competition for light, perhaps affecting species selection during seedling and sapling stages (Spasojevic et al. 2014).

Evidence showed, however, that facilitation may also structure plant communities in stressful environments (Bertness and Callaway 1994, Choler et al. 2001, Kikvidze et al. 2005). Generally, in dry environments, shade from taller trees allows retention of low levels of soil moisture at the soil surface, thereby facilitating the growth of neighbors with shallower roots (Maestre et al. 2009). However, in our case, it seems that stress in the Keys and the pine rocklands is driven by the lack of belowground resources (nutrients and water). Therefore, shifts in the balance of between competition and facilitation with increasing stress along the gradient are less likely.

## CONCLUSIONS

Both local and regional processes contributed to the filtering of species from the regional species pool into local hardwood hammock communities. The important role of environmental filtering across regions was observed primarily because of variation in the belowground environment across these areas. The observed shifts in trait values across the habitat gradient suggest that variation in individual physiology and morphology allows species to respond to different external filters along environmental gradients. Stressful environments in coastal and

pineland hammocks selected species with long-term investments in leaves and wood, while high-resource sites in Everglades hammocks filtered for species with fast-growth strategies. The external filtering process operated mainly on the level of individuals instead of species, and more plastic species exhibited traits most favorable to local environments. Furthermore, at the local scale, community assembly was driven by interspecific competition to acquire limited resources. Our findings reinforce that plasticity in resource use is an important mechanism of trait variation among trees across environmental gradients. Community assembly is most likely influenced by aboveground competition for light at the resource-rich end of the gradient, whereas it appears to be a product of belowground competition and abiotic filtering at the resource-poor end of the gradient, that is, species ability to tolerate extreme conditions. Furthermore, under climate change scenarios, sea level is expected to rise at an accelerating rate and also likely increases the frequency of storm and hurricane activities in coastal areas, which certainly influence local and regional processes of community assembly. Therefore, this study may provide further insight on how local and regional processes constrain community assembly patterns under changing climate scenarios.

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