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Abstract.   We aimed to determine the important functional dimensions that may drive forest succession and community assembly patterns in dry tropical forests. We investigated whether there were patterns in specific functional strategies during succession in the dry tropical forests of the Florida Keys, whose unique physical setting includes nutrient-stressed, salt-stressed, and water-limited environments. The study, which focused on ten traits, determined the leading trait dimensions by which species differentiate from one another in the study area. The general patterns of trait covariation at individual sites and among species were analyzed using principal component analysis. Trait niche overlap indices were calculated for all species sampled across all plots. Evidence for/against likely community assembly processes was tested using the coefficient of heterogeneity to determine whether variation within and among five key traits was clustered, random, or evenly distributed across young, old, or all measured forest stands. A combination of plant architecture, wood density, and three leaf traits (specific leaf area, leaf phosphorus, and leaf nitrogen) comprised a key set of functional traits that are important for understanding the community assembly process in dry tropical forest. Older forest stands were dominated by species with low specific area, low leaf nitrogen content, dense wood, and deeper and narrower canopies. Trees of old forests had leaves with lighter carbon isotope composition, suggesting that such individuals were making more efficient use of scarce water. Tests of trait distributions showed significant clustering across forests of all ages. When individual trait distributions in old stands were tested, they displayed either randomly or evenly distributed traits across trait niche space, indicating that resource partitioning was predominant in shaping community composition. Physical traits of trees in young communities are associated with resource acquisitive strategies, while old communities are dominated by species with traits that enhance survival in environments defined by competition or chronic resource scarcity.

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Introduction

Community assembly represents the outcome of differing strengths of competitive interactions and environmental filtering on a pool of candidate species present in an environment (Spasojevic and Suding 2012). Competitive interactions among co-occurring species are expected to produce at least some dissimilarity (Chesson 2000), while environmental filtering should lead

to high trait similarity among co-resident species (Mayfield and Levine 2010). Functional similarity indicates similar resource use strategies among individuals or species. Species with dissimilar traits should compete less, resulting in ecologically distinct resource use strategies among them. Therefore, the expectation of limiting similarity theory is that co-occurring species will exhibit less functional similarity than would occur by chance alone. In contrast, the environmental filtering concept posits that in stressful environments, species that cannot tolerate the local stressor will be excluded, resulting in a reduction in trait variation among species (Navas et al. 2010). In a few cases, community assembly processes such as facilitation or plant–pollinator interactions can also lead to trait similarity among species in a community (Cavender-Bares et al. 2009, Kraft et al. 2015). In general, these ideas have led to a widespread expectation that trait variation among species is low in regions of strong abiotic stress and increases in regions where competitive interactions are stronger (Spasojevic and Suding 2012). Variation among multiple traits can be considered in the context of the functional niche concept where species are represented by an n-dimensional hyper-volume in functional space and trait niche axes are functions or processes associated with different functional attributes (Rosenfeld 2002).

Succession is a sequential change over time in the relative abundance of dominant species (Shipley et al. 2006). Functional traits can help to define a species' position along a successional chronosequence, since variation along well-documented trait spectra (e.g., specific leaf area, maximum height, or seed mass) has been used to characterize the leading dimensions by which species differentiate from one another (Westoby et al. 2002, Díaz et al. 2016). These changes may reflect functional strategies for reproduction or resource capture (Baraloto et al. 2012). For instance, the high relative growth rates of pioneer species are associated with high photosynthetic capacity and allocation of leaves high in the forest canopy to maximize light interception (Poorter et al. 2006). Moreover, plant traits such as high specific leaf area and high leaf nitrogen concentrations allow pioneers to acquire resources rapidly and dominate the early stages following the disturbance. As succession proceeds, pioneer species are often replaced by species with lower specific leaf area and leaf nitrogen, which grow more slowly but are more efficient at conserving internal resources (Bazzaz 1996). However, some studies have found opposite patterns during secondary succession, such as specific leaf area increasing and wood density decreasing during succession (Lebrija-Trejos et al. 2010, Lohbeck et al. 2013).

Similarly, variation in plant architecture might have important implications for resource capture and survival after disturbance. For example, interspecific differences in height to crown length (Ht:CL) represent different strategies of light capture and diameter at breast height to crown area (dbh:CA) and height to diameter at breast height (Ht:dbh) are associated with structural stability, mechanical strength, and crown support (Sterck and Bongers 1998, King et al. 2006). When exposed to hurricanes or other types of windstorms, variation in such architectural traits may affect the likelihood that breakage will be limited to branches rather than the main stem (Zimmerman et al. 1994). Basal diameter increases with wind exposure in trees of similar height (King 1996), which is particularly relevant in the Florida Keys given the vulnerability to damage exhibited by large individuals of several early-successional species during Hurricane Andrew in 1992 (Ross et al. 2001). High proportions of multiple-stemmed trees are sometimes prevalent in dry tropical forest (Dunphy et al. 2000) and may be related to environmental stresses brought on by limited nutrients, drought, or excess salts, or a consequence of periodic hurricanes that may limit height growth.

Dry tropical forests of the Florida Keys differ from many other forests of their kind due to the wide range of physical limitations they face, including nutrient-stressed, salt-stressed, and water-limited environments (Bussotti et al. 1995, Redwine 2007) and frequent disturbance by storms and hurricanes. The organic soil layer is typically thin, causing trees to depend in varying degree on groundwater as their water source (Sternberg et al. 1991). However, in the upper Florida Keys even the water closest to the surface can be brackish, because the coralline limestone that forms these islands is extremely permeable, allowing groundwater to mix freely with surrounding seawater (Ross et al. 2003). Trees may

become drought-stressed when fresh soil water is exhausted, and thus, our hypothesis is that community assembly processes in this environment are strongly affected by the ability of different species to compete for scarce water and nutrients.

Previous work suggests that the successional-morphological changes in dry tropical forest involve trade-offs between traits enhancing growth in early-successional species—characterized by high specific leaf area, low wood density, and high concentrations of leaf nutrients (consistent with the findings of King et al. 2006)—and traits related to survival in late-successional species, such as long-lived leaves and high allocation to structural compounds, similar to the findings of Navas et al. (2010). While leaf habit alone is sometimes insufficient to distinguish plant functional groups in dry tropical forests, these groupings may be identified through the use of a database that includes other functional traits relevant to acquisition and use of resources (Powers and Tiffin 2010). This paper seeks to identify patterns of expression of important traits (particularly stem, leaf, and architectural traits) along successional gradients in dry tropical forests of the Florida Keys. To our knowledge, this is the first study to examine tropical dry forest succession using the combined approach of measuring changes in relative abundance of species along a chronosequence of forest patches and simultaneously measuring a set of architectural traits which correspond to resource acquisition strategies.

In this study, we assessed 10 traits in 26 species found in dry tropical forest stands in the Florida Keys to address three primary research questions: (1) What are the important trait niche axes among species in dry tropical forest? (2) Is there any pattern in community-weighted mean traits during the successional process in this forest? and (3) What does the important trait niche axes information reveal about the underlying mechanisms that may drive species assembly during forest succession? To address Question 1, we used multivariate analysis to identify a small number of orthogonal trait axes at both species and community levels and to define the level of evidence present to define trait niche axes. To address Question 2, we tracked community-weighted mean (CWM) traits along the successional gradient to determine if such pattern was associated with changes in environmental conditions during the successional process. To address Question 3, we inspected patterns in species niche overlap to evaluate how community assembly processes relate to forest succession in these forest stands. Early-successional species in recently disturbed areas experience severe and distinct environmental filtering, which is likely to structure early-stage development. Environmental conditions (e.g., greater soil depth, or higher moisture or nutrient availability) may become less stressful over time, allowing density-dependent processes such as competition to dominate the later stages of succession. Therefore, we expect younger stands and dominant early-successional species to show similar trait values (higher niche overlap), but as community development proceeds, trait values among coexisting species should become more dissimilar (lower niche overlap).

MATERIALS AND METHODS

Study area

A 15-km stretch of continuous forest in northern Key Largo, including portions of Crocodile Lakes National Wildlife Refuge and Key Largo Hammocks Botanical State Park, comprises the most extensive remaining example of dry tropical forest in southern Florida (Fig. 1). This forest features a diverse mixture of deciduous and evergreen tree species that are predominantly West Indian in origin. Soils are organic and rarely exceed 30 cm in depth. Elevations range from 0 to 5 m above sea level. Mean annual temperature is 25.1°C, and mean annual precipitation is about 1200 mm (Ross et al. 2001). Although occasional lightning fires and frequent windstorms are part of the disturbance regime, the ecological history of these hammocks is strongly influenced by clearance of many stands for farming early in the 20th century, and fires associated with these activities. Aerial photographs indicate that a large portion of the forest has been under cultivation or affected by roads, prospective residential development, oil exploration, or military use since that time (Ross et al. 2001).

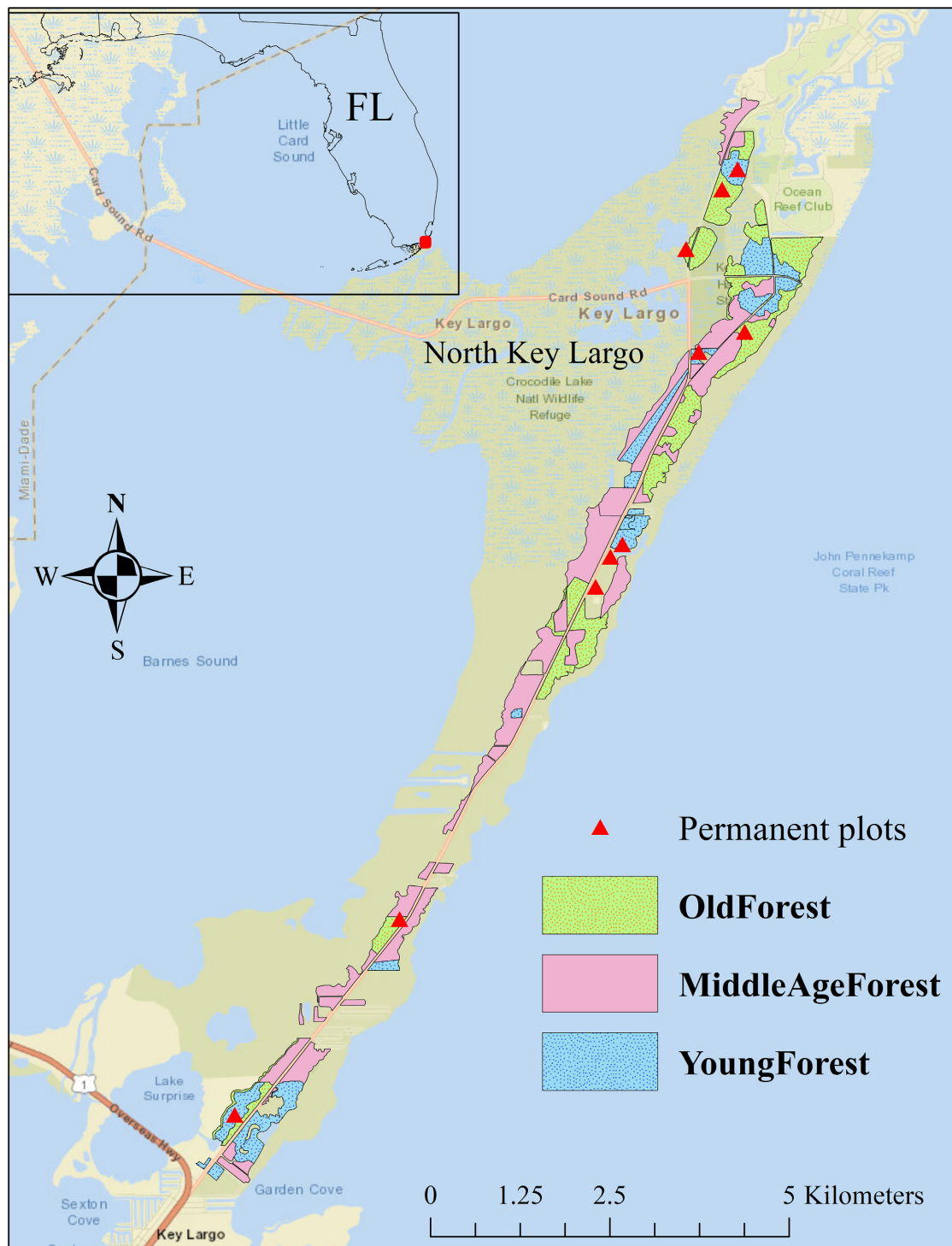Fig. 1. A 15-km stretch of continuous dry tropical forest in North Key Largo with forest age classes and location of plots. Trait data were collected from 20 × 20 m plots established, five in young forest stands (20–30 yr), and five in old forest stands (>100 yr). The year that each stand was cleared was estimated on the basis of the appearance of the site on black-and-white aerial photographs.

Study design

We used two distinct forest sampling approaches in this study. The first sampling approach was initiated in 2014–2015 to address research Questions 1 and 3 (plot-based data). Trait data were collected from ten 20 × 20 m plots: five in young forest (20–30 yr since abandonment, based on serial aerial photographs), and five in old-growth stands, believed to be 100 yr old or more based on aerial photographs (Fig. 1; see the next paragraph for more explanation on stand age). By collecting trait information on 3–5 individuals (mature trees <5 cm dbh) of each species present in each of these plots, we could employ linear mixed models and principal component analysis (PCA) to evaluate trait–forest type relationships for young and old sites, and enhance the strength of our inferences about correlations between traits and successional processes.

The second sampling approach was employed to address Question 2. Forest patches were sampled using transects 60–100 m in length in 23 separate stands (hereafter transect-based data), which were established in 1994 by Ross et al. (2001). In our nested belt sampling design, we recorded species and diameter at breast height (dbh at 1.45 m height) of all trees rooted within 1 m (stems 1.0–9.9 cm dbh), 2 m (stems 10.0–24.9 cm dbh) or 5 m (stems ≥25 cm dbh) of the center line of the transect. Then, we summarized tree species composition, basal area, and density of each transect. Stand age of each transect was obtained from earlier work by Ross et al. (2001) and Diamond and Ross (2016), which was estimated on the basis of historical photographs supplemented by reliable anecdotal information from each site. These stands have not experienced catastrophic disturbance after 1985 and are part of the Crocodile Lakes National Wildlife Refuge and Key Largo Hammocks Botanical State Park. If photographs from all years were not available, the date of stand initiation was estimated as the midpoint between the most recent year a stand exhibited full canopy cover and the latest year when it lacked tree cover. The successional status of tree assemblages in each transect (Appendix S1: Table S1) was already known from a previous study (Ross et al. 2001), in which abundance-weighted species means were determined from a 2013 calibration data set

in which stand ages were estimated as described above. In the Ross et al. (2001) study, stands with no evidence of clearing or fire as far back as the 1926 photograph were arbitrarily assigned an age of 100 yr. To address Question 2, we used transect-based data to examine correlations with species trait data.

Trait selection and measurement

The present study focused on ten traits that we expected to be especially important in dry tropical environments. Six of these traits are either direct measurements of plant tissues (wood density, specific leaf area, leaf nitrogen content, and leaf phosphorus) or indicators of a leaf's physiological function (the molar ratio of nitrogen/phosphorus and carbon stable isotope composition). Four of the ten measured traits describe architectural allometrics of the trees.

Due to its role in determining resistance to wind damage during storm events, and survival from intense droughts, wood density may be an important functional trait in dry tropical forest species in South Florida. Specific leaf area, leaf nitrogen content, and leaf phosphorus are correlated with primary productivity and nutrient cycling in many ecosystems (Aerts and Chapin 1999). Molar ratios of nitrogen and phosphorus in leaf tissues (leaf N:P) are often indicators of nutrient limitation (Koerselman and Meuleman 1996, Subedi et al. 2012). The carbon stable isotope ratio ($^{13}C/^{12}C$), expressed as $\delta^{13}C$, is an indicator of the strength of the diffusive gradient of CO_2 during leaf gas exchange and reflects intrinsic water use efficiency. Water use efficiency defines the leaf-specific trade-off between carbon gain and water loss during the interacting processes of photosynthesis and transpiration (Farquhar et al. 1982). These six characteristics of wood and leaves have been implicated as relevant to successional processes in previous studies (Bhaskar et al. 2014), but not many studies have used a shared sampling design that explicitly tested which ecological scale (site, species, or individual) explained the variability of the measured traits (Auger and Shipley 2013).

The remaining four traits, collectively described as "architectural," have been implicated in other studies as indicators of important life history strategies of dry tropical forest trees, for example, light capture strategies (Bohlman and O'Brien

2006). We tested four architectural traits: the ratios of diameter at breast height to crown area (CA:dbh), height to diameter at breast height (Ht:dbh), and height to crown length (Ht:CL), and the frequency of multiple-stem form.

Methods for measurement of plant traits followed standard methods (Pérez-Harguindeguy et al. 2013). Structural traits (height, height to crown, diameter at breast height, and crown dimensions) were determined for all trees greater than 1 cm diameter at breast height (dbh, measured in cm) in the ten plots. Total height (Ht, the shortest distance between the upper boundary of the main photosynthetic tissues on the plant and ground level, measured in m) and height to crown (first branch from the ground, measured in m) were measured using a telescoping height pole. Two crown dimensions (the longest and its perpendicular) were measured using measuring tapes, and dbh was measured using a tree caliper.

Assuming an elliptical crown shape (Sah et al. 2004), crown area (CA, m^2) was calculated as $CA = \pi((L1/2) + (L2/2))$, where L1 and L2 are the length at its widest point and the perpendicular crown extent at the same height, respectively. Crown length (measured in m) was calculated as the difference between total height and height to crown. Specific leaf area, leaf chemistry (leaf nitrogen, leaf phosphorus, and $\delta^{13}C$), and wood density were determined for 3–5 individuals of each species present in each plot. In rare cases in which there were fewer than three individuals of the species in the plot, we collected from trees near the plot boundary in the same stand. For analytical purposes, nutrient concentrations were expressed per unit leaf area ($\mu g/cm^2$). Six recently expanded sun leaves were sampled per tree, or in cases of understory species, we collected the most illuminated leaves on the plant. Specific leaf area (leaf area per unit mass) 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°C for 72 h before weighing. Wood density was determined for three 1–2 cm diameter branch samples per tree and calculated as the ratio of the oven-dried (at 100°C) mass of the bark-removed wood sample (30 cm long) divided by the mass of water displaced by its fresh (green) volume. All the individual trait values for each species were calculated as the average of the individuals within a plot.

Statistical analyses

Principal component analysis was used to identify a small number of orthogonal traits that defined trait niche axes at both species and community levels. For species-level analyses (Questions 1 and 3), all measured traits were included. At the species level, PCA combined mean trait values for 26 species in ten permanent plots (five in young and five in old forest) which covered about 82% of the total tree species occurred in the whole forest. At the community level, PCA was performed using CWM traits in ten permanent plots. Community-weighted mean of each trait was calculated for each plot as a weighted average of species traits, with weightings based on species' relative abundance (trees <1 cm dbh) in each plot (the same as transect data; see below). We also tested weighting CWM traits by basal area, but the results were similar, and are not discussed further.

To address Question 2, we examined correlations between CWM traits and age of the stands represented by the 23 transects. Community-weighted mean of each trait was calculated for each transect as a weighted average of species traits, average trait value from plot with weightings based on species' relative abundance (trees < 1 cm dbh) in each transect (Hulshof et al. 2013):

$$CWM_t = \sum_s \mu_i f_i$$

where t = transect, s = species, and μ_i and f_i are the mean trait value and relative abundance of the species i (proportion of total tree density). To assess trends identified via CWM, it is necessary to consider whether trait variation resides primarily at the site, species, or individual level. Linear mixed models were used to determine the proportion of the total variance expressed across these three levels among the traits we measured (Table 1). For each species, the total number of individuals sampled in the linear mixed model analyses varied from 36 to 45. The models were fit using the varcomp function of R (R Core Team 2015) with maximum-likelihood estimation, and site, species, and individual tree were specified as random variables for each trait.

Table 1. List of traits and percentage of their variation at three different scales (site, species, and intraspecific).

Trait	Unit	Site	Species	Intraspecific
Specific leaf area, SLA	cm^2/g	<1.0	90.37	9.2
Wood density, WD	g/cm^3	1.9	80.86	17.2
Leaf phosphorus, TP	μg/g	<1.0	20.95	78.6
Leaf nitrogen, TN	%	<1.0	98.88	<1.0
Leaf stable carbon isotope ratio, δ^{13}C	‰	<1.0	96.90	3.0
Leaf N:P	%	<1.0	95.94	3.06
Crown area:diameter at breast height, CA:dbh	m^2/cm	19.2	35.41	45.3
Height:diameter at breast height, Ht:dbh	m/cm	6.8	46.58	46.5
Height:crown length, Ht:CL	m/m	4.2	12.4	83.2

Note: Trait abbreviations and measured units are presented in the first and second columns, respectively.

Niche overlaps (NOs) and null models were computed using the R script provided by Geange et al. (2011). For each trait, a distribution was calculated using a kernel estimator (Mouillot et al. 2005), which is a density function that assumes measurement error around each data point and uses a smoothing function to estimate a distribution of all data for a given trait and community. Overlap is represented as the integral of the intersection of the species' respective kernel curves when overlaid on one another. The species kernels were then used to estimate pairwise NOs in trait space for all the coexisting species. Overlap indices were calculated for three data sets: for all species sampled across the ten plots, and separately for each successional category (young and old). Maximum variance occurs when all NOs are either 0 or 1. To test the community assembly processes, a test statistic (η), that is, the proportion of maximum variance (i.e., the coefficient of heterogeneity), was calculated to determine if the pattern in the data is random (the null model), clustered (η near 1), or evenly spaced (η near 0; Geange et al. 2011). If there are i species and t traits, each trait (as a niche axis) has $x = (i − 1)/2$ niche overlap values, represented as $x_1, x_2, ..., x_t$, with $\bar{x}$ and s^2 representing mean niche overlap and variance.

$$\eta = \sum \frac{s^2}{\bar{x}(1 - x)}$$

Once η is calculated for each niche axis, the average of η over the all trait niche axes gives an overall measure of clustering vs. regularity, or even spacing (Geange et al. 2011). All statistical analyses were carried out using R package version 3.4.1 (R Core Team 2015).

RESULTS

Variation in traits across the ecological scales

For the nine traits for which variances at the site, species, and tree (intraspecific) levels were all estimated (Table 1), linear mixed models indicate that traits varied dramatically across scales. Overall trait variation attributable to site was very low, exceeding 2% for only three architectural traits, in which site variation ranged from 4.24% to 19.22%. Variation was concentrated at the species level in five of the six morphological/chemical variables (specific leaf area, wood density, leaf nitrogen, leaf N:P, and δ^{13}C, above 80%). For five of the nine traits, intraspecific variation among trees occupying the same stand was <20%, while intraspecific trait variation exceeded 40% in leaf phosphorus as well as three architectural traits.

Correlation among species traits

In the species-level analysis of functional traits, the first three axes of the PCA of 10 traits explained 60% of the total variation and eigenvalues >1 (Table 2). Three traits (specific leaf area, wood density, Ht:CL, and multiple stem) were strongly associated with the first axis of the PCA. Leaf phosphorus was strongly associated with the second axis of the PCA, while leaf nitrogen loaded highly on the third PCA axis. Thus, the first PCA axis combined stem, leaf, and architectural traits, while the second and third axes were strongly related to leaf nutrient concentrations. On the basis of the contribution of traits to the first three principal components, specific leaf area, wood density, leaf nitrogen, leaf phosphorus, multiple stem, and Ht:CL shape the most important trait niche axes among the species found along the successional gradient.

In the community-level analysis of CWM traits, the first two principal component axes explained over 90% of the total variation in the sampled data (64.7% of variability in PC1 and 25.6% in PC2; Fig. 2; Appendix S1: Table S2). As in the species analysis, traits associated with Axis 1 were specific leaf area, wood density, and Ht:

Table 2. Principal component analysis results based on 26 species and their mean trait value.

Trait	Comp. 1 (24%)	Comp. 2 (22%)	Comp. 3 (14%)
Specific leaf area	0.46	0.19	<0.01
Wood density	−0.45	0.29	−0.16
Leaf phosphorus	−0.15	0.53	−0.31
Leaf nitrogen	0.18	0.15	−0.65
Leaf stable carbon isotope ratio	0.11	−0.26	<0.01
N:P	0.21	0.59	<0.01
Crown area:Diameter at breast height	−0.12	0.30	0.35
Height:Diameter at breast height	−0.14	0.25	−0.29
Crown length	0.50	<0.01	<0.01
Multiple stem	−0.42	0.12	−0.25

Notes: Trait contribution to the first three components contributed by each factor. Percentage of variation explained by each component is provided in parentheses.
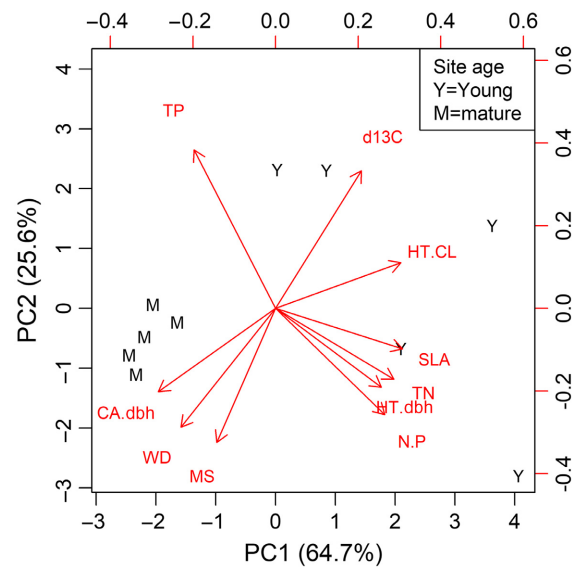

Fig. 2. Community-weighted trait bi-plot for principal component analysis of Key Largo dry tropical forests. The ordination is based on community-weighted mean traits, with traits weighted for each species by its relative abundance in the community. Trait abbreviations are given in Table 1.

CL, as well as leaf nitrogen and CA:dbh. Sites were grouped based on stand age along the first principal component axis, with young and old sites well separated on the *x*-axis. However, old sites grouped closely together, while young sites were scattered along the *y*-axis, which represented leaf phosphorus, $\delta^{13}C$, percentage of multiple stem, and Ht:dbh (Fig. 2).

Pattern of trait variation during the succession

Linear regression analyses between CWM traits and stand age showed significant trends along the successional gradient for all traits except leaf phosphorus and Ht:dbh (Fig. 3). The CWM of specific leaf area, leaf nitrogen, leaf N:P, $\delta^{13}C$, and Ht:CL decreased with increasing stand age, while wood density, multiple-stem frequency, and CA:dbh increased significantly from young to old sites (Fig. 3).

Niche overlap between species in important functional traits

Since the species-level PCA showed that specific leaf area, wood density, leaf phosphorus, leaf nitrogen, leaf N:P, multiple stem, and Ht:CL formed the most important niche axes and explained most of the variation among species, we based our analyses of niche overlap on those traits. It is noted that inclusion of multiple stem and leaf N:P traits did not show any significant results and did not change our overall results of

species overlap for any three analyses, that is, all plots, young, and mature; thus, we excluded those traits in community assembly analysis. Analysis of the five traits across 26 tree species considered in the Key Largo dry tropical forest yielded an average local realized niche overlap of 0.39 (0 is no overlap while 1 is complete overlap; Appendix S1: Tables S1 and S3). *Simarouba glauca* was a conspicuous outlier among its associates, exhibiting a niche overlap of only 0.16. *Reynosia septentrionalis* Urb., *Drypetes lateriflora* (Sw.) Krug & Urb., *Ficus citrifolia* Mill., and *Calyptranthes pallens* (Poir.) Griseb. were also notably dissimilar from their associates. Species with high mean NOs were *Sideroxylon salicifolium* (L.) Lam., *Swietenia mahogani* (L.) Jacq., *Metopium toxiferum* (L.) Krug & Urban, and *Coccoloba diversifolia* Jacq (Appendix S1: Table S1).

To answer whether resource acquisition (in response to environmental stress as exemplified by trait convergence) or resource partitioning (in response to competition as exemplified by trait differentiation) predominates in shaping community composition, the proportion of maximum variance (i.e., the coefficient of
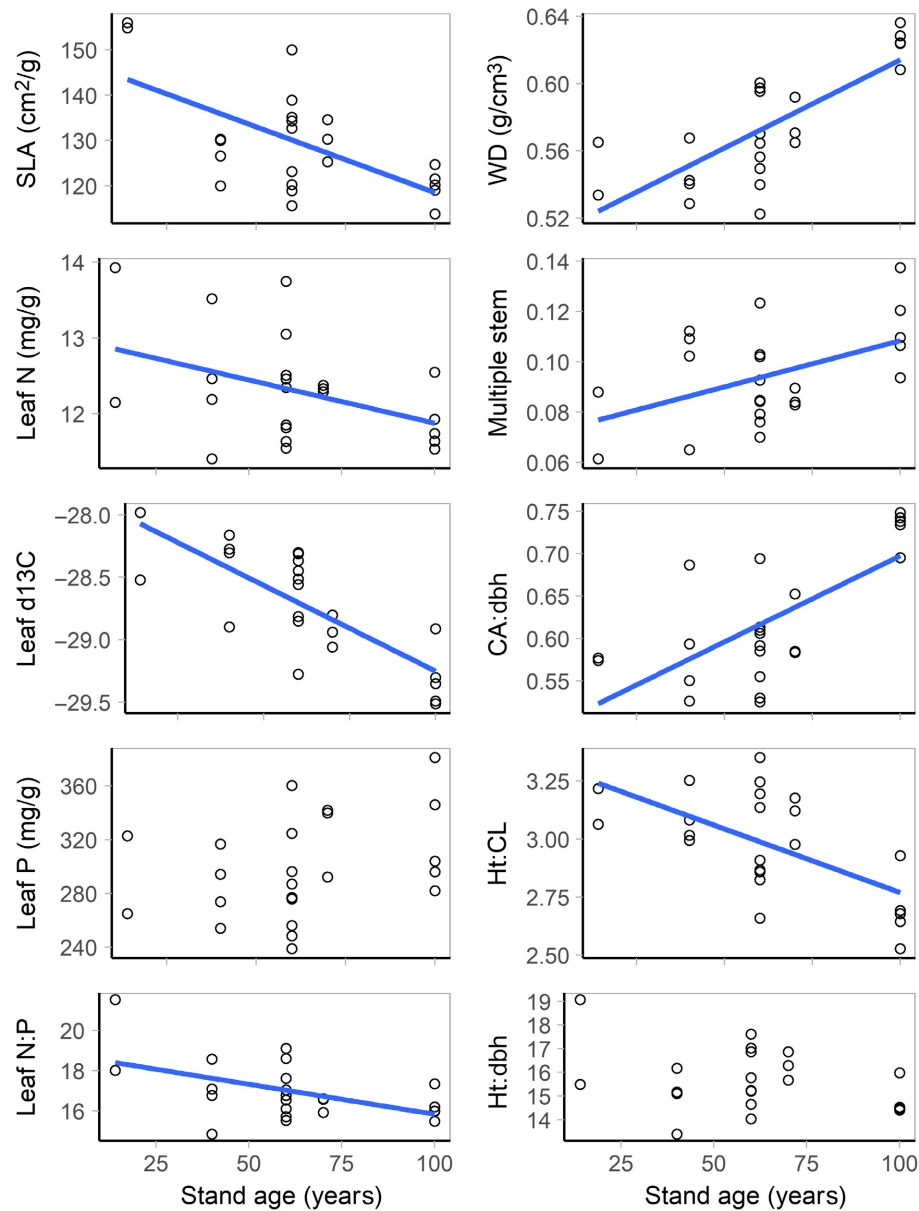
Fig. 3. Community trait shifts during forest succession. Each point represents one of the 23 sites in a 15-km continuous secondary forest in north Key Largo. The dependent variables are the community-weighted mean trait values of the vegetation at that site. The linear regression line is shown only for traits exhibiting a significant pattern ($P < 0.05$).

heterogeneity) among species was calculated for the five traits evaluated above (Table 3). When all plots and traits were considered together, species displayed significant clustering across niche space. When mean niche overlap was analyzed separately for each trait across all plots, significant clustering was also observed in three traits, that is, specific leaf area, wood density, and leaf phosphorus, but no departures from random expectations were observed for leaf nitrogen and Ht:CL. Similarly, when niche overlap was analyzed separately

for young stands, species displayed significant multivariate clustering across trait niche space, and in this case, all five individual traits followed suit (*P*-value <0.05). In contrast, when niche overlap was calculated for old plots only, species were more evenly distributed across trait niche space than expected based on the null model. Community assembly patterns for individual traits in old plots differed from the null model in only one trait (leaf nitrogen), which was more evenly distributed than expected, that is, exhibited significant niche differentiation (Table 3).

DISCUSSION

Our investigation demonstrated that a combination of plant architecture (Ht:CL), wood density, and leaf traits (specific leaf area, leaf phosphorus, leaf nitrogen) comprises a key set of functional traits that are important for understanding succession and the community assembly process in dry tropical forest of the Florida Keys. The patterns in community-weighted mean traits indicate that species experience stressful conditions during the dry early stages of succession and drought stress may gradually decrease as succession proceeds. A strong clustering pattern in traits of young communities suggests that environmental filtering is important in the early stages of succession, while a significant niche differentiation pattern in older communities suggests that community assembly was strongly influenced by competition for limiting resources in the late stages of succession.

Major trait niche axes (Question 1)

The PCA results showed that principal components of multiple niche trait axes represent important species differences across the forested mosaic that we sampled in Key Largo (Table 2, Fig. 2). Expectations based on the leaf economics spectrum concept are that leaf nitrogen and phosphorus contents will be strongly positively correlated with specific leaf area for tree species found in dry tropical forests (Wright et al. 2004). Typically, low leaf nitrogen and low specific leaf area are characteristic of species with long-lived leaves, whereas high leaf nitrogen and high specific leaf area are associated with ephemeral leaves that live less than one year (Wright et al. 2004).

The sampling approach we employed allows for differentiation among site-specific and species-specific patterns in morphological, physio-chemical, and architectural characteristics. Results indicate an orthogonal relationship among specific leaf area, leaf phosphorus, and leaf nitrogen (Table 2), with each weighted strongly on a different PCA axis, indicating that these traits are not strictly correlated at the stand level in the regional mosaic of forest patches occurring in Key Largo. These results suggest that the way that chemical traits vary is not universal, and that observed patterns of variation may provide unique insight into how specific resource limitations are operating in each community. Our results, therefore, reflect the different roles these traits play in dry tropical forest, where species response to seasonal resource limitation (water and nutrients) is critical.

Table 3. Measures of the evenness vs. clustering of all 23 transects, young stands, and old stands of Key Largo tree species across niche space incorporating five functional traits: (1) SLA, (2) WD, (3) TP, (4) TN, and (5) Ht:CL, with the average coefficient of heterogeneity over the five traits giving an overall measure of clustering vs. even spacing.

Community	Test	Overall	SLA	WD	TP	TN	Ht:CL
All plots	Evenness	ns	ns	ns	ns	ns	ns
	Clustering	<0.01	0.01	0.02	0.001	ns	ns
Young	Evenness	ns	ns	ns	ns	ns	ns
	Clustering	<0.01	0.02	0.03	0.03	0.04	0.02
Old	Evenness	0.03	ns	ns	ns	0.02	ns
	Clustering	ns	ns	ns	ns	ns	ns

Notes: Statistically significant evenly spaced or clustered distributions, as identified by null model tests, are indicated by *P*-values (*P* < 0.05), while non-significant *P*-value is presented as ns. SLA, Specific leaf area; WD, Wood density; TP, Leaf phosphorus; TN, Leaf nitrogen; Ht:CL, Height:Crown length.

In Florida Keys' dry tropical forest, community assembly appears to be driven mainly by species-level responses to light, nitrogen, and freshwater availability, and species–individual interactive responses to phosphorus. Previous investigations demonstrate that dry tropical forests in the Florida Keys appear to be water- and nutrient-limited systems (Redwine 2007). We expected a strong negative correlation between specific leaf area and wood density, as slow-growing species in water-limited environment with low specific leaf area typically allocate photosynthate to the production of dense wood (Reich et al. 2003, Baraloto et al. 2010). The relationship between these important traits was supported by results of the correlation analysis at the forest stand level (Appendix S1: Table S4). Interpretation of wood-related traits may need to account for a few different trait axes as coastal forests in the Florida Keys are frequently disturbed by storms and hurricanes. While the wood density spectrum was explored in this study, other potentially relevant traits of wood were not. For example, light wood may be either soft or brittle (Chave et al. 2009), and variation in this trait spectrum may contribute to a species' inherent capacity to resist windstorm damage and/or support multiple stem or spreading canopies; a significant negative correlation of wood density with Ht:CL and a positive correlation with CA:dbh were observed (Appendix S1: Table S4). Moreover, multiple-stem form is common in the Florida Keys dry tropical forest and is a characteristic feature of Caribbean dry forests (Dunphy et al. 2000). The factors most likely to be responsible for the multiple-stem species may include prolonged drought and salt stress, and phosphorus limitation as well as periodic hurricane disturbances in coastal environment (Dunphy et al. 2000, Bellingham and Sparrow 2009). Therefore, our architectural traits results indicate that future studies investigating biomechanical properties of tree species in this forest may be particularly useful in clarifying relationships between wood properties and canopy architecture/stability (Fournier et al. 2013).

Prior knowledge of intra- and interspecific trait variation is essential for studying community assembly patterns (Albert et al. 2010, Messier et al. 2010). In some cases, variation occurring at different levels may affect the results obtained and the conclusions drawn for community assemblages (Messier et al. 2010). The orthogonality between key traits with relatively high interspecific variation observed in this study (Tables 1 and 2) indicates that species may respond to different selective pressures of the environment through these functional traits. The finding that the amount of intraspecific variation is negligible in key traits compared to interspecific variation indicates that species differ distinctly from one another in these traits. Therefore, intraspecific variation would have little effect on the outcome of assembly rules determined on the basis of species mean trait values in this forest. On the other hand, the high intraspecific variation observed in this study for a few traits, particularly in Ht:CL and leaf phosphorus (Table 1), indicates the importance of individual variation in acquiring resources, mainly light and phosphorus within and across the sites, thereby reflecting trees' plastic responses to the environments to which they are exposed (Sultan 2000).

The PCAs help to determine important niche axes that correlate strongly with aspects of whole-plant performance. The presence of complex interactions between traits and species composition indicates that no single trait adequately captures community dynamics, and highlights the importance of trait selection that captures multiple niche axes for the exploration of community assembly mechanisms. Therefore, a combination of plant architecture, stem, and leaf traits comprises key functional niches that are important for understanding the community assembly process in dry tropical forest. Different assembly processes may be operating simultaneously along these distinct niche axes (Spasojevic and Suding 2012); therefore, an understanding of the functional roles of each of the traits under study is important in interpreting relationships between niche axes and assembly processes.

Pattern of trait variation across the successional gradient (Question 2)

The shifts in CWM traits along the successional gradient in dry tropical forest (Fig. 3) represent responses to stress. In dry forest, succession may be driven by an increase in water availability over time (Pineda-García et al. 2013). In such forests, species experience stressful

conditions during the dry and hot early stages of succession and drought stress may gradually decrease toward later stages of succession as soils build up and canopy cover increases (Lebrija-Trejos et al. 2010, Lohbeck et al. 2013). Previous studies in the Florida Keys have shown that canopy trees undergo a gradual change in leaf traits from deciduous (short-lived leaves) to evergreen (long-lived leaves) by the time of stand maturity (Ross et al. 2001, Redwine 2007). In the young forest, trait values related to drought tolerance (less negative δ^{13}C) and optimal light acquisition (high specific leaf area and leaf nitrogen) prevailed (Fig. 3), reflecting an acquisitive strategy to maximize photosynthesis (Poorter et al. 2009) when water is available and to minimize water loss and respiration costs during dry periods. In old forests, the evergreen leaf habit, which is typically accompanied by lower nutritional values (carbon–nitrogen ratio), slow growth, and conservative strategies (low specific leaf area and leaf nitrogen, and increased structural toughness), appears to be a strategy to survive in nutrient-poor soils (Givnish 2002). In order to maintain maximum leaf area year-round, the evergreen species that occupy older forests have high wood density (Fig. 3), which allows them to resist drought stress by maintaining high water potentials during the dry season (Westoby et al. 2002). The pattern in water use economy we observed, that is, a decrease in leaf δ^{13}C across the successional gradient (Fig. 3), nevertheless suggests that moisture availability in old-growth forests is higher than in young stands. A similar study in southern Mexico dry tropical forest found mixed patterns in traits during succession (Lebrija-Trejos et al. 2010, Lohbeck et al. 2013), demonstrating inconsistencies between acquisitive and conservative trait patterns. However, our findings clearly show that acquisitive traits decreased while conservative traits increased with succession, as predicted.

Our data also suggest that as a result of differences in light demand, variation in architectural traits may be important for resident species in the Key Largo forest. High Ht:CL was observed in young communities (Appendix S1: Table S4) that are dominated by shade-intolerant early-successional species. In contrast, shade-tolerant species in old stands (late-successional species)

tend to have wider crowns (high CA:dbh; Appendix S1: Table S4) that increase interception of diffuse light. Early-successional species in young stands are therefore must grow quickly, overtopping neighbors, and attaining or maintaining occupancy of the canopy following gap formation that results from storm and hurricane disturbance (Diamond and Ross 2016). As in our study, others have also found that early-successional species do so by developing both a slender stem (high Ht:dbh) and a shallow crown (high Ht:CL; Poorter et al. 2006). In contrast, species in old stands dominated by shade-tolerant understory species that regenerate in shaded environments may not attain great height, but have wide crowns that allow them to intercept light over a large area. Similarly, our results showed that multiple-stem species were more frequent in mature stands. Multiple-stem characteristic in trees may be associated with available resources (Bellingham and Sparrow 2009) and/or wind disturbances (Van Bloem et al. 2006). Soil moisture is expected to increase with stand age in these forests as both soil depth and canopy cover increase with stand age. In contrast, studies in dry tropical forest (Puerto Rico) showed that soil moisture and nutrients only play a secondary role in selecting for multiple-stem trees, as hurricane winds appear to serve as a filter promoting smaller multiple-stem species over long periods (Van Bloem et al. 2006). Therefore, our observation of higher frequency of multiple-stem species in mature forest may also be explained by the legacy of hurricane winds, as most of the species studied (similar to Caribbean dry tropical forest) sprout prolifically after wind breakage (Van Bloem et al. 2003, 2006).

Therefore, given long seasonal drought (4–7 months) in the Florida Keys, young stands experience extreme drought stress as well as more exposure to wind disturbances due to their shallow soils and open canopies, favoring species with acquisitive strategies, that is, short-lived leaves, high nutrient values, shallow crown, and slender stems. In contrast, in old stands, where soils are deeper and insolation is reduced by a more closed forest canopy, nutrient availability tends to be reduced, water availability remains a challenge, and species with conservative strategies bear long-lived leaves with low leaf nitrogen concentrations and higher wood density.

Community assembly patterns (Question 3)

Overall, a significant trait clustering pattern (Table 3) suggests strong environmental filtering of trait values. Such trait similarity supports the expectation that differences in local environment influence which trait values, filtered out of the regional pool, perform best under local conditions. At a finer scale, our results showed that the patterns of trait niche overlap in young and old stands differed. The observed trait similarity in younger stands provides strong evidence that environmental filtering is important in the early stages of succession. Convergence toward trait values that maximize resource acquisition is the dominant assembly process in early stages of forest succession. In contrast, a significant niche differentiation pattern in older communities suggests species differences that lessen competition among them, in which resource competition acts to constrain local neighborhoods to certain traits or trait combinations, producing lower niche overlap than expected by chance. On the basis of trait patterns, filtering at this end of the gradient was likely the result of competition for limiting resources, water and nutrients (high wood density, low leaf nitrogen; Fig. 3). Our results appear to confirm a general tenet of competition theory identified by Chesson (2000) which predicts some level of limitation on functional similarity among co-occurring species as abiotic stresses, competition, or pest pressures increase. In the case of the Florida Keys' dry tropical forests, competition for light and nutrient limitation both clearly increases as forest stands age through a successional process (Redwine 2007). Water supply may increase marginally as soils develop, although increased demand associated with larger trees may be offset by species-based coping strategies (as indicated by CWM of δ^{13}C which suggests decreased water use efficiency of older stands). In any event, severe water stress is clearly occurring for weeks–months each year in all dry tropical forest types in the study area (Ross et al. 2003).

Additional insights about changes in the community assembly processes can be drawn from individual trait patterns across the environmental gradient. Overall, environmental filtering plays an important role in this forest, as only the best suited species in the local environment are successful. Our results showed a significant clustering pattern in three traits (specific leaf area, wood density, and leaf phosphorus) across all stands. Limiting conditions, mainly water and nutrients, are likely to determine the success of tree species in becoming established in Florida Keys' dry tropical forests, as indicated by their functional traits (low specific leaf area, high wood density, and less leaf phosphorus). A strong clustering pattern suggests an intense pressure for a common resource use strategy to acquire limiting resources regardless of forest age, where productivity is limited, as in Florida Keys forests (Ross et al. 2003). Similarly, a significant clustering pattern in all key traits in young communities suggests that dominant species in young forests have similar leaf, stem, and architectural traits. As hypothesized, the early-successional stands in our system were dominated by species with traits that control extreme water and nutrient stress. Many of these species are capable of photosynthesizing and accumulating biomass at high rates (high specific leaf area and leaf nitrogen) during the wet season, and subsequently increase dry-season survival by dropping leaves, that is, mostly deciduous species (Appendix S1: Table S1).

In older communities, however, leaf nitrogen showed significant niche differentiation, while overlaps in the other four traits we tested were not different from expectations of the null model. The observed niche differentiation in leaf nitrogen among species may reflect spatiotemporal differences in preferential uptake in nitrogen through different sources such as microorganisms, soil, and/or groundwater (Beyschlag et al. 2009). Leaf nitrogen may not be directly associated with nutrient availability per se, which may depend on other factors such as moisture availability and other nutrient supply (Wright et al. 2001). Therefore, the ability of species to access other resources such as water and phosphorus may also play a significant role in accessing nitrogen. The concentration of variation of leaf nitrogen (almost 99%) at the species level (Table 1) may indicate the conservative nature of leaf nitrogen within species. A previous study in this forest suggests that symbiotic associations with microorganisms are widespread (Redwine 2007). Similarly, differences in rooting depth and physiology may affect tree species' capacities to access water from soil and groundwater.

Considering the nature of the karst substrate and very thin soil layer in the study area, some tree species might use groundwater, particularly during the long dry season (Ewe et al. 1999). The depth of the water table below the rock surface, ranging from a few cm to 4 m, may not prevent the majority of tree species from reaching the groundwater. Fine root placement and ability of species to access freshwater at small scale could also be occurring at different depths leading to differential access to nutrient supplies (Hooper and Vitousek 1997). However, groundwater across the study region is brackish in nature (Ross et al. 2003), and freshwater species in this forest may have very little ability to tolerate salts. Nevertheless, even slight variation in salt tolerance among species might preclude some species from accessing water/nutrients from groundwater. Thus, one important aspect of the observed trait differentiation among coexisting species in old-growth forest may be partitioning of alternative sources of nitrogen among coexisting species. However, current knowledge about nitrogen cycling processes in the study area is very limited.

In some settings, trait differentiation among coexisting species in a community may result from dispersal limitation rather than environmental differentiation (Hubbell 2006). However, one may reason that dispersal limitation may not be as important in explaining spatial pattern in the study area, a contiguous area of 875 ha, populated mostly by tree species with fleshy fruits likely to be dispersed by birds and small animals (Redwine et al. 2007, Ross et al. 2016). In their seed dispersal activities, birds and animals move easily across the whole forest exploiting most or all available habitat (Humphrey 1988, Strong and Bancroft 1994). Furthermore, a parallel study in the same forest showed that trait–species relationships were not strong for dispersal traits (i.e., seed mass and number; Subedi 2017).

CONCLUSIONS

We report a key set of morphological, chemical, and architectural traits that are important for understanding the community assembly process in the dry tropical forest of the Florida Keys. Species traits in young stands are mostly associated with resource acquisitive strategies, while old stands are dominated by species with conservative traits. Our results support the hypothesis that younger stands in our study area are predominantly shaped by environmentally driven processes, while old stands are shaped by competitively driven processes that lead to limiting similarity at the site level. This seems to be caused by changes in abiotic conditions such as soil nutrient, water, and light availability, which favor more conservative strategies of resource use as succession proceeds. Trees in young stands (early-successional species) emphasize nutrient and water acquisition as they have less competition after disturbance. In contrast, trees from old stands (late-successional species) compete with one another for resources as stands age and become more diverse. The overall trait similarities among the species present in these forests suggest that they are mostly specialists on the local environment, and species' tolerances for limiting resources such as nutrients and moisture, and survival during wind disturbance may be more important than competition for resources at the regional scale.

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Supporting Information

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