



Inferring implications of climate change in south Florida hardwood hammocks through analysis of metacommunity structure

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ABSTRACT

Aim In order to explore how variation in regional biogeography would affect forest responses to climate change, we analysed metacommunity structure of trees in natural forest fragments across a boundary between tropical and subtropical temperature regimes. We wished to determine whether species assemblages were constrained by periodic cold temperatures, dispersal limitation and/or local processes associated with fragment size, and consider how these influences might affect future species migration and community reassembly.

Location Southeastern Florida, USA.

Methods We collected complete tree species lists for 144 forest fragments, from our own surveys supplemented by publicly available sources. The resulting species-by-site data matrix was re-ordered based on an ordination that identified the latent environmental axis most responsible for variation in composition, and metacommunity structure was analysed for coherence, turnover and range boundary clumping. Matrix structure was tested for associations with site variables, and with community-aggregated functional traits related to cold tolerance, dispersal limitation and fragment size.

Results Forest patch size was the strongest single correlate with composition and species richness, but mean January temperature and a neighbourhood index denoting degree of isolation from other patches contributed significantly to regression models. The species-by-site matrix was highly nested, with trees common to small upland fragments in the Everglades interior representing a distinct subset of the richer assemblages found in sites closer to the coast. Interior forests were smaller, more isolated, and subject to cooler minimum temperatures than more coastal forests, and were comprised primarily of early-successional, animal dispersed species.

Main conclusions While warming winter temperatures may relax some constraints on the northward migration of tropical species through the region, sea level rise will raise ground water levels, decreasing the size and number of suitable mesic patches, and increasing their isolation. The result will be a loss in tree species diversity, especially among late-successional, edge-sensitive species.

Keywords

community-aggregated functional traits, dispersal limitation, metacommunity structure, nestedness, species-area relationship, tree islands.

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INTRODUCTION

Biogeographic ecotones between tropical and temperate floras are likely to experience rapid and broadly predictable change with climatic warming (Box *et al.*, 1999). However, these changes will take on increasing complexity at finer scales, where they will be mediated through metacommunity processes, i.e., context-specific biotic interactions within individual patches along with propagule exchange among them. To the extent that current processes, filters and constraints continue to operate, interpretation of existing metacommunity structure may provide insights into likely changes to local communities affected by global climate change.

The concept of the metacommunity (“... a set of local communities linked by the dispersal of multiple potentially interacting species”; Leibold *et al.*, 2004) focuses on scale-dependent interactions within and among local communities that occupy discrete patches. Metacommunity studies address intra-regional patterns in species composition and richness, along with their causes and consequences (Leibold, 2011). An analytical sequence proposed by Presley *et al.* (2010) seeks to integrate important environmental drivers, by linking traditional gradient analysis methods with tests of hypotheses about metacommunity structure. The procedure begins with ordination of a site-by-species data matrix, which identifies the latent environmental axes responsible for variation in site composition, and provides a basis for re-ordering the matrix so that both species and sites are arranged according to their positions along the selected ordination axis. By framing structural hypotheses within the context of this ordination, with its interpretable environmental drivers, the analysis may point to the mechanisms that underlie structure in the regional landscape.

Metacommunity analysis can inform considerations of species movements in response to climate change if the processes that have driven species to their current distributions can be inferred from the observed patterns. It addresses cross-scale interactions, examining the structure resulting from both within-patch and among-patch processes. Its perspective is regional, from a distance at which both landscape-scale processes (e.g., seed dispersal among patches) and local relationships that seem random when viewed at close range sometimes display interpretable pattern (Levin, 1992).

Besides reflecting ongoing processes, metacommunity structure bears the imprint of bioclimatic trajectories that extend well beyond the focal region, and stretch back in time. For instance, the lower quarter of the Florida peninsula, including the archipelago of the Florida Keys, occupies a tension zone between freeze-free and freeze-prone sites, and hence between tropical and temperate biotas. This is evident among assemblages of broadleaved tree species growing on well-drained, mesic substrates, known in the region as hardwood hammocks. Excellent distribution maps of Florida tree species are available (e.g., Little, 1978), and the tropical elements and transitional nature of the south Florida flora have been recognized in several biogeographic treatments (Schwartz, 1988;

Box *et al.*, 1993). The landscape itself is geologically youthful, with its most prominent feature, the Everglades wetland, having formed only six thousand years ago, in response to changing climatic conditions (Willard & Bernhardt, 2011).

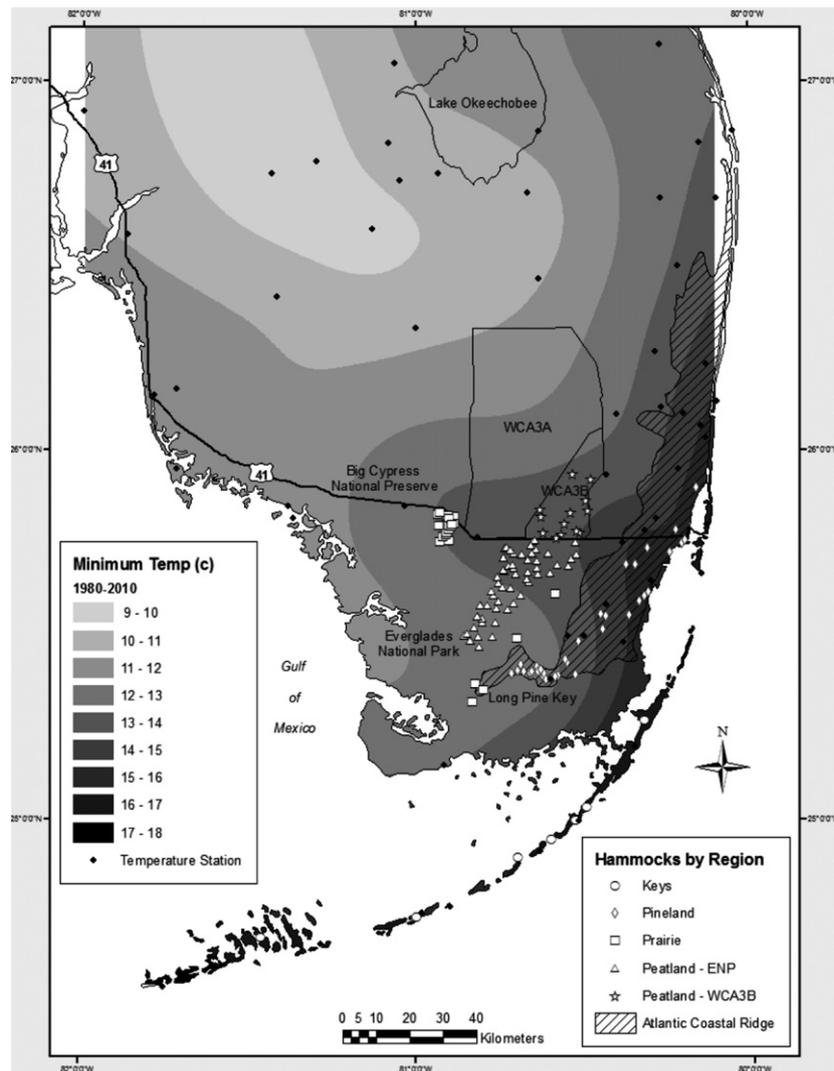
In this article, we present an analysis of the metacommunity structure of trees in a network of hardwood hammocks in southeastern Florida, based on an extensive regional database. We ask whether the revealed structure is a product of global, landscape-scale or local forces, and consider how these scale-related issues inform our expectation of species and community responses to further climatic warming. We examine several readily available site attributes relevant to south Florida and other sub-tropical areas: winter temperature, proximity to nearby seed sources, and patch size. We then link site analyses to community characteristics by examining three parallel community-aggregated traits that reflect the expected effects of chilling, dispersal limitation, and fragment size on forest composition: cold tolerance, seed dispersal mode and successional status, respectively.

METHODS

The study area comprises the Florida Keys plus a $\sim 5 \times 10^5$ ha area at the southeast corner of the Florida peninsula (Fig. 1). The region's climate is influenced by surrounding marine waters, which are warmed by the passage of the Gulf Stream on the south and east. Coastal effects cause mean minimum temperatures to vary by more than 4 °C across the study area, with the northwest experiencing the coldest temperatures and the south and east the warmest. Mean annual precipitation decreases from about 1400 mm per year in the northeast to 1100 mm in the southwest (Moses *et al.*, 2013). Seasonality in rainfall is pronounced, with 60 percent of annual rainfall concentrated between June and September (Duever *et al.*, 1994).

The area's hardwood hammocks are mostly found as forest fragments, also referred to as tree islands, on shallow soils above limestone bedrock, where the water-table is typically 0.5 m or more below the surface, and fires are infrequent. Nearer to the coast, the outcropping limestone forms extensive, raised ridges surrounded by open water or wetlands. Prior to human intervention, these surfaces were occupied almost exclusively by hammocks (upper Florida Keys) or by a mixture of pine forest and hammock (Atlantic Coastal Ridge and its extension on Long Pine Key, Everglades National Park). Consequently, hammocks in coastal areas tend to be large and relatively close together, while hammocks in the interior Everglades are rooted above isolated limestone outcrops, remnants of massive erosion that took place late in the Pleistocene epoch (Meeder *et al.*, unpublished manuscript). Embedded in freshwater prairies and marshes, outcrops high enough to support mesophytic trees are small and far apart. The co-variation in pattern between landform and climate means that interior hammocks are not only small and sparsely distributed, but also relatively cold, while coastal hammocks are warm, large and closely spaced.

Figure 1 Map showing the location of study sites (144 hammocks) overlaid on the Local Minimum Temperature (LMT) surface derived by interpolating minimum daily temperature of the coldest south Florida month (January) during the period 1976–2005.



Natural disturbances, especially freezes, hurricanes and fires play important roles in south Florida hammocks. Freeze events are rare or absent in the Florida Keys, but occur several nights per year in the northern Everglades, and about once every 2 years at the southern end of the peninsula (Duever *et al.*, 1994). Temperature is moderated in the interior of established hammocks, but tropical hardwood stems near the forest edge are vulnerable (Olmsted *et al.*, 1993). Major hurricanes recur at about 15-year intervals (Keim *et al.*, 2007), damaging or killing many individuals (Slater *et al.*, 1995; Ross *et al.*, 2001), but community reassembly proceeds rapidly (Kwit *et al.*, 2000). Fires are infrequent in hammocks, as their microclimate (moist and cool in summer) confers substantial fire-resistance. However, under very dry conditions, fires may enter the forest and smoulder for weeks in limestone cavities, leading to loss of organic soils. Vegetation recovery following such fires is exceedingly slow (Wade *et al.*, 1980).

Since the initiation of the Everglades peatland ~6K years ago, hardwood hammocks of the study area have experienced several enduring environmental perturbations, including: (1)

a slow rise in sea level, averaging about 10 cm per 100 years over the period, but accelerating during the last century (Lidz & Shinn, 1991); (2) a long decline in temperature, culminating 200–500 years ago in the “Little Ice Age”, followed by the sharp rise evident in recent years (Mann *et al.*, 2008; Marcott *et al.*, 2013); (3) intensified human use of hammocks in the interior Everglades as human populations burgeoned 2–3 thousand years ago (Griffin, 2002); (4) Everglades drainage, beginning in 1891 and largely completed by 1970 (McVoy *et al.*, 2011); and (5) 20th century development of the coastal ridge for agriculture and urban uses. However, the inherent patterns of hammock fragmentation within the wetland and other landscapes remain today.

Data acquisition

Data were collected on species occurrence in 144 South Florida forests (Fig. 1). During 2001–2011 we identified all tree species present in 77 hardwood hammocks embedded in the prairies and marshes of Everglades National Park (ENP), Big

Cypress National Preserve, and Water Conservation Area 3B (WCA3B). The 74 sites in the peatlands of ENP and WCA3B comprised a complete survey of all hardwood hammocks in those sub-regions. We thoroughly searched each hammock, spending an hour or so in the larger stands, less in the smaller ones. We excluded species capable of survival to maturity in hydric conditions, as well as non-native trees, which were uncommon. While the influence of non-native species on forest composition is an important topic, our study design was not suitable to address it, and inclusion of such species in the analysis might obscure relationships among the native species that were of primary interest. Data were supplemented from several sources. The first was the online database of the Institute for Regional Conservation (IRC: <http://www.regionalconservation.org/>), from which complete tree species lists for 26 natural areas in metropolitan Miami-Dade County and the Florida Keys were extracted. Tree species categorized as 'cultivated' at each site were excluded from consideration. We also included complete species lists from 18 tree islands within the pine-dominated matrix on Long Pine Key, Everglades National Park, collected by the noted Everglades ecologist Frank Craighead during the 1960s. Finally, we incorporated published comprehensive species lists from two forests on Long Pine Key (Olmsted *et al.*, 1980) and 21 sites in the eastern Big Cypress National Preserve (Gunderson & Loope, 1982). Species taxonomic authority was Wunderlin & Hansen (2011).

Lacking uniform and comprehensive data on edaphic, hydrologic or topographic characteristics across all sites, we examined one climatic and two geographic variables with potential to influence stand composition. We determined hammock area (AREA) for all fragments, based on screen-digitization from the most recent available aerial photo using ESRI® ArcMap™ 9.2. Area is often considered a proxy for site heterogeneity (Brose, 2001), but in some cases, small and large fragments also differ predictably in modal habitat characteristics (e.g., Vallan, 2000). We also calculated Neighbour Proximity Index (NPI), a metric of connectivity to nearby seed sources. We created a 2-km buffer around the centroid of each hammock fragment, and gridded it into 100 × 100 m cells. NPI was calculated as:

$$NPI = k * \sum \left(\frac{1}{D} \right)$$

where D was the distance in meters from the target fragment centre to the centre of each cell occupied by another hammock patch, and k was an arbitrary scaling constant set to 1000. NPI was only derived for hammocks < 1 ha, because the index is confounded with AREA at larger sizes, where cells near the centre of the target hammock are commonly self-occupied, and thus cannot be occupied by a neighbouring fragment. Finally, we estimated the Local Minimum Temperature (LMT), representing a stress factor that might influence the success of cold-sensitive Florida tree species. Defined as the mean minimum daily temperature of the coldest south Florida month (January), averaged across

30 years (1976–2005), LMT was estimated for each site by interpolating among 22 weather stations distributed throughout south Florida (Fig. 1).

To explore responses of the tree communities to the site variables described above, we summarized several attributes of the tree assemblage, including indices of successional condition and cold-hardiness, as well as the relative abundance of species with animal-dispersed fruit. We reasoned that these three community-aggregated trait characteristics (Shipley *et al.*, 2006) might reflect adaptations to fragment size, frequency/severity of chilling temperatures and isolation from nearby seed sources, respectively.

Tree species composition is subject to edge influences that may extend many meters into the forest (Matlack, 1994; Harper *et al.*, 2005), or encompass the entirety of small fragments. In some cases, the high mortality rates associated with these environments can favour early successional over late successional species (Chen *et al.*, 1992). To capture this characteristic at the stand level, we calculated a Successional Position Index (SPI), defined as the mean successional age optimum (Ross *et al.*, 2001) across all resident species, as determined from a chronosequence of Florida Keys hammocks in different stages of recovery from catastrophic disturbance (e.g., fire, farming, or land clearing).

Despite large variation associated with propagule size or dispersal vector, tree seeds moved by birds and medium/large mammals are generally dispersed farther than wind-dispersed species (Vittoz & Engler, 2007). We determined the percent of species per stand with zoochorous fruits, based on the assumption that fleshy fruits (drupes, berries, acorns, some achenes) are animal-dispersed, primarily by birds or mammals.

Finally, we estimated a Cold Tolerance Index (CTI) as

$$CTI_j = 100 * \frac{\sum_{i=1}^n (RMT_{max} - RMT_i)}{n(RMT_{max} - RMT_{min})}$$

where CTI_j is the value of the index in hammock j , RMT_i

is the Rangewide Minimum Temperature of resident Species i (defined as the lowest mean minimum daily temperature of the coldest local month recorded anywhere within the range of Species i over the period 1981–2010), and RMT_{max} and RMT_{min} are the highest and lowest RMT values, respectively, among all species in the data set. RMT values were determined by layering species' ranges (US Geological Survey, 1999; Wunderlin & Hansen, 2008) on interpolated temperature rasters derived from NOAA weather stations.

Data analysis

Metacommunity analysis followed the EMS (Elements of Metacommunity Structure) approach outlined in Presley *et al.* (2010). Three characteristics of species distributions are derived: *coherence*, *range turnover*, and *range boundary clumping*. *Coherence* is a measure of how completely species fill their realized niches along the environmental gradient that emerges in latent form in the compositional ordination.

Coherence is assessed by comparing the number of embedded absences (absences from sites located between the species' first and last occurrences along the gradient) to the number of absences in randomly generated matrices. *Range turnover* is a measure of the frequency in which species' pairs exhibit a "replacement", such that the distribution of Species A extends beyond that of Species B at one end of the dominant environmental gradient, while Species B extends further than Species A in the opposite direction. Finally, *range boundary clumping* is a measure of the frequency of co-occurrences of species range boundaries along the environmental gradient. Collectively, these three structural metrics address some of the mechanisms underlying species and community distributions within the landscape, with coherence and range turnover reflecting species responses to environmental gradients, and range boundary clumping reflecting on the nature of species assemblages.

Metacommunity analysis was applied to a presence-absence matrix of 144 sites \times 77 species present in at least three stands. Analysis was done in MATLAB R2011a (The Mathworks, Inc. 2011), using a program described in Presley *et al.* (2009), available at <http://faculty.tarleton.edu/higgins/metacommunity-structure.html>. The matrix was first arranged according to species and site positions along Axis 1 of a reciprocal averaging (RA) ordination. Statistics for coherence, range turnover, and range boundary clumping were calculated for the matrix, and for 1000 matrices randomly generated from it. Random matrices were constructed on the basis of a null model in which species richness per site was constrained to equal the observed number of taxa, while the probability of a species' occurrence at each site equalled its proportional incidence in the observation matrix. A metacommunity exhibited significantly positive coherence when the probability of fewer embedded absences in randomly generated matrices than in the empirical matrix was ≤ 0.05 ($\leq \alpha/2$ for two-tailed test). Positive species turnover was present if the likelihood of having more replacements in randomly generated matrices than expected by chance was $\leq \alpha/2$, and negative turnover, or nestedness, was present if the converse was true. Finally, range boundary clumping was assessed using the Morisita Index (I), whose significance was examined using a χ^2 test following methods described in Presley *et al.* (2011).

A hierarchical agglomerative clustering method was used to identify groups of hammocks with distinctive species composition. We used Bray–Curtis dissimilarity as our distance measure, and the flexible beta (-0.25) linkage method to calculate relatedness among individual sites or groups (McCune *et al.*, 2002).

Factors responsible for metacommunity structure were assessed by several means. We used multiple regression to examine the relationship between the three site variables (AREA, NPI and LMT) and RA Axis 1. When necessary, variables were log transformed to normalize the data and minimize heteroscedasticity. Because NPI could not be calculated for large tree islands, the relationships between the

three site variables and RA Axis 1 scores were explored through two sets of regressions. In the first set, all tree islands were considered, and the effects of AREA, LMT, and their 2-factor combination were assessed as predictors. In the second set of analyses, only stands with AREA < 1 ha were considered, and all 1-, 2-, and 3-factor combinations of AREA, LMT, and NPI were tested. For both data sets, we selected the best model based on the minimum Akaike Information Criterion (AIC) score.

Compositional variation among tree islands was also analysed for spatial structure, which provides some indication of the importance of inter-patch dispersal across scales. We examined the relationship between Jaccard dissimilarities and linear distances among all pairs of sites. Site pairs were grouped by distance into 2-km bins, and an exponential model was fit to the distance \times dissimilarity vector.

Variation in values of community-aggregated traits was examined by applying analysis of variance to groups of sites defined in the classification procedure. Several variables that failed to meet ANOVA assumption after the application of data transformation were tested with the non-parametric Kruskal–Wallis test, followed by a multiple comparison 'Z'-test if the overall effect was statistically significant.

RESULTS

Axis 1 (Eigenvalue = 0.284) of the reciprocal averaging ordination explained 16 percent of total inertia, and Axis 2 explained an additional 11 percent. Due to the distortion (i.e., "Arch effect"; Hill & Gauch, 1980) to which secondary axes in RA analysis are susceptible, Axis 2 was not examined further. With species and sites arranged according to their ordination positions, hammock metacommunity structure was revealed to be positively coherent, with negative turnover (nested structure) along the underlying gradient, and clumped species loss at range boundaries (Table 1; Fig. 2). Although positive range boundary clumping is commonly reported where species turnover is positive, metacommunities with nested structure can also exhibit clumped range boundaries (Presley *et al.*, 2010). Such a pattern signifies that the effect of the filtering process that created nestedness does not change smoothly or randomly, but in successive jumps.

Cluster analysis (Fig. 3) identified four distinct groups that corresponded with the discontinuities in the nested pattern of species occurrence evident in Fig. 2. These units were associated with sub-regions within the study area; hammocks of the Florida Keys, peatlands of ENP, and peatlands of WCA3B formed three groups, while hammocks of the pine forest and prairie landscapes formed a fourth, mixed class. Species of tropical origin predominated throughout, comprising 71 of the 77 species represented.

Based on Indicator Species Analysis, 40 species exhibited significant associations with one of the four regional groups (Table 2). Most indicator species (28) were associated with the Keys group. About half of these were uncommon (< 20

Table 1 Coherence, turnover and range boundary clumping statistics for matrix of south Florida hammocks rearranged based on RA Axis-1 ordination scores.

Axis	Coherence				Turnover				Clumping	
	EA	Mean	SD	<i>P</i>	RE	Mean	SD	<i>P</i>	M	<i>P</i>
1	3440	6869	235	<0.001	255,318	967,530	93,978	<0.001	3.98	<0.001

Means and standard deviations (SD) are calculated from 1000 null simulations with fixed row totals and equiproportional species totals. The *P*-value represents the significance of the difference between actual number of embedded absences or replacements and mean number of embedded absences or replacements in the null matrices. EA = embedded absences; RE = species replacements; M = Morisita's index.

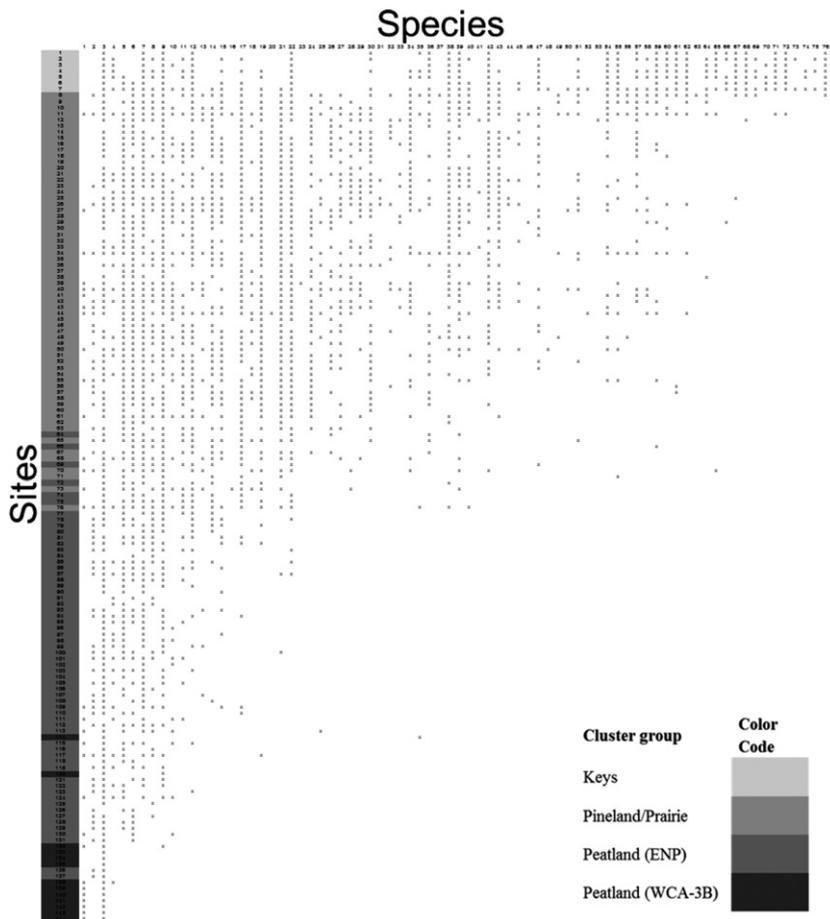


Figure 2 Metacommunity matrix of 144 sites and 77 species. Matrix is packed by arranging sites and species based on reciprocal averaging (RA) ordination Axis-1 scores. Filled cells indicate species presence. Cluster analysis identified four groups of sites (left column), each associated with a sub-region of the study area.

percent occurrence) outside the Keys, while the remainder were well-represented in the pine forests and prairies of Everglades National Park. Indicators for the Keys group included major canopy trees (e.g., *Bursera simaruba*, *Exothea paniculata*, *Ficus citrifolia* and *Metopium toxiferum*) as well as species important in the sub-canopy (e.g., *Ardisia escallonioides*, *Coccoloba diversifolia*, and *Eugenia axillaris*). Only a few Keys indicators (*B. simaruba*, *C. diversifolia*, *E. axillaris* and *Solanum* spp.) occupied more than 20 percent of hammocks in the ENP peatland group, and only one species (*B. simaruba*) was found in more than one WCA3B-peatland site.

Ten species were associated with the pine forest/prairie landscapes of ENP (Table 2). Only one of these (*Myrcianthes*

fragrans) was entirely absent from the Keys, while *Quercus virginiana*, a temperate-origin tree found in all hammocks within the group, was present in only one Keys site. Five pineland/prairie indicators, including both canopy (*Sabal palmetto*, *Sideroxylon salicifolium* and *Simarouba glauca*) and sub-canopy species (*Chrysophyllum oliviforme* and *Myrsine floridana*), were also present in 15 percent or more of ENP peatland hammocks. No indicators of the pineland/prairie group were observed in WCA3B forests.

Celtis laevigata and *Sambucus nigra* subsp. *canadensis* were the sole indicators for ENP-peatland and WCA3B-peatland groups, respectively (Table 2). In the canopy of the species-poor ENP-peatland hammocks, *C. laevigata* shared dominance with a few species more indicative of Keys or

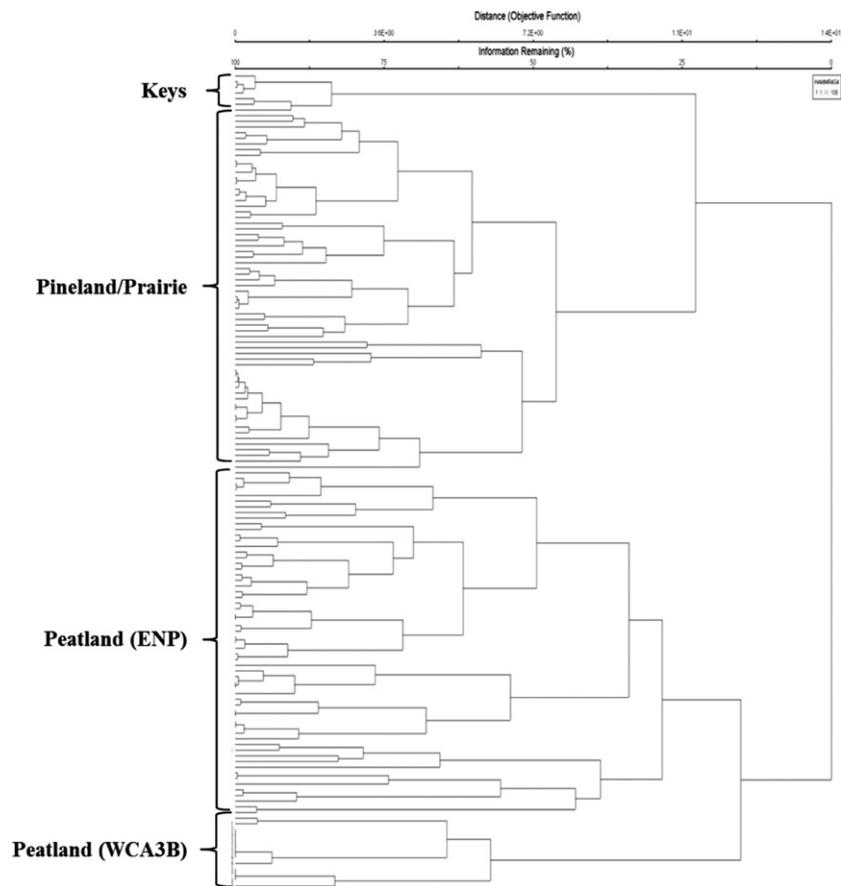


Figure 3 Dendrogram produced from agglomerative cluster analysis, showing sites clustered in four major groups. The dendrogram was pruned at the distance (Wishart's objective function) where 25% of information remained (McCune *et al.*, 2002). A presence-absence data matrix of 144 sites x 77 species was used for classification.

pineland/prairie forests (cited above), and with *Ficus aurea*, an epiphytic tree evenly distributed across all hammock types. *F. aurea* was usually the only tree to occupy the canopy of WCA3B hammocks.

Hammocks ranged in size from 50 m² to nearly 1000 ha, with a distribution skewed strongly toward the smaller sizes (mean = 12.41 ha; median = 0.59 ha). NPI values were also non-normal, so both variables were log-transformed for use, along with LMT, in multiple regression models predicting RA Axis 1 scores. For the 79-site small hammock data set, the best single predictor was log NPI, and the model with lowest AIC included log AREA as well (Table 3). Inclusion of LMT added negligibly to the variance explained by the two-variable model (39 percent). For the full data set of 144 hammocks, AIC was lowest for a two-variable model that included both log AREA and LMT (Table 3). Log AREA provided the best one-variable model, but the inclusion of LMT as an additional predictor improved the variance explained from 55 to 70 percent. The strong effect of hammock area on the regional compositional gradient is illustrated in Fig. 4, as is the decrease in hammock size from the Keys through the pinelands and prairies to the interior peatlands.

Spatial autocorrelation in tree composition was pronounced (Fig. 5), suggesting the importance of dispersal in community assembly. Mean dissimilarity increased from 50 percent for neighbouring tree islands to 75 percent for tree

islands 20 km apart; for more distant sites, the increase in dissimilarity with distance slowed somewhat, reaching 90 percent at 50 km.

A Kruskal–Wallis test followed by multiple comparison tests showed that the four hammock categories defined in the cluster analysis differed significantly in the fraction of species that produce zoochorous fruit, and in indices of successional status (SPI) and cold tolerance (CTI). Most species produce fleshy fruits likely to be transported by birds or mammals, but dry-fruited species (e.g., *Swietenia mahogani*, *Piscidia piscipula*, *Gymnanthes lucida* and *Lysiloma latisiliquum*) were more prevalent in the hammocks of the Keys and pineland/prairies than the interior peatlands (Fig. 6a, Table 2). Likewise, the relative abundance of large, early- to mid-successional tree species (e.g., *Bursera simaruba*, *Celtis laevigata*, *Ficus aurea*) was higher in peatland hammocks than in Keys or pineland/prairie forests (Fig. 6b, Table 2), where site occupancy was shared with many late-successional sub-canopy associates. Finally, CTI values increased continuously from Keys assemblages to the peatland communities at the north end of the study area (Fig. 6c).

DISCUSSION

The metacommunity concept is readily applicable to South Florida hardwood hammocks, whose distinctiveness from surrounding ecosystems serves to separate the local and

Table 2 Species associations with four compositional groups of south Florida trees. Significance of associations ($P < 0.05$) are based on Indicator Species Analysis (McCune *et al.*, 2002). Data are based on percent occupancy in 144 sites distributed among four vegetation groups (Keys, $n = 7$; Pineland/Prairie, $n = 63$; Peatland-ENP, $n = 61$; and Peatland-WCA-3B, $n = 13$). Only species with five or more total occurrences are included.

Species	Percent Occupancy			
	Keys	Pineland/ Prairie	Peatland- ENP	Peatland- WCA3B
Species associated with the Florida Keys group				
<i>Amyris elemifera</i>	100	6	0	0
<i>Ardisia escallonioides</i>	100	89	13	0
<i>Bursera simaruba</i>	100	94	57	15
<i>Bourreria succulenta</i>	100	3	0	0
<i>Canella winterana</i>	71	2	0	0
<i>Capparis cynophallophora</i>	86	3	0	0
<i>Coccoloba diversifolia</i>	100	76	33	0
<i>Coccoloba uvifera</i>	100	19	0	0
<i>Drypetes diversifolia</i>	100	2	0	0
<i>Drypetes lateriflora</i>	57	21	0	0
<i>Eugenia axillaris</i>	100	89	72	0
<i>Eugenia foetida</i>	100	16	2	0
<i>Exothea paniculata</i>	100	62	0	0
<i>Ficus citrifolia</i>	100	52	2	0
<i>Guapira discolor</i>	100	30	0	0
<i>Guettarda elliptica</i>	71	29	0	0
<i>Gymnanthes lucida</i>	86	11	0	0
<i>Krugiodendron ferreum</i>	86	37	2	0
<i>Manilkara jaimiqui</i> subsp. <i>emarginata</i>	100	2	0	0
<i>Metopium toxiferum</i>	100	63	2	0
<i>Piscidia piscipula</i>	100	10	0	0
<i>Reynosia septentrionalis</i>	100	2	0	0
<i>Schaefferia frutescens</i>	57	2	0	0
<i>Sideroxylon celastrinum</i>	100	3	0	0
<i>Solanum spp</i>	71	29	30	8
<i>Swietenia mahagoni</i>	57	14	0	0
<i>Thrinax radiata</i>	71	6	0	0
<i>Ximenia americana</i>	86	30	2	0
Species associated with mainland pine forest and prairie group				
<i>Chrysophyllum oliviforme</i>	14	73	18	0
<i>Citharexylum spinosum</i>	43	52	0	0
<i>Lysiloma latisiliquum</i>	57	59	0	0
<i>Myrcianthes fragrans</i>	0	67	0	0
<i>Myrsine floridana</i>	43	95	67	0
<i>Nectandra coriacea</i>	43	94	8	0
<i>Quercus virginiana</i>	14	100	3	0
<i>Sabal palmetto</i>	29	92	59	0
<i>Sideroxylon salicifolium</i>	57	90	18	0
<i>Simarouba glauca</i>	57	67	15	0
Species associated with ENP peatland group				
<i>Celtis laevigata</i>	0	37	54	0
Species associated with WCA-3B peatland group				
<i>Sambucus canadensis</i>	0	24	11	62
Very abundant species that lack significant group association				
<i>Ficus aurea</i>	100	83	89	100

Table 3 Regression models explaining the variation in reciprocal averaging (RA) ordination Axis-1 scores. Spatial variables were log-transformed hammock size (LogArea) and Neighbor Proximity Index (LogNPI), and environmental variable was Local Minimum Temperature (LMT). Analysis was carried in two steps: i) for all islands, and ii) for islands <1 ha in size. The Akaike information criterion (AIC) was used to select the best model (bold figures).

Predictors	r^2	P	AIC
All islands			
Log Area + LMT	0.70	<0.0001	1465.0
Log Area	0.55	<0.0001	1522.4
LMT	0.36	0.0001	1572.9
Islands (size < 1 ha)			
Log Area + Log NPI	0.39	<0.0001	758.9
Log Area	0.20	<0.0001	777.9
LMT	0.01	0.491	794.9
Log NPI	0.23	<0.0001	774.4

landscape-scale processes that determine forest composition. This network of forest patches is also of biogeographic and conservation interest, in that it links the rich woody flora of the tropical Caribbean with the less speciose temperate forests of North America. Our research objective was to evaluate current metacommunity processes for what they might portend about species movements through this or other subtropical landscapes as climate changes. We found little turnover from tropical to temperate flora within our study area; instead metacommunity structure was highly nested, with species-poor sites occupied by a small suite of ubiquitous tropical trees. In addition, site variables and attributes of local species assemblages suggested that stand composition was influenced not only by tolerance to cold temperature, but also by dispersal limitation, and especially by habitat characteristics associated with patch size. Local effects associated with small patch size are likely to constrain the northward movement of tropical species, even as macroclimatic conditions become more favourable to them.

Metacommunity structure

The EMS analytical approach used in this study is an effective method to evaluate competing hypotheses about metacommunity structure (Willig *et al.*, 2011). We supplemented the EMS sequence with (1) multiple regressions that clarified the relationships of geographic and climatic variables with the primary ordination axis, (2) classification analysis that defined the units suggested by the positive range boundary clumping result from EMS, and (3) statistical comparison of three community-aggregated trait characteristics among the classification groups discussed above.

Although RA Axis 1 explained only one-sixth of the correspondence between site and species, the matrix organized in accordance with it exhibited high coherence, indicating that

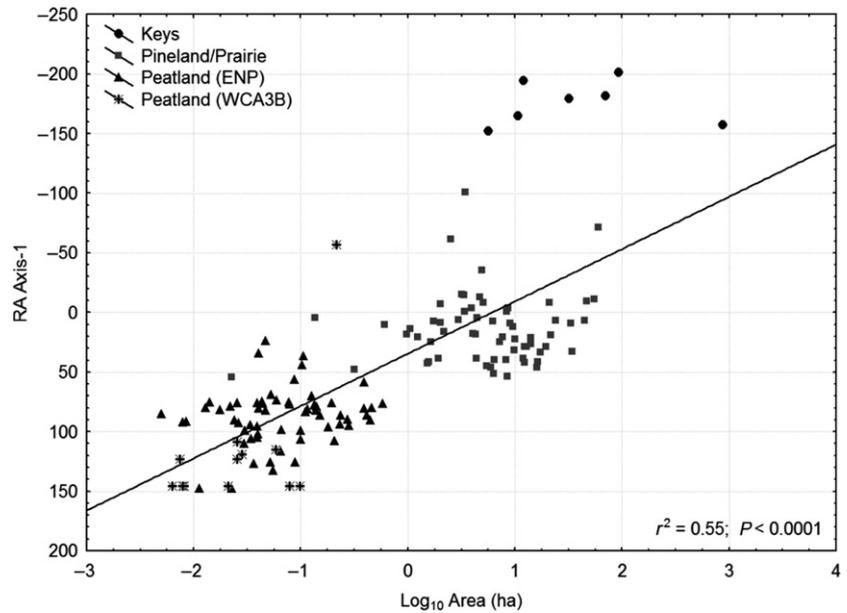


Figure 4 Scatterplot showing the relationship between hammock area and RA Axis-1 scores.

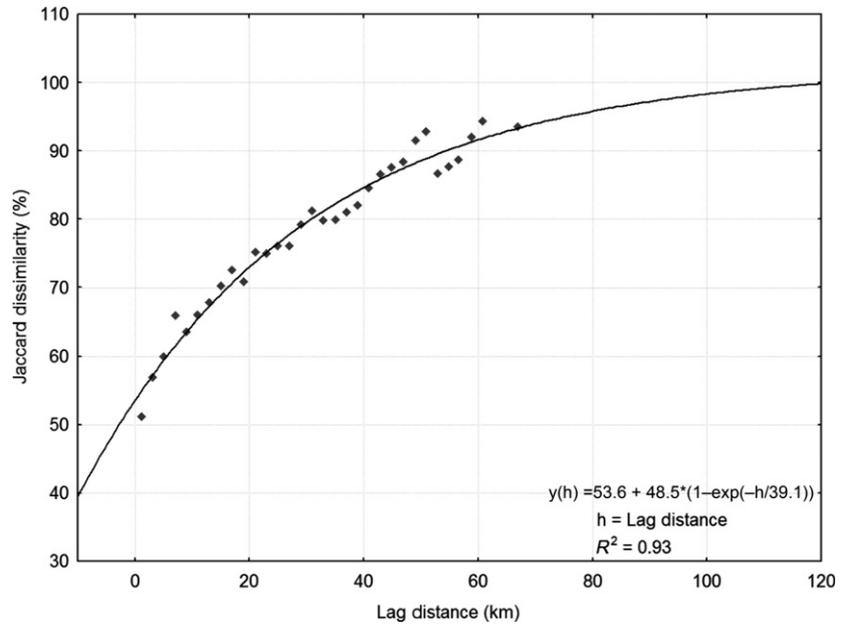


Figure 5 Spatial pattern in forest compositional dissimilarity with distance in the study area.

the environmental factors that drive tree species distributions are common across most taxa. According to Presley *et al.* (2010), positive coherence is widespread among well-sampled metacommunities that encompass broad environmental gradients. Still, it is noteworthy that the coherence evident here applies within a single forest type, in which the range in environmental conditions is not enough to incorporate other recognized plant communities. Moreover, RA Axis 1 is interpretable through its strong relationships with site variables such as hammock size, minimum winter temperature, and NPI, an index of the proximity of neighbouring seed sources. These variables exhibit parallel decreases from the Keys through the interior Everglades, but represent distinct processes affecting hammock composition.

Perhaps the most notable characteristic of the metacommunity we studied was the nested structure that emerged when species and sites were arranged according to their positions along the dominant ecological axis. According to Matthews *et al.* (2015), nestedness is uncommon in both oceanic and habitat island data, even when the matrix is arranged optimally to produce the pattern (but *cf.* Wright *et al.*, 1998). Why then did nestedness emerge in this forest metacommunity? Presley *et al.* (2010) suggested that dispersal ability (Kadmon, 1995; Ganzhorn & Eisenbeiss, 2001), tolerance to abiotic conditions (McAbendroth *et al.*, 2005) or habitat specialization (Vallan, 2000) may allow certain species to navigate past ecological filters that create nested structure. In south Florida forests, the conditions for habitat

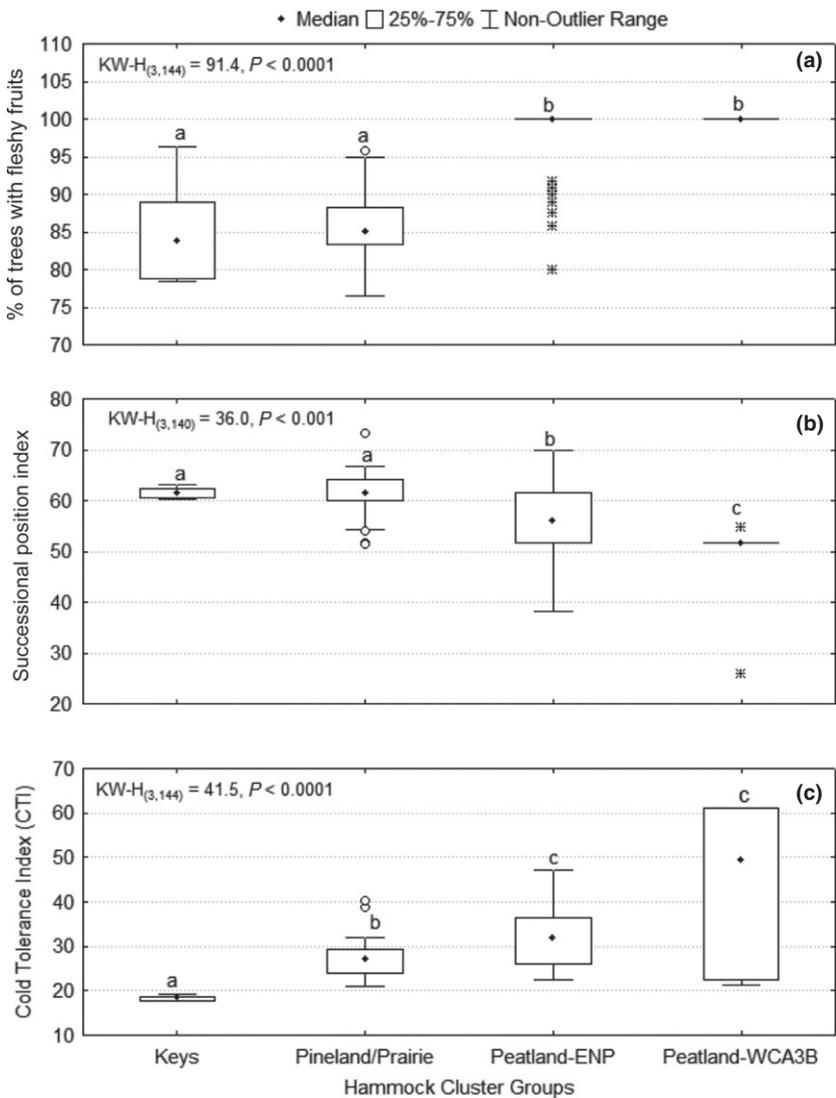


Figure 6 Box-plots showing the (a) percent of trees with fleshy fruits, (b) Successional Position Indices (SPI), and (c) Cold Tolerance Indices (CTI) for four hammock groups. Sub-regions followed by the same letter did not differ at $\alpha = 0.05$ (Kruskal-Wallis test, followed by a multiple comparison 'Z'-test).

specialization may be fixed by hammock size, which was the best predictor of RA score, and which decreased precipitously from the extensive and species-rich Keys hammocks to the small and depauperate tree islands of the Everglades interior. According to niche-based concepts of community assembly, increasing patch area may incorporate additional habitat variation, presenting suitable conditions for a broader range of species (MacArthur & Wilson, 1967; Crawley & Harral, 2001). In our network, which encompassed a gradient from edge-only stands as small as 50 m² to extensive hammocks exceeding 10 ha, large fragments include a greater proportion of forest core environments that enable edge-averse species to persist (Honnay *et al.*, 1999). The ecological stresses to which edge environments are prone vary: fire or freeze on the mainland, storm tides and salt spray in the Keys, and wind damage throughout. In all instances, recolonization following disturbance is apt to come from shade-intolerant, well-dispersed, early-successional species.

Augmented by classification analysis, our analysis of range boundary clumping indicated that the nested pattern of species loss along the environmental gradient occurred in

sub-regionally defined, compositionally similar sets of tree islands. Evidence of range boundary clumping in more continuous landscapes usually implies strong biotic integration, featuring interdependencies among species within local neighbourhoods, and has been described as ‘‘Clementsian’’ (Leibold & Mikkelsen, 2002). For forest fragments separated by wetland expanses, however, compositional similarity must be driven by processes operating across patches, e.g., seed dispersal (Levey *et al.*, 2008), historical biogeographical dynamics (Henriques-Silva *et al.*, 2013), or simply by distinctive physical conditions or disturbance regimes. In south Florida, hydrologic condition and nutrient availability certainly differ among sub-regions, though tree islands may be somewhat insulated from these differences due to their elevated landscape position. Moreover, human occupancy varies sharply, with tree islands in WCA3B and, to a lesser extent, ENP peatlands receiving the most concentrated and recent use. Due to the lack of suitable data sources, we did not attempt to account for these influences, and focused our analysis on factors that were both quantifiable throughout the region, and might be linked to current and future metacommunity development.

To interpret hammock metacommunity patterns, we used publicly available sources, e.g., aerial photography and meteorological data, to derive ecologically pertinent habitat-, dispersal- and climate-related site variables, and paired them with related community-aggregated functional traits. We found that as tree islands became smaller, more isolated, and cooler along the regional gradient, resident tree assemblages became more exclusively animal-dispersed, dominated by early-successional species, and comprised of species that experience colder winter temperatures within their range limits. This association between site characteristics and the composite trait mixture of resident tree assemblages is consistent with the hypothesis that dispersal limitation, edge environments, and periodic freezing temperatures are ecological filters that prevent all but a small subset of species from occupying interior Everglades hammocks, thereby producing the strongly nested metacommunity structure. Importantly, the scope and resolution of these filters differ. Climate variation extends to the broadest scales of time and space, while influencing species distributions down to the local level. The seed dispersal process, whether by water, wind or animals, is best viewed as a landscape-scale attribute that applies to multiple sites within and across sub-regions. In contrast, the size and shape of surfaces suitable for mesic tree species are locally idiosyncratic, and their ecological effects are directed at each fragment independently. Each of these processes is likely to affect the future dynamics of tree species in the region.

Implications for forest response to climate change

In considering the effect that warmer temperatures will have on Florida forests, Box *et al.* (1999) reasoned that the northward recession of temperate species would be relatively prompt and predictable, as they would find themselves outside their climatic limits. In contrast, the extension of tropical species to the north would likely be less predictable and rapid, i.e., limited by species' capacities to disperse as well as by local biological and physical factors. Difference in expected response between populations at the trailing versus leading edges of species distributions is not unique to temperate-tropical interfaces. Niches vacated by the recession of one set of species are filled by new arrivals or species already present in the area. If advancing species are slow in arriving, the result might be a loss in diversity and ecosystem services, or perhaps an expansion of weedy native or non-native species (Crumpacker *et al.*, 2001).

The current south Florida forest is a product of changing climate. During the late Pleistocene, the regional climate was cool and dry, supporting oak scrub vegetation, but by the early Holocene (~10K BP) temperatures were not much different from today's (Watts, 1980). Worldwide temperatures warmed by ~0.6 °C early in the Holocene, followed by a cooling period in which temperatures dropped by 0.7 °C (Marcott *et al.*, 2013). The Everglades wetland began to form about 6300 BP, when temperatures were warm, precipitation was relatively high, and seas were steadily rising (Gleason &

Stone, 1994). Everglades tree islands were present as early as 4K years ago, with formation and subsequent expansion associated with periods of relative regional aridity (Bernhardt, 2011). Pollen from sediments deposited in these early Everglades hammocks does not contain evidence of tropical species (Willard *et al.*, 2006; Bernhardt, 2011). However, the absence of pollen does not necessarily signify that the first Everglades hammocks lacked tropical trees, which are mostly insect-pollinated and under-represented in the pollen record; notably, pollen of several tropical tree species was found in a layer dating to 2300 BP in the Florida Keys (Winkler *et al.*, 2001). Nevertheless, the region's forest landscape appears to be a relatively recent construct that developed under fluctuating temperature and moisture conditions.

Our data shows that temperature variation is a high order driver of metacommunity structure in south Florida, whose importance is likely to persist into the future. However, the relationship between rising global temperatures and the occurrence of locally damaging cold temperature events is complicated by teleconnections with broad circulation patterns. For instance, cold temperature extremes in Florida are strongly associated with the negative phase of the North Atlantic Oscillation (Hagemeyer, 2006), and warmer winters associated with La Nina may actually increase the frequency of extreme cold events (Stefanova *et al.*, 2013). While freeze events are likely to become a less potent ecological force, their frequency in the near term is not easily predicted and their effect on the metacommunity uncertain.

In contrast, changes in water regime occasioned by global sea level rise may have a larger and more predictable impact on the forests of the region. Currently rising globally at a rate of 2.6–2.9 mm.year⁻¹ (Watson *et al.*, 2015), sea level in south Florida is expected to rise at an accelerating rate, increasing by a cumulative 46 cm during the 2010–2060 period (Obeysekera *et al.*, 2015). Rising groundwater levels will eliminate small upland patches and cause larger ones to decrease in size, thereby limiting their suitability for edge-sensitive species. With increasing isolation, seed dispersal among the remaining fragments may also decrease, depending on the responses of zoochorous birds and mammals to the associated landscape changes. The result will be a loss in the diversity of the region's forests in the interim before surrounding waters transgress onto the emergent south Florida land mass. Due to the region's low topography and coastal setting, the prognosis for its forests is gloomier than for many sub-tropical areas. However, its metacommunity structure provides a dramatic lesson regarding local constraints on species migration and community reassembly with changing climate, and reminds us that these responses will unfold in real landscapes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Site characteristics.

Table S2. Species characteristics.

BIOSKETCH

The authors are current or former staff of Florida International University's South Florida Terrestrial Ecosystem Lab (softel.fiu.edu), a research group that takes a field-oriented,

multi-disciplinary approach to the study of south Florida and the Caribbean environments. The group studies ecological processes in the coastal and freshwater landscapes of the Everglades and Florida Keys, as well as the adjacent urban areas, focusing most recently on the region's dry tropical forests. Author contributions: M.S.R, J.P.S. and P.L.R. conceived the ideas; P.L.R., M.S.R., A.A.S., S.S. and J.P.S. collected the data; J.P.S. and M.S.R. analysed the data; M.S.R. and J.P.S. wrote the paper.

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