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Community assembly of the ferns of Florida

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PREMISE OF THE STUDY: Many ecological and evolutionary processes shape the assembly of organisms into local communities from a regional pool of species. We analyzed phylogenetic and functional diversity to understand community assembly of the ferns of Florida at two spatial scales.

METHODS: We built a phylogeny for 125 of the 141 species of ferns in Florida using five chloroplast markers. We calculated mean pairwise dissimilarity (MPD) and mean nearest taxon distance (MNTD) from phylogenetic distances and functional trait data for both spatial scales and compared the results to null models to assess significance.

KEY RESULTS: Our results for over vs. underdispersion in functional and phylogenetic diversity differed depending on spatial scale and metric considered. At the county scale, MPD revealed evidence for phylogenetic overdispersion, while MNTD revealed phylogenetic and functional underdispersion, and at the conservation area scale, MPD revealed phylogenetic and functional underdispersion while MNTD revealed evidence only of functional underdispersion.

CONCLUSIONS: Our results are consistent with environmental filtering playing a larger role at the smaller, conservation area scale. The smaller spatial units are likely composed of fewer local habitat types that are selecting for closely related species, with the larger-scale units more likely to be composed of multiple habitat types that bring together a larger pool of species from across the phylogeny. Several aspects of fern biology, including their unique physiology and water relations and the importance of the independent gametophyte stage of the life cycle, make ferns highly sensitive to local, microhabitat conditions.

KEY WORDS community assembly; community phylogenetics; ferns; functional diversity; mean pairwise dissimilarity; mean nearest taxon distance; phylogenetic diversity; species richness.

Studies of community assembly attempt to understand how the organisms present in a regional species pool assemble into smaller species groups, or local assemblages (Connor and Simberloff, 1979; Cornell and Lawton, 1992; Kraft and Ackerly, 2014). Numerous evolutionary and ecological factors influence community assembly processes and affect which sets of species form particular local assemblages. In general, more closely related species are often expected to be similar ecologically and in their morphological and functional traits and are therefore expected to compete strongly, leading to competitive exclusion and ultimately an assemblage composed of species less closely related to one another than would be expected by chance (phylogenetic overdispersion) (Webb, 2000; Webb et al., 2002; Cahill et al., 2008; Cavender-Bares et al., 2009). In contrast, if abiotic phenomena (e.g., climate, soils, disturbance) in a particular location select strongly for species with similar morphological or ecological traits, the assemblage in that location may

consist of species that are more closely related to one another than would be expected by chance (phylogenetic underdispersion or clustering; used interchangeably sensu Swenson, 2014), assuming there is evolutionary conservation, or phylogenetic signal, for the traits in question (Webb, 2000; Webb et al., 2002; Cavender-Bares et al., 2009). Another possibility is that stochastic processes may cause local assemblages and their phylogenetic and/or functional composition to be no different than expected for an assemblage based on random draws from the regional species pool (Drake, 1991; Hubbell, 2001; Chase, 2007).

A key question in community assembly is whether the filtering process is biased toward members of certain lineages (Silvertown et al., 2006) or toward species with particular traits (de Bello et al., 2016) and to what extent phylogenetic signal in traits conflates these two patterns. While evolutionary processes largely determine the traits of organisms, ecological and biotic interactions among species in an assemblage also influence those species' evolution (Cavender-Bares et al., 2006; Vamosi et al., 2009; Gerhold et al., 2015). In addition, the framework described above for predicting over vs. underdispersion makes several assumptions about the relationship between traits and phylogenetic signal that are not often tested directly (Mayfield and Levine, 2010; Gerhold et al., 2015; Narwani et al., 2015). These assumptions include that there *is* phylogenetic signal in functional and morphological traits, that trait similarity correlates with phylogenetic relatedness (i.e., that close relatives are more similar than distant relatives), and that habitat filtering selects for species with similar traits while competition selects for divergent traits. The extent to which species assemblages will show evidence of over vs. underdispersion has also been shown to be strongly influenced by the scale at which the assemblages are defined, both in terms of taxonomy and geography (Cavender-Bares et al., 2006, 2009; Swenson et al., 2006; Vamosi et al., 2009; Kraft and Ackerly, 2014). The assumptions described above are likely strongly scale-dependent, and this dependence may lead directly to differences in phylogenetic or functional structure at different scales. We may be able to better understand these effects by simultaneously investigating patterns of phylogenetic structure and functional diversity across assemblages to estimate the extent to which evolutionary vs. ecological processes are driving assembly at different scales.

In the current study, we address these questions by exploring community assembly of ferns across the state of Florida. Florida is one of the most plant-species-rich regions in the United States, with more than 4700 native and naturalized species of plants (Wunderlin et al., 2017). The state has the highest fern diversity in the continental United States (Nelson, 2000), with ca. 140 species, including more than 100 native plus ca. 40 naturalized species. The fern species present in Florida vary in their distributions across the state and in their habitat preferences and morphological and ecological traits (Fig. 1), making them an excellent group with which to explore how species' phylogenetic relationships and traits shape community assembly. Although in reality ferns belong to natural communities composed of many types of organisms, a study focused on a particular group of interest can facilitate insights into the assembly rules acting on that group that account for unique aspects of their biology and evolution. Such has been the case for community phylogenetic analyses focused on organisms as diverse as lizards (Losos et al., 2003), salamanders (Kozak et al., 2005), birds (Lovette and Hochachka, 2006), snails (Astor et al., 2014), insects (Hembry et al., 2013), tropical rainforest trees (Webb, 2000; Chazdon et al., 2003; Kembel and Hubbell, 2006; Swenson et al., 2006, 2007), other woody plants (Herrera, 1992; Cavender-Bares et al., 2004; Ackerly et al., 2006; Verdú and Pausas, 2007; Naaf and Wulf, 2012), and all vascular plants (J. Allen et al., Florida Museum of Natural History, University of Florida, personal communication). Compared to other plants, ferns are unique in a number of characteristics that may influence community assembly processes. Physiologically, for example, ferns have much lower rates of stomatal and hydraulic conductance than most angiosperms (Brodribb and Holbrook, 2004; Brodribb et al., 2005; McAdam and Brodribb, 2013; Martins et al., 2016), which likely has profound effects on aspects of their habitat and climatic demands that relate to precipitation and water availability. Ferns also have two free-living, nutritionally and ecologically independent life cycle stages, the sporophyte and gametophyte, each of which may follow its own assembly rules (Haufler et al., 2016; Nitta et al., 2016). Ferns have been the subjects of only a handful of community assembly studies (Karst et al., 2005; Jones et al., 2006; Kluge and Kessler, 2011; Hennequin et al., 2014; Nitta et al., 2016), and there is reason to suspect that their unique biology may lead to novel assembly patterns. While several of these studies have examined the impact of elevational gradients on fern community assembly, our study is the first to investigate the potential effects of spatial scale on analyses of fern species assemblages.

We assessed phylogenetic and functional diversity of Florida ferns using the mean pairwise dissimilarity and mean nearest taxon distance metrics (Webb et al., 2002; Tucker et al., 2017) with comparisons to null models calculated as standardized effect sizes (SES) (Kembel, 2009). To understand the extent to which spatial scale might influence our findings, we conducted our analyses at two non-overlapping spatial scales: a larger scale corresponding to counties (average size 2088 km^2) and a smaller scale corresponding to a set of conservation areas in south Florida (average size 15 km^2). We asked whether the species present in county-level and conservation area-level assemblages differ from a random selection of species from their corresponding regional species pool (either all species present in the state or all species present in the conservation areas, respectively) in terms of phylogeny and morphological traits, and whether the direction of non-random assembly (overdispersion vs. underdispersion) is scale-dependent.

MATERIALS AND METHODS

Taxon sampling, DNA extraction, and amplification

We included 125 of the 141 species of ferns present in Florida. We arrived at the number 141 by consulting the *Ferns of Florida* (Nelson, 2000), the *Flora of Florida* volume on pteridophytes (Wunderlin and Hansen, 2000), the *Flora of North America* volume on pteridophytes (Flora of North America Editorial Committee, 1993) and the online Atlas of Florida Plants (Wunderlin et al., 2017; http://florida.plantatlas.usf.edu/). We omitted taxa that are known or suspected to be hybrids. Of the total 141 species (Table 1), we were unable to obtain DNA or sequences for 16 species; for the remaining 125 species, data were available in GenBank, or we were able to collect material. Ferns and seed plants are sister clades (Pryer et al., 2001), and so we used the angiosperm *Amborella trichopoda* as the outgroup for our phylogenetic analyses.

For newly collected species, we used a DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) to extract total genomic DNA following the manufacturer's protocols. We amplified and

FIGURE 1. Photographs and county-level locality/voucher information for several ferns found in Florida. Species in A–D have wide ranges in the eastern United States; those in E–H are generally found farther south, typically belonging to tropical rather than temperate floras. (A) *Osmundastrum cinnamomea*, (B) *Polystichum acrostichoides*, (C) *Asplenium platyneuron*, (D) *Woodwardia areolata*, (E) *Psilotum nudum*, (F) *Anemia adiantifolia*, (G) *Vittaria lineata*, (H) *Asplenium dentatum*. Voucher information is from the Atlas of Florida Vascular Plants (Wunderlin et al., 2017; http://florida.plantatlas.usf.edu/). *Photo credits:* E.B. Sessa (A, B, D, F, G) and L. Trotta (C, E, H).

TABLE 1. List of 141 species of ferns that occur in Florida and their assigned family (PPG 1, 2016). The "Incl.?" column indicates whether or not the species was included in our analyses (125 species).

No.	Family	Taxon	Incl.?	No.	Family	Taxon	Incl.?
1	Anemiaceae	*Anemia adiantifolia*	yes	72	Osmundaceae	*Osmundastrum cinnamomeum*	yes
2	Anemiaceae	*Anemia wrightii*	yes	73	Polypodiaceae	*Campyloneurum angustifolium*	yes
3	Aspleniaceae	*Asplenium abscissum*	yes	74	Polypodiaceae	*Campyloneurum costatum*	yes
4	Aspleniaceae	*Asplenium cristatum*	yes	75	Polypodiaceae	*Campyloneurum phyllitidis*	yes
5	Aspleniaceae	*Asplenium erosum*	yes	76	Polypodiaceae	*Neurodium lanceolatum*	yes
6	Aspleniaceae	*Asplenium heterochroum*	yes	77	Polypodiaceae	*Pecluma plumula*	yes
7	Aspleniaceae	*Asplenium monanthes*	yes	78	Polypodiaceae	*Pecluma ptiloton*	yes
8	Aspleniaceae	*Asplenium platyneuron*	yes	79	Polypodiaceae	*Phlebodium aureum*	yes
9	Aspleniaceae	*Asplenium resiliens*	yes	80	Polypodiaceae	*Phymatosorus scolopendria*	yes
10	Aspleniaceae	*Asplenium serratum*	yes	81	Polypodiaceae	*Platycerium bifurcatum*	yes
11	Aspleniaceae	*Asplenium trichomanes*	yes	82	Polypodiaceae	*Pleopeltis astrolepis*	yes
12	Aspleniaceae	*Asplenium dentatum*	—	83	Polypodiaceae	*Pleopeltis polypodioides*	yes
13	Aspleniaceae	*Asplenium pumilum*	—	84	Polypodiaceae	*Serpocaulon triseriale*	yes
14	Aspleniaceae	*Asplenium verecundum*	—	85	Polypodiaceae	*Microgramma heterophylla*	—
15	Athyriaceae	*Athyrium filix-femina*	yes	86	Polypodiaceae	*Pecluma dispersa*	—
16	Athyriaceae	*Deparia petersenii*	yes	87	Psilotaceae	*Psilotum nudum*	yes
17	Athyriaceae	*Diplazium esculentum*	yes	88	Pteridaceae	*Acrostichum aureum*	yes
18	Blechnaceae	*Blechnum occidentale var minor*	yes	89	Pteridaceae	*Acrostichum danaeifolium*	yes
19	Blechnaceae	*Blechnum serrulatum*	yes	90	Pteridaceae	*Adiantum capillus-veneris*	yes
20	Blechnaceae	*Stenochlaena tenuifolia*	yes	91	Pteridaceae	*Adiantum caudatum*	yes
21	Blechnaceae	*Woodwardia areolata*	yes	92	Pteridaceae	*Adiantum tenerum*	yes
22	Blechnaceae	*Woodwardia radicans*	yes	93	Pteridaceae	*Adiantum trapeziforme*	yes
23	Blechnaceae	*Woodwardia virginica*	yes	94	Pteridaceae	*Adiantum villosum*	yes
24	Cystopteridaceae	*Cystopteris protrusa*	yes	95	Pteridaceae	*Ceratopteris pteridoides*	yes
25	Dennstaedtiaceae	*Hypolepis repens*	yes	96	Pteridaceae	*Ceratopteris thalictroides*	yes
26	Dennstaedtiaceae	*Pteridium aquilinum* var. *caudatum*	yes	97	Pteridaceae	*Myriopteris alabamensis*	yes
27	Dennstaedtiaceae	*Pteridium aquilinum* var. *latiusculum*	yes	98	Pteridaceae	*Myriopteris lanosa*	yes
28	Dennstaedtiaceae	*Pteridium aquilinum* var. *pseudocaudatum*	yes	99	Pteridaceae	*Myriopteris microphylla*	yes
29	Dennstaedtiaceae	*Dennstaedtia bipinnata*	—	100	Pteridaceae	*Pellaea atropurpurea*	yes
30	Dryopteridaceae	*Ctenitis sloanei*	yes	101	Pteridaceae	*Pellaea viridis*	yes
31	Dryopteridaceae	*Ctenitis submarginalis*	yes	102	Pteridaceae	*Pityrogramma calomelanos*	yes
32	Dryopteridaceae	*Cyrtomium falcatum*	yes	103	Pteridaceae	*Pityrogramma trifoliata*	yes
33	Dryopteridaceae	*Dryopteris ludoviciana*	yes	104	Pteridaceae	*Pteris bahamensis*	yes
34	Dryopteridaceae	*Polystichum acrostichoides*	yes	105	Pteridaceae	*Pteris cretica*	yes
35	Dryopteridaceae	*Polystichum tsus-simense*	yes	106	Pteridaceae	*Pteris grandifolia*	yes
36	Dryopteridaceae	*Rumohra adiantiformis*	yes	107	Pteridaceae	*Pteris multifida*	yes
37	Equisetaceae	*Equisetum hyemale* var. *affine*	yes	108	Pteridaceae	*Pteris quadriaurita*	yes
38	Equisetaceae	*Equisetum ramosissimum*	yes	109	Pteridaceae	*Pteris tripartita*	yes
39	Gleicheniaceae	*Dicranopteris flexuosa*	yes	110	Pteridaceae	*Pteris vittata*	yes
40	Hymenophyllaceae	*Trichomanes holopterum*	yes	111	Pteridaceae	*Vittaria lineata*	yes
41	Hymenophyllaceae	*Trichomanes krausii*	yes	112	Pteridaceae	*Adiantum anceps*	—
42	Hymenophyllaceae	*Trichomanes lineolatum*	—	113	Pteridaceae	*Adiantum melanoleucum*	—
43	Hymenophyllaceae	*Trichomanes petersii*	—	114	Salviniaceae	*Azolla filiculoides*	yes
44	Hymenophyllaceae	*Trichomanes punctatum* subsp. *floridanum*	—	115	Salviniaceae	*Salvinia minima*	yes
45	Lindsaeaceae	*Odontosoria clavata*	yes	116	Salviniaceae	*Salvinia molesta*	yes
46	Lomariopsidaceae	*Lomariopsis kunzeana*	yes	117	Schizaeaceae	*Schizaea pennula*	yes
47	Lygodiaceae	*Lygodium japonicum*	yes	118	Tectariaceae	*Tectaria fimbriata*	yes
48	Lygodiaceae	*Lygodium microphyllum*	yes	119	Tectariaceae	*Tectaria heracleifolia*	yes
49	Marsileaceae	*Marsilea hirsuta*	yes	120	Tectariaceae	*Tectaria incisa*	yes
50	Marsileaceae	*Marsilea macropoda*	yes	121	Tectariaceae	*Tectaria coriandrifolia*	—
51	Marsileaceae	*Marsilea minuta*	yes	122	Thelypteridaceae	*Macrothelypteris torresiana*	yes
52	Marsileaceae	*Marsilea oligospora*	yes	123	Thelypteridaceae	*Phegopteris hexagonoptera*	yes
53	Marsileaceae	*Marsilea vestita*	yes	124	Thelypteridaceae	*Thelypteris augescens*	yes
54	Marsileaceae	*Marsilea ancylopoda*	—	125	Thelypteridaceae	*Thelypteris dentata*	yes
55	Nephrolepidaceae	*Nephrolepis biserrata*	yes	126	Thelypteridaceae	*Thelypteris grandis*	yes
56	Nephrolepidaceae	*Nephrolepis multiflora*	yes	127	Thelypteridaceae	*Thelypteris hispidula* var. *versicolor*	yes
57	Nephrolepidaceae	*Nephrolepis cordifolia*	yes	128	Thelypteridaceae	*Thelypteris interrupta*	yes
58	Nephrolepidaceae	*Nephrolepis exaltata*	yes	129	Thelypteridaceae	*Thelypteris kunthii*	yes
59	Nephrolepidaceae	*Nephrolepis falcata*	yes	130	Thelypteridaceae	*Thelypteris opulenta*	yes
60	Onocleaceae	*Onoclea sensibilis*	yes	131	Thelypteridaceae	*Thelypteris ovata*	yes
61	Ophioglossaceae	*Botrychium biternatum*	yes	132	Thelypteridaceae	*Thelypteris palustris* var. *pubescens*	yes

(Continued)

TABLE 1. (Continued)

No.	Family	Taxon	Incl.?	No.	Family	Taxon	Incl.?
62	Ophioglossaceae	*Botrychium lunarioides*	yes	133	Thelypteridaceae	*Thelypteris patens*	yes
63	Ophioglossaceae	*Botrychium virginianum*	yes	134	Thelypteridaceae	*Thelypteris reptans*	yes
64	Ophioglossaceae	*Ophioglossum crotalophoroides*	yes	135	Thelypteridaceae	*Thelypteris reticulata*	yes
65	Ophioglossaceae	*Ophioglossum engelmannii*	yes	136	Thelypteridaceae	*Thelypteris sancta*	yes
66	Ophioglossaceae	*Ophioglossum nudicaule*	yes	137	Thelypteridaceae	*Thelypteris serrata*	yes
67	Ophioglossaceae	*Ophioglossum palmatum*	yes	138	Thelypteridaceae	*Thelypteris tetragona*	yes
68	Ophioglossaceae	*Ophioglossum pendulum*	yes	139	Thelypteridaceae	*Thelypteris resinifera*	—
69	Ophioglossaceae	*Ophioglossum petiolatum*	yes	140	Thelypteridaceae	*Thelypteris sclerophylla*	—
70	Ophioglossaceae	*Botrychium jenmanii*	—	141	Woodsiaceae	*Woodsia obtusa*	yes
71	Osmundaceae	*Osmunda regalis* var. *spectabilis*	yes				

sequenced five chloroplast markers: coding regions *atpA*, *atpB*, and *rbcL* and the spacers *rps4-trnS* and *trnL-trnF*. Primer information and polymerase chain reaction (PCR) protocols were given by Sessa et al. (2012a, b). Clean PCR products were sequenced at the Interdisciplinary Center for Biotechnology at the University of Florida. All accession numbers (for new sequences and sequences obtained from GenBank) are provided in Appendix S1 (see the Supplemental Data included with this article).

Spatial scale

There are 67 counties in Florida, which range in size from 622 km^2 (Union County) to 5268 km^2 (Palm Beach County), with an average size of 2088 km^2. We split Monroe County into two units, one each for the mainland and the Florida Keys, for a total of 68 units in the county-level data set (see Appendix S2 for a labeled map of the counties in Florida). We obtained data on species' presence/absence in each county for this larger-scale data set from the online Atlas of Florida Plants (Wunderlin et al., 2017; http://florida.plantatlas.usf.edu/). We also obtained plant species lists for 446 conservation areas in South Florida from a database managed by the Institute for Regional Conservation in Miami, Florida (IRC: http://regionalconservation.org/ircs/database/site/ConservationAreas.asp) for the smaller-scale data set. For each conservation area, we extracted ferns from the species list and then excluded conservation areas with fewer than three fern species from further analyses. We also removed the eight conservation areas greater than 70,000 acres in size, leaving only areas that were less than half the size of the smallest county, so that the two data sets did not overlap in terms of the sizes of the included units (counties or conservation areas). The final data set included 178 conservation areas that range in size from 0.6 to 26,481 hectares (approximately 265 km^2). We note that both counties and conservation areas are arbitrary units, and they may not always correspond to non-overlapping size bins, but they were useful units for the present study. We also note that a large apparent gap between conservation areas in the east and west parts of South Florida (see Fig. 3B) is caused by the presence of the Everglades, which occupy most of the south and southwestern parts of the state. This region is one of the largest conservation areas and was excluded from the study for that reason.

Phylogenetic analyses

We edited sequences and assembled contigs using Geneious v. 9. We aligned sequences for each plastid region using the plugin for MAFFT (Katoh and Standley, 2013) in Geneious (Kearse et al., 2012) and then concatenated the alignments for the five loci (plastids are maternally inherited in ferns and do not recombine [Vogel et al., 1998]). We identified the best nucleotide substitution model, as well as the optimal partitioning scheme for the entire data set, using PartitionFinder v. 1.1.1 (Lanfear et al., 2012). For *rps4-trnS* and *trnL-trnF*, which included portions of the coding regions of *rps4* and *trnL*, respectively, we delimited the noncoding and coding portions separately in the PartitionFinder control file.

Some phylogenetic and functional diversity metrics (e.g., Faith's PD; Faith, 1992) can be calculated using either a phylogram or an ultrametric tree. We used an ultrametric chronogram as the phylogeny in our downstream analyses because the metrics we used (in particular, mean nearest taxon distance) require ultrametricity. To produce an ultrametric tree for subsequent analyses, we used BEAST v. 2.4.2 (Bouckaert et al., 2014) to perform a molecular dating analysis with fossil calibrations. We referred to several previous fern-wide molecular dating analyses (Schuettpelz and Pryer, 2009; Rothfels et al., 2015; Testo and Sundue, 2016) when selecting fossil constraints. We followed the taxonomy for families and orders described by the Pteridophyte Phylogeny Group (PPG 1, 2016). Based on the species included in our data set, the constraints were set as follows: (1) the crown node of leptosporangiate ferns to 299 Myr based on the oldest inferred divergences within leptosporangiates (e.g., the split between Osmundales and all other leptosporangiates) (Miller, 1971; Zhaoqi and Taylor, 1988; Phipps et al., 1998; Galtier et al., 2001; Rößler and Galtier, 2002); (2) the crown node of Schizaeales to 167.7 Myr based on a fossil of *Stachypteris* (Van Konijnenburg-Van Cittert, 1981; Wikström et al., 2002); (3) the crown node of Salviniales to 140.2 Myr based on a fossil of *Regnellites* (Yamada and Kato, 2002); (4) the node uniting *Ceratopteris* and *Acrostichum* to 37.2 Myr based on a fossil allied to *Ceratopteris* (Dettmann and Clifford, 1992); (5) the node uniting Onocleaceae and Blechnaceae to 55.8 Myr based on a fossil assigned to *Onoclea sensibilis* (Rothwell and Stockey, 1991); and (6) the crown node of Polypodiaceae to 33.9 Myr based on a fossil *Protodrynaria* (Van Uffelen and van Uffelen, 1991). We modeled each calibration point using a gamma prior distribution. The gamma is a flexible, continuous probability distribution that can assume a number of shapes, from normal to exponential, depending on the values of its two parameters (alpha/shape and beta/rate). With alpha = 1, for example, gamma approximates an exponential distribution, and with values much greater than 1, a normal distribution. For each calibration point, we set alpha and beta to 2.0 and 5.0, respectively, with the offset equal to the age of the fossil. This centered the bulk of each age distribution at slightly older than the age of the fossil, with a relatively long tail. We also constrained several nodes that have proven difficult to resolve in previous broad-scale analyses of ferns, but without assigning fossils to them (see Fig. 2).

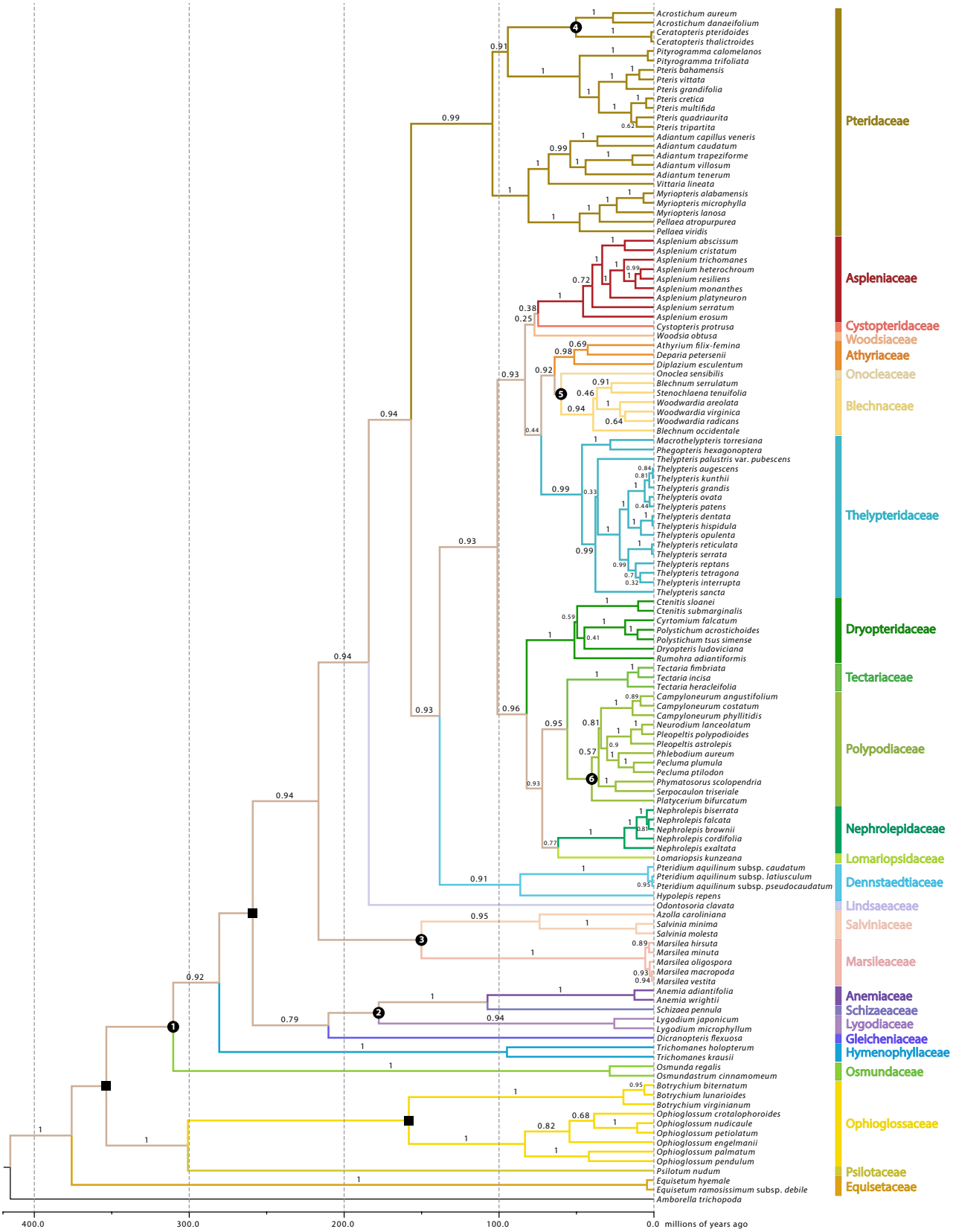

FIGURE 2. Maximum clade credibility chronogram from BEAST analysis of 125 species of Florida ferns. Posterior probabilities are given above each branch. Six fossil calibration points are indicated with black circles (see methods for details), and three additional constrained nodes are indicated with black squares. Branches are colored by family, following the PPG classification (PPG 1, 2016).

We used an uncorrelated, lognormal relaxed clock model and a birth–death process speciation prior, with clock and tree models linked across data partitions. We ran the analysis for 50,000,000 generations, with parameters sampled every 1000 generations and trees every 10,000 generations. We assessed convergence from the log file using Tracer 1.6 (Rambaut et al., 2014), examining the distribution of the posterior and the estimated sample sizes (ESS) of all parameters. We determined that the analysis had run for sufficiently long if all ESS values were above 200. We used TreeAnnotator v. 2.4.2 (Bouckaert et al., 2014) to summarize a post burn-in set of trees and annotate a maximum clade credibility chronogram with mean divergence times and 95% highest posterior density (HPD) intervals for the age of each node.

Functional traits

We used a natural language processing (NLP) approach to transform taxonomic descriptions for our 125 fern taxa into taxon-by-character matrices. First, we obtained 205 taxonomic descriptions written in a formal telegraphic style. These included descriptions of 27 families and 53 genera in addition to the 125 sampled species, since the familial and generic descriptions include traits relevant for each species. The majority of descriptions came from the *Flora of North America* volume on pteridophytes (Flora of North America Editorial Committee, 1993), with some additional descriptions from the *Flora of China* volume on ferns and lycophytes (Wu et al., 2013). We transformed the text file descriptions into eXtensive Markup Language format (XML) using the Text Capture Input Generator Tool v. 1.0 that is part of the Explorer of Taxon Concepts (ETC) toolkit (http://etc.cs.umb.edu/etcsite/). We used the ETC Text Capture Tool (v. 0.1.127-SNAPSHOT) to parse and semantically annotate the text descriptions using the "Plant" setting option (OTO Glossary v. 0.19), which leverages a botanical glossary with >9000 terms (Endara et al., 2017). The parsed descriptions were then converted into a taxon-by-character matrix using the ETC Matrix Generator (v. 0.1.38-SNAPSHOT) using the "Inherit Values" option, which propagates values from familial and generic descriptions to lower levels. We used MatrixConverter (Liu et al., 2015) to evaluate the characters and character states in the resulting matrix using the raw matrix numbers, and checked the matrix manually by comparing values with the original text (Flora of North America Editorial Committee, 1993) as well as with the *Flora of Florida* volume on pteridophytes (Wunderlin and Hansen, 2000). Characters were chosen for inclusion in the final matrix based on coverage across species and relevance for physiology/function (e.g., traits relating to color of hairs or scales were considered purely morphological and were not included). In addition to the traits obtained from the taxonomic descriptions, we manually scored additional data on habitat and substrate (e.g., average soil pH) from the *Flora of Florida* pteridophytes volume (Wunderlin and Hansen, 2000). Data on wetland designation according to the National Wetland Plant List (Lichvar et al., 2014) were obtained from the Atlas of Florida Plants (Wunderlin et al., 2017; http://florida.plantatlas.usf.edu/).

We constructed a species by trait matrix, which we then converted to a species by species distance matrix using Gower's general coefficient of similarity (Gower, 1971), a measure of proximity between all pairs of sample units in a data matrix, including mixed data types. The Gower coefficient allows for both qualitative and quantitative trait data as well as missing values.

Statistical analyses

We conducted all statistical analyses in R (R Core Team, 2016), using the picante package (Kembel et al., 2010). To measure fern biodiversity in each county and conservation area, we calculated species richness, functional diversity, and phylogenetic diversity. Many indices exist for measuring functional and phylogenetic diversity (see Miller et al., 2017; Tucker et al., 2017; Villéger et al., 2017 for review and commentary on these metrics; note that we use "phylogenetic diversity" in a general sense and are not referring specifically to Faith's PD (Faith, 1992), a commonly used metric of phylogenetic diversity). We opted to use mean pairwise dissimilarity (MPD) and mean nearest taxon distance (MNTD) (Webb et al., 2002) because both can be used to calculate both functional and phylogenetic diversity, making our results for the two directly comparable to one another. In addition, MPD is independent of species richness (de Bello et al., 2016), a desirable property when calculating functional and phylogenetic diversity. Mean pairwise dissimilarity is the average of the dissimilarities in functional or phylogenetic distance between all pairs of species found within a given sample unit (e.g., county or conservation area):

$$\mathrm{MPD} = \frac{\Sigma_i^n \Sigma_j^n \delta_{i,j}}{n}, i \neq j,$$

where $\delta_{i,j}$ is the functional or phylogenetic distance between species i and j, and n is the number of species in the sample unit. Mean nearest taxon distance is the average minimum distance between species pairs within an assemblage:

$$\mathrm{MNTD} = \frac{\Sigma_i^n \min\delta_{i,j}}{n}, i \neq j$$

where $min\delta_{i,j}$ is the minimum functional or phylogenetic distance between species i and all other species in the assemblage, and n is the total number of species in the assemblage.

For calculating MPD and MNTD of functional diversity (referred to hereafter as $\mathrm{MPD}_{\mathrm{Fun}}$ and $\mathrm{MNTD}_{\mathrm{Fun}}$), the functional distance matrix is the Gower distance matrix of species by species trait data; for MPD and MNTD of phylogenetic diversity (hereafter, $\mathrm{MPD}_{\mathrm{Phy}}$ and $\mathrm{MNTD}_{\mathrm{Phy}}$), the phylogenetic distance matrix is the pairwise cophenetic distance of all species in the phylogeny, using the ultrametric phylogeny from the BEAST analysis. We used simple linear regression to determine whether species richness was correlated with geographic size, functional diversity, or phylogenetic diversity at both the county and conservation area scales.

Although MPD/MNTD values are not necessarily correlated with species richness, their variances show a systematic relationship with species richness (Swenson, 2014). When species richness is low, MPD/MNTD values usually have high variance and vice versa. Therefore, we also conducted null model analyses with 999 randomizations by shuffling species names in the functional and phylogenetic distance matrices. For each sample unit, we then calculated a standardized effect size (SES) for its functional and phylogenetic MPD/MNTD value using the equation:

$$\mathrm{SES} = [X_{\mathrm{obs}} - mean(X_{\mathrm{null}})]/\mathrm{SD}(X_{\mathrm{null}}),$$

where X_{null} is a vector of MPD or MNTD values from all null model randomizations. A positive SES indicates that the observed functional/phylogenetic diversity in a site is higher than expected given

the species richness of that site. To test for significance of SES, we calculated one-tailed *P*-values based on the rank of the observed value across all X_{null}. *P*-values lower than 0.025 (to match alpha = 0.05 for two-tailed *P*-value) indicate that functional diversity or phylogenetic diversity is *significantly* higher or lower, respectively, than expected. These *P*-values correspond roughly to SES values ±2. The regional species pools used for these calculations were either all species present in the state (for the county-level analyses) or all species present in the conservation areas (essentially all species that occur below 27.5°N in Florida). We used the smallest regional species pool possible (e.g., only those species present in the conservation areas, as opposed to all species present in the state, for the conservation-area-level tests) to avoid an artifical trend toward underdispersion that could have been driven by the use of an inappropriately large species pool. To test whether the overall SES across all sample units was significantly different from zero, we used a simple *t*-test. Significant overall SES values (greater or lower than zero) in these tests suggest that functional or phylogenetic diversity is higher or lower than would be expected at random given the species richness across all sample units.

A potential concern in our study is the tendency to see underdispersion at larger spatial scales and overdispersion at smaller spatial scales. We should be able to identify a signal of overdispersion if it is present, however, as previous work has demonstrated that overdispersion can also be seen at large spatial scales. For example, Cooper et al. (2008) found phylogenetic overdispersion of mammalian assemblages at large scales (10 km^2 to 440,000 km^2), and Bennett et al. (2013) found that overdispersion was rarely caused by competition even at small scales (4 m^2). To test for a relationship between area and SES, we plotted the area of sample units for the conservation areas against the SES values for each metric. If small areas are required to detect overdispersion, then we should observe a negative relationship between area and SES. Positive SES indicates that species have larger distance between them than expected, and thus the higher the SES, the larger the distance (hence overdispersion). If small areas are not necessary to detect overdispersion, we should not see a negative relationship between the two.

RESULTS

Phylogeny

The final aligned DNA data matrix for the five chloroplast regions was 7025 bp long. PartitionFinder identified the following as the best set of nucleotide substitution models and overall partitioning scheme for the data set: partition 1, *atpA*, *atpB*, and *rbcL* (GTR+I+G); partition 2, *trnL* (HKY+G); partition 3, *rps4-trnS* and *trnL-trnF* (GTR+I+G); and partition 4, *rps4* (GTR+I+G). The molecular dating analysis recovered a tree (Fig. 2) congruent at the generic, familial, and ordinal levels with recently published phylogenies of ferns (Schuettpelz and Pryer, 2009; Rothfels et al., 2015; Testo and Sundue, 2016) and the most recent classification for all ferns (PPG 1, 2016). The XML file used in the BEAST analysis is included as a supplementary document (Appendix S3). Alignments and trees are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.66v6k.

Species richness

Average fern species richness was 28 ± 14.1 species/county (mean ± SD) and 10 ± 5.8 species/conservation area. At the county level, species richness ranged from seven species in Madison and Gulf counties to 77 species in Miami-Dade County (Fig. 3A). A total of 61 fern species was present in the 178 included conservation areas, and fern species richness ranged from the minimum allowed of three species (18 conservation areas) to 29 species at John D. MacArthur Beach State Park (Fig. 3B). Species richness was positively correlated

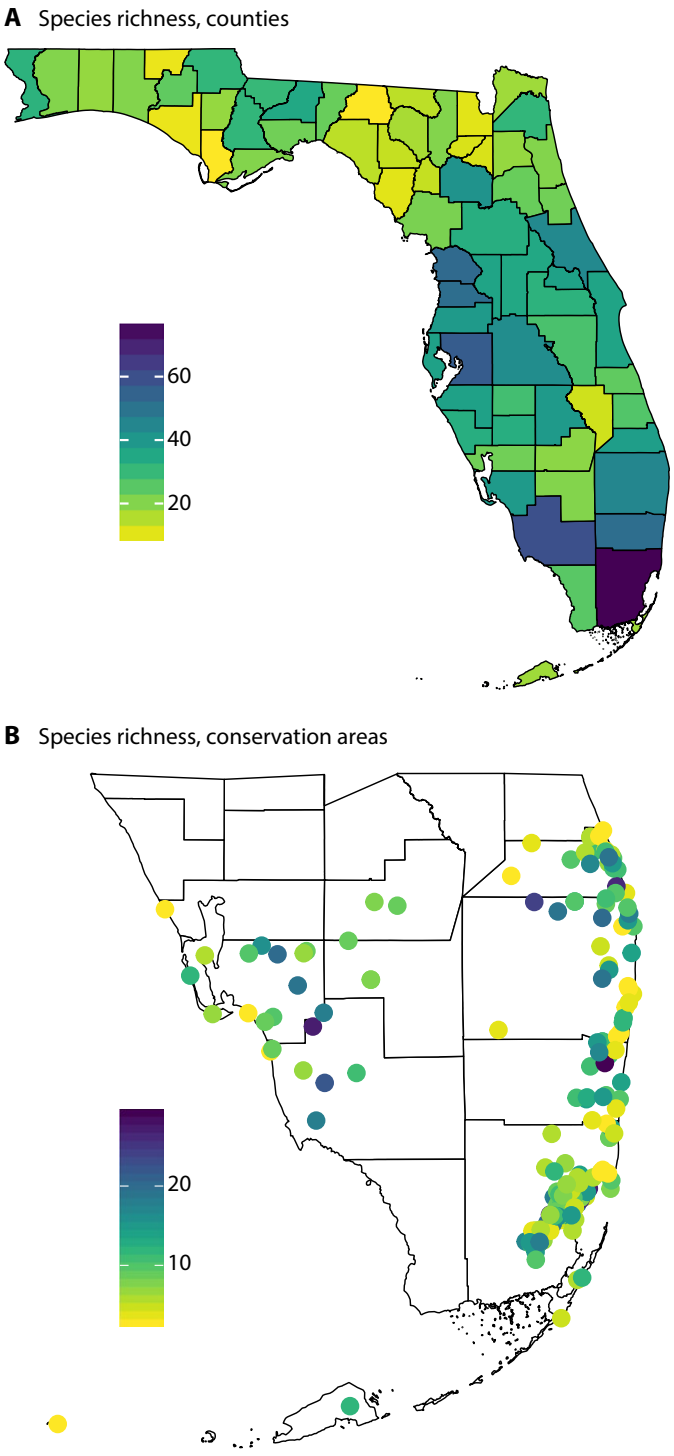

FIGURE 3. Species richness of ferns across (A) 68 counties (Monroe County is split into two units, the Florida Keys and the mainland) and (B) 178 conservation areas in south Florida.

with geographic area for counties (i.e., larger counties generally had more species than smaller counties, $P = 3.59e^{-6}$, $r^2 = 0.28$, df = 67), but not for conservation areas ($P = 0.171$, $r^2 = 0.01$, df = 176).

Phylogenetic diversity

For the full data set, across counties the lowest MPD_{Phy} was 0.66, in Okeechobee County, and the highest was 1.18, in Bradford County, with an average across all counties of 0.87 (Fig. 4A). The lowest $MNTD_{Phy}$ was 0.14, in Collier County, and the highest 0.78, in Gulf County, with an average across counties of 0.28 (Fig. 4C). At the county level, both MPD_{Phy} and $MNTD_{Phy}$ were negatively correlated with species richness: counties with more species had lower phylogenetic diversity (MPD_{Phy}: $P < 0.001$, $r^2 = 0.15$, df = 66; $MNTD_{Phy}$: $P < 0.001$, $r^2 = 0.45$, df = 66).

For the conservation areas, the lowest MPD_{Phy} was 0.19, in Holey Land Wildlife Management Area, and the highest was 1.21, in both Delray Beach (Lake Ida Parcel) and Virginia Key and Marine Stadium, with an average MPD_{Phy} across conservation areas of 0.70 (Fig. 4E). The lowest $MNTD_{Phy}$ was 0.12, again in Holey Land Wildlife Management Area, and the highest was 0.92, again in Delray Beach (Lake Ida Parcel), with an average $MNTD_{Phy}$ across conservation areas of 0.377 (Fig. 4G). At the conservation area scale, MPD_{Phy} was not related to species richness ($P = 0.852$, $r^2 < 0.001$, df = 176), but $MNTD_{Phy}$ was negatively correlated with species richness: parks with more species had lower $MNTD_{Phy}$ ($P < 0.001$, $r^2 = 0.26$, df = 176).

The SES values for MPD_{Phy} across counties (Fig. 4B) indicate that for most counties in Florida, phylogenetic diversity is higher than expected based on species richness (values above zero) but only significantly so ($P < 0.025$) in seven counties in North Florida (Bradford, Escambia, Gadsden, Jackson, Leon, Union, and Wakulla Counties). MPD_{Phy} is lower than expected (values below zero) in 10 counties, mostly in Central and South Florida, but is not significantly lower than expected in any county. Across all counties, in the *t*-test, SES of MPD_{Phy} was significantly positive, suggesting higher phylogenetic diversity than expected across the state (phylogenetic *overdispersion*; $P < 0.001$, $t = 8.24$) (Table 2). In contrast, SES of $MNTD_{Phy}$ was significantly negative in three counties in North and Central Florida (Columbia, Escambia, and Martin), and only above zero in a total of 18 counties (Fig. 4D). The remaining 50 counties were below zero, with only one of these below –2 (Martin). Across the state, in the *t*-test, SES of $MNTD_{Phy}$ was significantly negative, suggesting lower phylogenetic diversity in this metric than expected (phylogenetic *underdispersion*; $P < 0.001$, $t = -4.28$) (Table 2).

In the conservation areas, SES of MPD_{Phy} was significantly different from zero ($P < 0.025$) in only two areas (High Ridge Scrub Natural Area and Holey Land Wildlife Management Area), both of them below zero, with the majority of conservation areas (110/178) having SES values below zero but not significant (Fig. 4F). Sixty-eight conservation areas had higher than expected MPD_{Phy} values (above zero). Across all the conservation areas, the *t* for SES of MPD_{Phy} was significantly negative ($P < 0.001$, $t = -3.94$), suggesting that phylogenetic diversity is lower than expected across

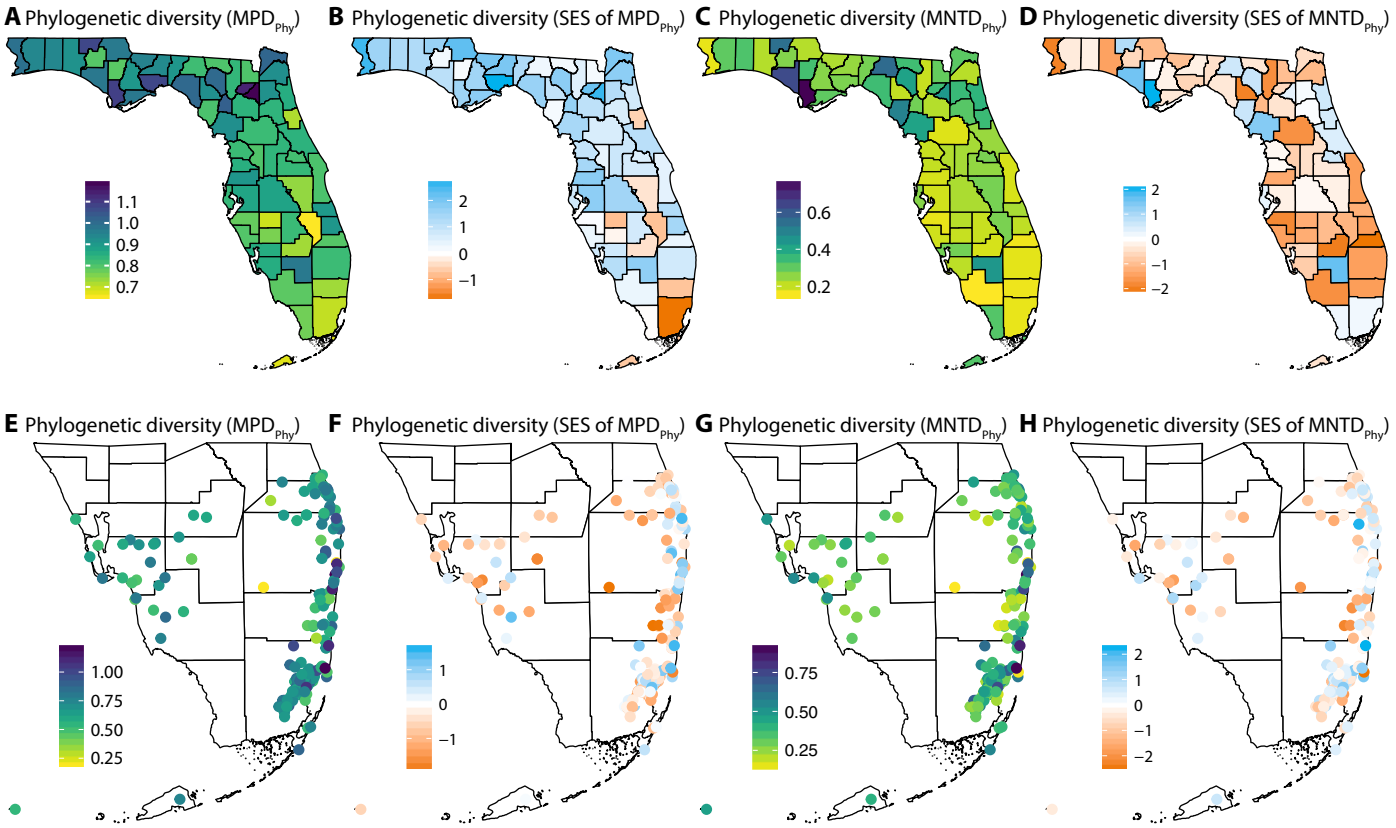

FIGURE 4. Phylogenetic diversity results. (A) MPD_{Phy} of counties, (B) SES of MPD_{Phy} of counties, (C) $MNTD_{Phy}$ of counties, (D) SES of $MNTD_{Phy}$ of counties, (E) MPD_{Phy} of conservation areas, (F) SES of MPD_{Phy} of conservation areas, (G) $MNTD_{Phy}$ of conservation areas, (H) SES of $MNTD_{Phy}$ of conservation areas. MPD: mean pairwise dissimilarity, MNTD: mean nearest taxon distance, Phy: phylogenetic diversity, SES: average standard effect size.

TABLE 2. Summary of statistical results from analyses of mean pairwise dissimilarity (MPD) and mean nearest taxon distance (MNTD) for both phylogenetic diversity ($_{Phy}$) and functional diversity ($_{Fun}$) across all counties or conservation areas. Average standard effect size (SES) values for each analysis are given, along with the *P*-values and *t*-statistics from *t*-tests, and the conclusion based on those tests, at both spatial scales.

	Average SES	*P*	*t*	Conclusion
Mean pairwise dissimilarity				
County level	$MPD_{Phy} = 0.896$	<0.001	8.24	Phylogenetic overdispersion
	$MPD_{Fun} = -0.185$	0.077	−1.79	Not different from random
Conservation area level	$MPD_{Phy} = -0.277$	<0.001	−3.94	Phylogenetic underdispersion
	$MPD_{Fun} = -1.365$	<0.001	−18.04	Functional underdispersion
Mean nearest taxon distance				
County level	$MNTD_{Phy} = -0.378$	<0.001	−4.28	Phylogenetic underdispersion
	$MNTD_{Fun} = -0.315$	0.003	−3.09	Functional underdispersion
Conservation area level	$MNTD_{Phy} = -0.100$	0.311	−1.02	Not different from random
	$MNTD_{Fun} = -0.923$	<0.001	−16.34	Functional underdispersion

the conservation areas (phylogenetic *underdispersion*) (Table 2). Standardized effect size of $MNTD_{Phy}$ in the conservation areas was below zero in 98 areas and significantly negative in six areas; it was above zero in the remaining 80 areas and significantly positive in two areas (Loxahatchee Slough Natural Area and Oleta River State Park) (Fig. 4H). The *t*-test for SES of $MNTD_{Phy}$ across all conservation areas suggested that there was no difference from random ($P = 0.311$, $t = -1.02$) (Table 2).

Functional diversity

The final trait matrix included 19 traits (Appendix S4). The matrix was 83% complete; the average percentage missing data per trait was 16.84%, ranging from no missing data (habit) to 61.6% missing data (average soil pH). The latter was the only trait with more than 50% missing data.

For the county data set, the lowest MPD_{Fun} among the counties was 0.33 (Columbia), and the highest was 0.42 (Holmes) (Fig. 5A), with an average of 0.38. The lowest $MNTD_{Fun}$ was 0.11 (Miami-Dade), the highest was 0.30 (Gulf), with an average of 0.18 (Fig. 5C). The MPD_{Fun} was not correlated with species richness at the county scale ($P = 0.609$, $r^2 = 0.004$, df = 66), but $MNTD_{Fun}$ was negatively correlated with species richness at the county scale ($P < 0.001$, $r^2 = 0.64$, df = 66).

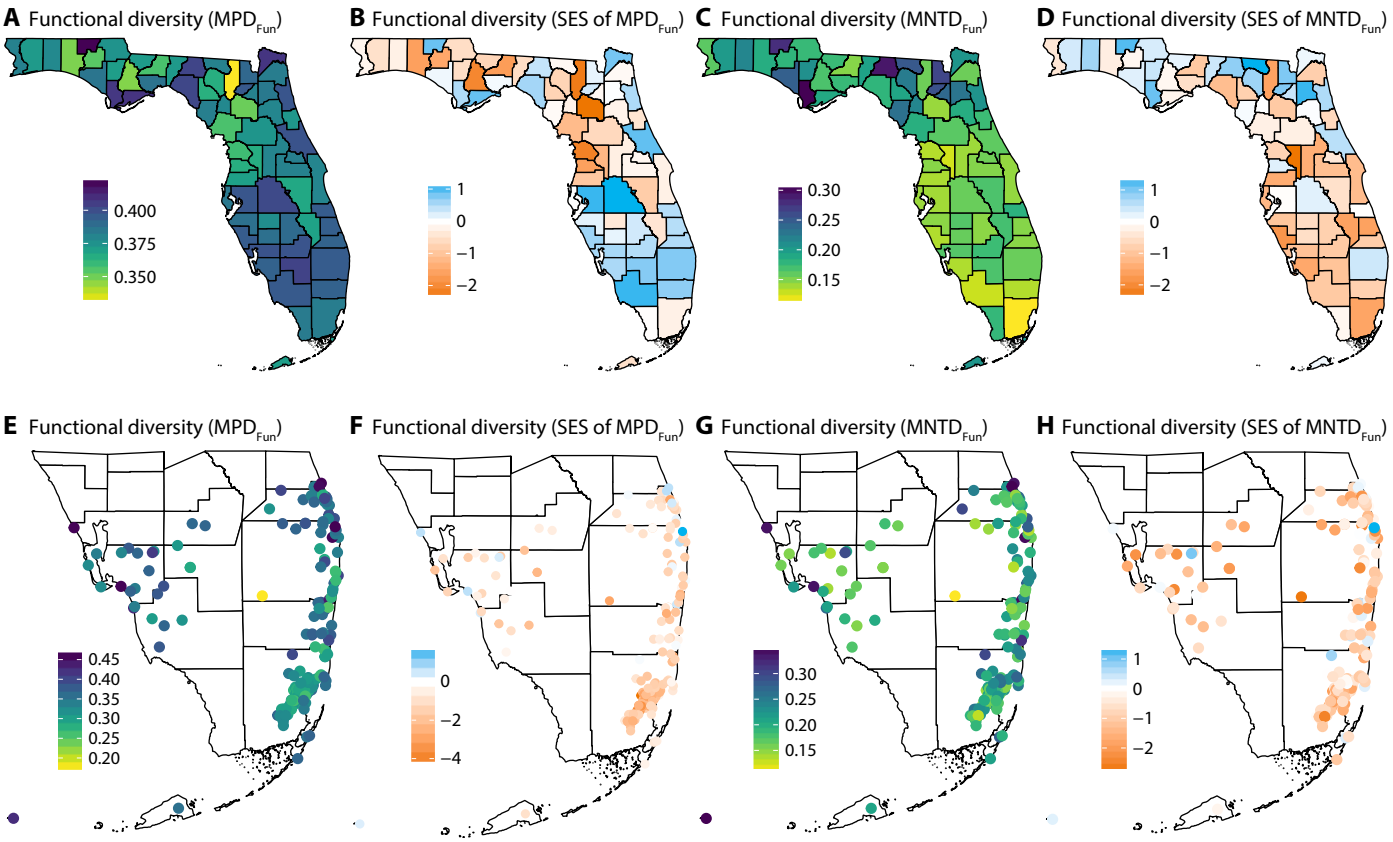

FIGURE 5. Functional diversity results. (A) MPD_{Fun} of counties, (B) SES of MPD_{Fun} of counties, (C) $MNTD_{Fun}$ of counties, (D) SES of $MNTD_{Fun}$ of counties, (E) MPD_{Fun} of conservation areas, (F) SES of MPD_{Fun} of conservation areas, (G) $MNTD_{Fun}$ of conservation areas, (H) SES of $MNTD_{Fun}$ of conservation areas. MPD: mean pairwise dissimilarity, MNTD: mean nearest taxon distance, Fun: functional diversity, SES: average standard effect size.

In the conservation areas, the Holey Land Wildlife Management Area had the lowest MPD_{Fun} (0.18), and Jupiter Ridge Natural Area the highest (0.46) (Fig. 5E), with an average 0.34. The Holey Land Wildlife Management Area also had the lowest $MNTD_{Fun}$ (0.11), and Dry Tortugas National Park the highest (0.35) (Fig. 5G), with an average of 0.21. MPD_{Fun} was positively correlated with species richness at the conservation area scale ($P = 0.038$, $r^2 = 0.024$, df = 176), while $MNTD_{Fun}$ was negatively correlated with species richness at this scale ($P < 0.001$, $r^2 = 0.44$, df = 176).

The SES values for MPD_{Fun} across counties are nearly an even mix of values above (27/68) and below (41/68) zero, with four counties showing significant underdispersion: Alachua, Columbia, Citrus, and Liberty (Fig. 5B). No counties were significantly overdispersed (values above 2). For SES of $MNTD_{Fun}$ (Fig. 5D), 41 counties were below zero, and 27 were above (Fig. 5D). Only one county was significantly underdispersed (Sumter), and none were significantly overdispersed. Across all counties, the *t*-test found that SES of MPD_{Fun} was not significantly different from zero ($P = 0.077$, $t = -1.79$), while SES of $MNTD_{Fun}$ was significantly underdispersed ($P = 0.003$, $t = -3.09$) (Table 2).

For the conservation areas, the SES of MPD_{Fun} values indicate that functional diversity is lower than expected in the majority of conservation areas (159/178), and significantly lower than expected in 49 areas (Fig. 5F). SES values for MPD_{Fun} are above zero in only 19 conservation areas and are not significantly different from random in any conservation area. SES of $MNTD_{Fun}$ was below zero in 155/178 conservation areas, with 13 areas significantly negative; it was above zero in the remaining 23 areas, but not significant in any area (Fig. 5H). For SES of both MPD_{Fun} and $MNTD_{Fun}$ across all the conservation areas, *t* was significantly negative (MPD_{Fun}: $P < 0.001$, $t = -18.04$; FD-MNTD: $P < 0.001$, $t = -16.34$) (Table 2), suggesting that functional diversity is lower than expected based on species richness across the conservation areas for both metrics (functional *underdispersion*).

Effect of scale

We did not see a negative relationship between conservation area size and SES for any of the four metrics (Appendix S5), and therefore the lack of observed overdispersion in our study is not due to the areas being too large. In panel C of Appendix S5, for example, large SES values (ca. 2.3, indicating overdispersion) can be found in both small and large conservation areas, supporting our hypothesis that overdispersion can be possible in both small and large scales.

DISCUSSION

Our analyses of functional diversity, and particularly phylogenetic diversity, for Florida ferns show different patterns of overdispersion versus underdispersion depending on the spatial scale and diversity metric considered. At the larger scale, mean pairwise dissimilarity (MPD_{Phy}) recovers a pattern of significant phylogenetic overdispersion across all counties in the state (Fig. 4B), while mean nearest taxon distance ($MNTD_{Phy}$) finds significant phylogenetic underdispersion across all the counties (Fig. 4D) (Table 2). In contrast, at the smaller scale, MPD_{Phy} shows evidence of phylogenetic underdispersion (Fig. 4F), while $MNTD_{Phy}$ did not differ from random (Fig. 4H) (Table 2). As Cavender-Bares et al. (2006, p. S109) noted, abiotic filtering and competitive interactions "can operate simultaneously in real communities, but have greater influence at different scales", and our results seem to demonstrate this. Overall, our results are consistent with environmental filtering being most important at the smaller, more local scale. The smaller conservation areas each likely encompass less habitat diversity than do the larger counties and may comprise only one or a few local habitat types (e.g., prairie, pinelands, oak scrub, hardwood hammocks, salt marsh, swamp). These local habitats can differ strongly from one another, however, and if abiotic conditions differ between conservation areas as a result (in terms of microclimate or soil/substrate, for example), that may lead to strong selection for groups of species that are closely related and thus share traits suited to each local habitat type, resulting in underdispersion at the smaller scale. As the spatial scale increases, the larger units (counties) are more likely to be composites of many different local habitat types, and so diverse habitat specialists are brought together at the county level, resulting in overdispersion in MPD but underdispersion in MNTD at this larger scale. If each county consisted of only one habitat type, we would expect to see phylogenetic and functional underdispersion in both metrics at this scale.

Mean pairwise distance and MNTD are fundamentally different metrics, which contributes to the contrasting results that we recovered; MPD measures the mean distance in branch length between all taxa in an assemblage, while MNTD considers only the closest relatives of each taxon in that assemblage (i.e., the shortest distances in the tree) (Tucker et al., 2017). In general, this difference in how the metrics are calculated leads to MNTD values emphasizing the tipmost relationships in a phylogeny, while MPD extends down the branches to capture relationships that are more basal within the tree. We would expect to see overdispersion in MPD and underdispersion in MNTD at the county level if each county includes species from across the phylogeny, but with each species having one or more close relatives also present in the county, rather than county-level assemblages consisting of singleton species from across the tree. This pattern would result in deep relationships at the county level that are recovered by MPD, but with each taxon (on average) only a short phylogenetic distance from its closest relative that is also in that assemblage. If these sets of close relatives assort into separate conservation areas due to environmental filtering at the smaller scale, the result would be the pattern of underdispersion at the conservation area level that we also recovered, at least for MPD_{Phy} ($MNTD_{Phy}$ did not differ from random across conservation areas). One county that is consistent with this pattern is Lee County, although neither its MPD_{Phy} nor $MNTD_{Phy}$ values differed significantly from random at either scale (Fig. 6). The metrics demonstrate the overall trend, however, with broad representation in Lee County of species from across the phylogeny (overdispersion in MPD_{Phy}), but with each species generally present along with close relatives, grouping into clades across the tree (underdispersion in $MNTD_{Phy}$). The conservation areas that occur in Lee County have multiple species present that belong to several clades (consistent with underdispersion in MPD). The trends in this county and its conservation areas are thus consistent with the overall pattern in the state for both metrics and scales.

Our results are somewhat at odds with classical theory, which suggests that biotic interactions have the strongest influence locally, leading to overdispersion at small scales, while environmental filtering due to climatic conditions or other abiotic phenomena is dominant at larger, more regional scales, leading to underdispersion (Weiher and Keddy, 1995; Webb et al., 2002; Cavender-Bares

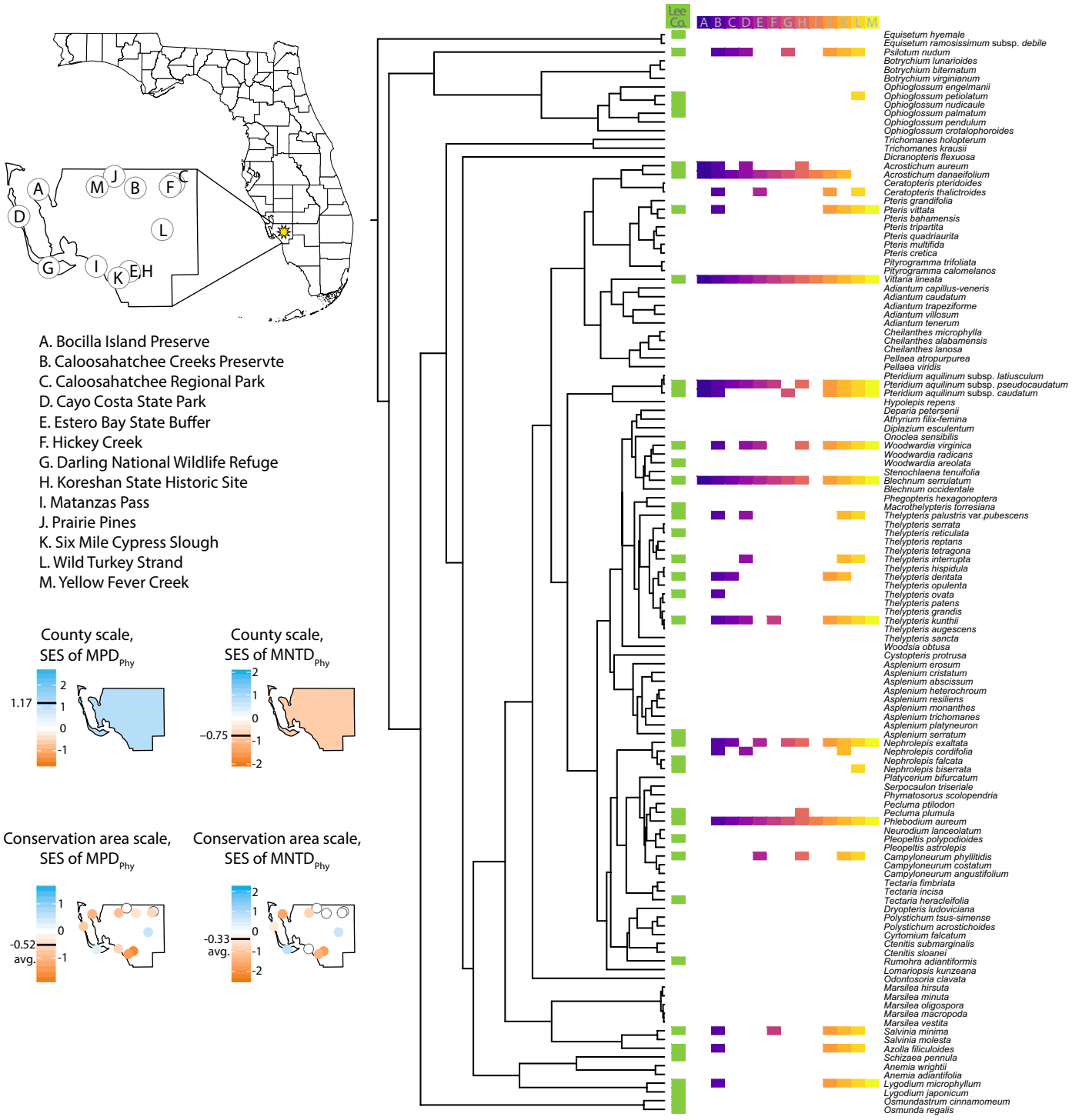

FIGURE 6. Lee County, Florida, exemplifies the contrasting patterns of over and underdispersion in phylogenetic diversity that we recover depending on the metric and spatial scale considered: county-level MPD_{Phy} trends toward overdispersion and $MNTD_{Phy}$ toward underdispersion, while MPD_{Phy} averaged across conservation areas trends toward underdispersion ($MNTD_{Phy}$ does not differ from random). The phylogeny at right includes all species present in the state, though only the subset present in the conservation areas was used as the regional species pool for those analyses. Species present in Lee County and in each conservation area in the county are indicated by colors in the columns, which are labeled according to the map at left. Conservation areas with SES values near zero are outlined in gray in the maps at lower left to make them easier to see. MPD: mean pairwise dissimilarity, MNTD: mean nearest taxon distance, Phy: phylogenetic diversity, Fun: functional diversity, SES: average standard effect size.

et al., 2006, 2009; Silvertown et al., 2006). The results reported here demonstrate the sensitivity of community phylogenetic analyses to the specific metrics that are used and correlate previous studies that have stressed the importance of scale and how it is defined in these studies (Cavender-Bares et al., 2006, 2009; Swenson et al., 2006; Vamosi et al., 2009; Kraft and Ackerly, 2014). Biotic and abiotic interactions work synergistically to shape the assemblages of species present in a community, and our results speak to the importance of considering multiple metrics and being mindful of the spatial scale in question to understand how processes are shaping species assembly across assemblages.

The biology of the organisms under study will also determine how they respond to biotic vs. abiotic pressures, and ferns are unique among plants in several aspects of their biology and physiology that may affect how species group into local and regional assemblages. Two features in particular stand out that would potentially make ferns more sensitive to environmental filtering at smaller vs. larger spatial scales. The first involves physiological ecology and specifically the water relations of ferns. Although many correlations among foliar traits related to gas exchange are consistent between ferns and seed plants (Karst and Lechowicz, 2007), ferns have long been known to differ dramatically from seed plants when it comes to water transport and water-use efficiency (Brodribb and Holbrook, 2004; Brodribb et al., 2005, 2009). While some ferns have vessel elements in their vascular tissue, the majority transport water exclusively via tracheids (Brodribb and Holbrook, 2004; Pittermann et al., 2013), which are narrower and therefore more resistant to cavitation than are vessel elements, but at the expense of water volume moved per unit time (Brodribb et al., 2005). As a result, ferns generally have much lower rates of hydraulic conductance than angiosperms, although they can be on par with gymnosperms (Brodribb et al., 2005; Pittermann et al., 2011). In addition, rather than the active, abscisic acid (ABA)-mediated control over stomatal response seen in seed plants, fern stomata respond passively, opening and closing based on changes in leaf water potential (McAdam and Brodribb, 2012a, b, 2013, 2014; Martins et al., 2016). Because ferns cannot adapt as quickly to water stress as seed plants can, they operate with a higher overall "safety margin" when it comes to local water availability (Brodribb and Holbrook, 2004). These water-related traits may result in ferns tracking local environmental conditions more closely than do seed plants. Jones et al. (2014) reached this conclusion in a study of fern and angiosperm herb-layer communities in Indonesia. While these authors did not find direct evidence of physiological differences between the two groups, they did find that community composition and species turnover between sites was tied more closely to local environmental conditions for ferns than for flowering plants. This study and many others have also shown that ferns are very sensitive to soil traits (Karst et al., 2005; Zuquim et al., 2012, 2014; Jones et al., 2013, 2014; Tuomisto et al., 2014; Lehtonen et al., 2015), which can vary extensively over small spatial scales. If ferns are highly sensitive to local environmental and soil conditions, we might expect these abiotic factors to override competitive interactions in terms of importance at the local scale. Such a shift in relative importance of abiotic vs. competitive effects with spatial scale would explain our findings of phylogenetic and functional underdispersion at the smaller spatial scale and overdispersion at the larger scale in terms of MPD, with the opposite occurring for MNTD.

The second feature of ferns that may strongly influence their spatial patterns of community assembly is their life cycle. Ferns (and lycophytes) are unique among land plants in having two completely independent stages of the life cycle, the haploid gametophyte and diploid sporophyte (Haufler et al., 2016). These stages are distinct from one another physiologically and in terms of their niche preferences. At the extreme, some fern species have little or no range overlap between their gametophytes and sporophytes, presumably because their ecological and microhabitat demands are so different (Pinson et al., 2017). Nitta et al. (2016), in the only study of fern community structure to date that has examined both gametophytes and sporophytes, found substantial differences between the two life stages in terms of species composition across sites. This study, like many other studies of fern diversity and community composition (Kluge and Kessler, 2006, 2011; Watkins Jr. et al., 2006; Kluge et al., 2008; Salazar et al., 2015; Kessler et al., 2016), focused on changes in species composition and richness over an elevational gradient. In general, these studies have inferred that changes in fern species composition between sites are primarily driven by differences in microclimate across elevations (e.g., relative humidity and temperature), emphasizing the strong relationship between local climate variables and fern community dynamics. Nitta et al. (2016) found that the level of phylogenetic clustering differed between the life stages and with elevation, with sporophytes showing evidence of phylogenetic clustering that grew stronger with increasing elevation, while gametophytes showed no evidence of phylogenetic clustering at any elevation. These authors also found, strikingly, that gametophytes showed no evidence of the mid-elevation peak in species richness that is a hallmark of fern species distributions across elevational gradients in the tropics, based entirely on studies of sporophytes (Cardelus et al., 2006; Kluge and Kessler, 2006; Watkins et al., 2006; Kluge et al., 2008; Kessler et al., 2011; Pouteau et al., 2016). These findings together strongly suggest that gametophytes are governed by different assembly rules than are sporophytes. As with sporophyte traits related to water use, physiology likely plays a role here. Recent studies on gametophyte physiology have demonstrated that this stage of the life cycle is more ecologically complex than was long suspected and that gametophytes can be long-lived and desiccation tolerant (Watkins, 2006; Watkins et al., 2007a, b; Chambers et al., 2017). Establishment limitation at the gametophyte stage is almost certainly more important for ferns than is dispersal limitation (Flinn, 2007), as ferns produce highly dispersible, dust-like spores that are desiccation tolerant and capable of long-distance dispersal (Tryon, 1970, 1986). Because every sporophyte must have been preceded by at least one gametophyte, traits related to gametophyte establishment and that allow them to persist long enough for successful sexual reproduction may be reflected in the patterns of small-scale underdispersion that we recovered, even though we did not include traits related to gametophytes in our dataset.

CONCLUSIONS

We found that inferences about community assembly of ferns benefit from using multiple diversity metrics and considering assemblages at different spatial scales. We interpret our results as suggesting that fern assembly is shaped most strongly by microhabitat conditions on a local scale, which likely reflects the importance for ferns of microclimate and the gametophyte stage of the life cycle. We did not include data on climate or soils directly in our analyses, and it is clear that future testing of our hypotheses will require fine-scale data collection on these aspects of the abiotic environment,

ideally from exact occurrences of specimens. We also note that most of the traits we measured were morphological in nature rather than strictly physiological (Appendix S4), and it would be valuable to see whether the same patterns are recovered for traits more directly related to physiological functioning (e.g., specific leaf area, stomatal density, vein density). In addition, traits that influence stress tolerance and competition have been hypothesized to follow a unimodal pattern of distribution in relation to microenvironment, with convergence in these traits expected at both ends of a gradient spanning disturbed, severe environments to productive sites (Navas and Violle, 2009; Naaf and Wulf, 2012). To test this hypothesis for ferns would require data collection focused on environmental conditions related to site richness and productivity, as well as traits tied to competition and stress response, ideally in both life stages. Understanding how fern communities assemble and the ways in which their assembly processes are governed by local vs. regional factors will help us to use functional and phylogenetic diversity data predictively (Cadotte et al., 2015) to anticipate how ecological and evolutionary traits and the environment will interact in the future to shape fern community assembly under changing climates.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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