

# Community phylogeny of the globally critically imperiled pine rockland ecosystem

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**PREMISE OF THE STUDY:** Community phylogenetic methods incorporate information on evolutionary relationships into studies of organismal assemblages. We used a community phylogenetic framework to investigate relationships and biogeographic affinities and to calculate phylogenetic signal of endemism and invasiveness for the flora of the pine rocklands—a globally critically imperiled ecosystem with a significant portion of its distribution in South Florida, United States.

**METHODS:** We reconstructed phylogenetic relationships of 538 vascular plant taxa, which represent 92.28% of the vascular flora of the pine rocklands. We estimated phylogenetic signal for endemism and invasiveness using phylogenetic generalized linear mixed models. We determined the native range for each species in the data set and calculated the total number of species sourced from each region and all possible combinations of these regions.

**KEY RESULTS:** The pine rockland flora includes representatives of all major vascular plant lineages, and most species have native ranges in the New World. There was strong phylogenetic signal for endemism, but not for invasiveness.

**CONCLUSIONS:** Community phylogenetics has high potential value for conservation planning, particularly for fragmented and endangered ecosystems like the pine rockland. Strong phylogenetic signal for endemic species in our data set, which also tend to be threatened or endangered, can help to identify species at risk, as well as fragments where those species occur, highlighting conservation priorities. Our results indicate, at least in the pine rockland ecosystem, no phylogenetic signal for invasive species, and thus other information must be used to predict the potential for invasiveness.

**KEY WORDS** community phylogeny; endemic species; invasive species; phylogenetic signal; pine rockland; systematics.

Community phylogenetic approaches are powerful tools for exploring the effect of evolutionary relationships on interactions between species that are occurring on ecological timescales (Connor and Simberloff, 1979; Webb et al., 2002; Cavender-Bares et al., 2009; Vamosi et al., 2009). Phylogenetic relationships provide an alternative to species richness, which has historically been the most commonly used means of quantifying diversity. However, species richness provides an incomplete picture of biodiversity in natural systems because it fails to take into account the evolutionary relationships between species (Webb et al., 2002; Cavender-Bares et al., 2009; Miller et al., 2018). A community phylogeny is generally constructed for a group or assemblage of species that co-occur within a local area. These species are a subset of those found in a larger

regional pool, and are treated as their own unit when assessing relatedness (Purvis, 2008; Vamosi et al., 2009). Particular traits or designations of interest can also be used to subset and study groups of species belonging to the larger regional pool (Miller et al., 2016; Tucker et al., 2017). Adding a phylogenetic component to biodiversity analysis complements more traditional measures of species richness (Mazel et al., 2014; Li et al., 2018), and can elucidate drivers of community assembly, persistence, and disassembly because both environmental influences and competitive interactions can leave behind phylogenetic signal in the observed community (Cavender-Bares et al., 2009). Community phylogenetic approaches have been used to detect evolutionary signal underlying species extirpations and invasions in the face of global climate change (MacArthur and

Wilson, 1967; Fargione et al., 2003; Olden, 2006; Morlon et al., 2011), and have been used to understand the assembly rules governing a number of biological systems, including meadows, grasslands, pine forests, and tropical rainforests (Webb, 2000; Kembel and Hubbell, 2006; Silvertown et al., 2006; Swenson et al., 2007; Kress et al., 2009; Fine and Kembel, 2011; Sollenberger et al., 2016; Li et al., 2017).

Community phylogenies are typically used to describe the assembly of species groups and discern the relative roles of long-term evolutionary and short-term ecological processes, which may have different and sometimes conflicting influences (Webb, 2000; Webb et al., 2002; Cavender-Bares et al., 2004, 2006, 2009; Mayfield and Levine, 2010; Narwani et al., 2015). Unlike taxonomically focused phylogenetic studies, which try to understand the evolutionary processes shaping diversity of a specific clade, community phylogenies include all species that persist in a geographic area or system of interest (Webb et al., 2002; Cavender-Bares et al., 2009; Kress et al., 2009). Community phylogenies can be used to examine patterns of phylogenetic or functional under or overdispersion (i.e., whether species in an assemblage are more or less closely related to one another than would be expected by chance (Webb et al., 2002; Cavender-Bares et al., 2009; Kress et al., 2009; Swenson, 2014)), and to ask specific questions about the relationship between assemblage members and ecosystem-level processes. For example, community phylogenies have been used to understand effects of microbial communities on ecosystem functioning (Maherali and Klironomos, 2007), the effects of phylogenetic and functional diversity on plant community assembly and productivity (Cadotte et al., 2009; Pavoine et al., 2011; Liu et al., 2015; Sessa et al., 2018), and the importance of considering phylogenetic and other diversity metrics when designing conservation strategies (Devictor et al., 2010; Rosauer and Mooers, 2013; Winter et al., 2013; Buerki et al., 2015; Forest et al., 2015; Hipp et al., 2015; Laity et al., 2015).

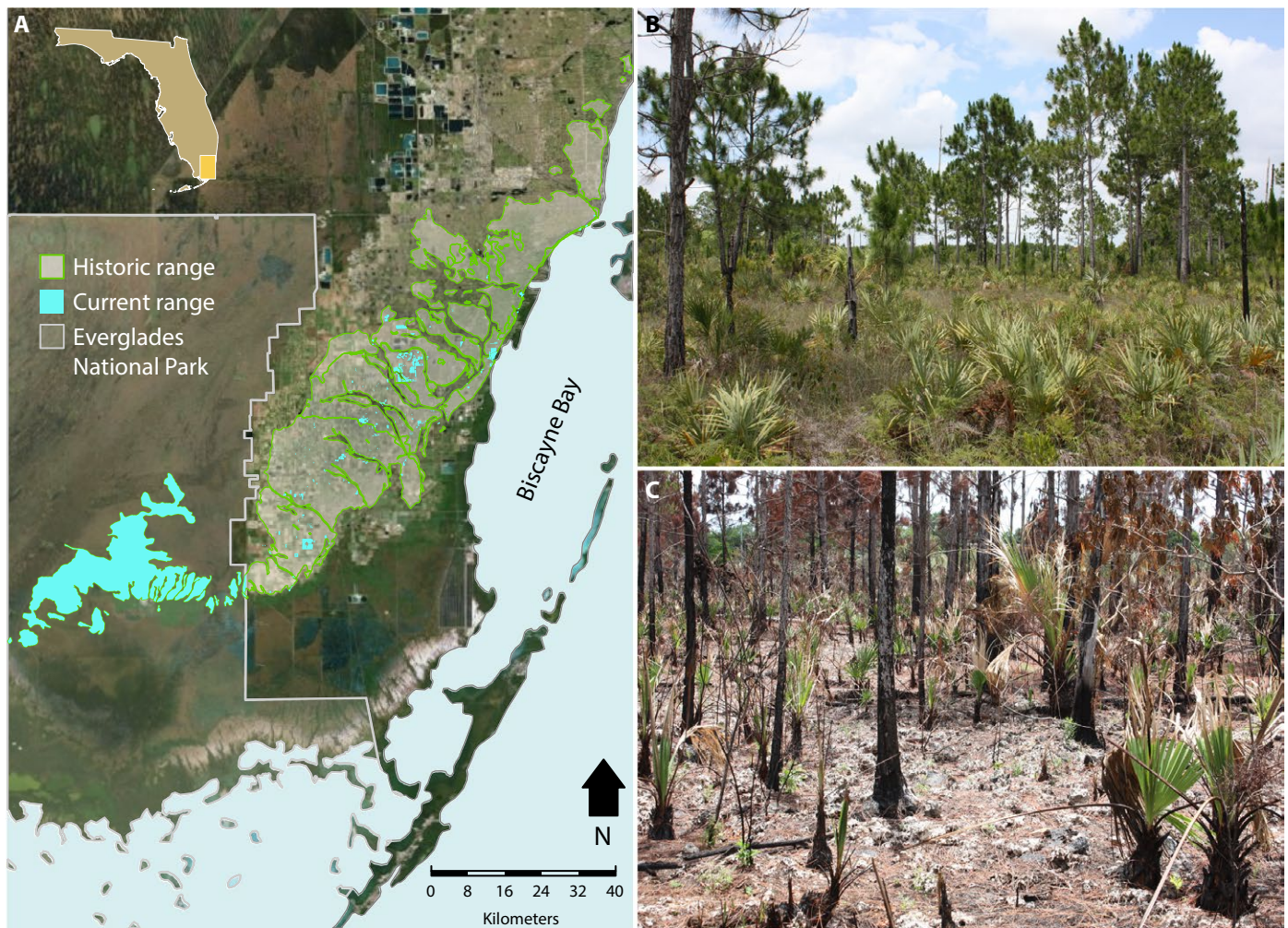
Like taxonomically focused phylogenies, community phylogenies can also be used to test for phylogenetic signal of traits of interest. Phylogenetic signal is the tendency for evolutionarily related organisms to resemble each other (Blomberg and Garland, 2002; Blomberg et al., 2003), and can be used to determine whether species are more likely to possess a particular trait or feature simply by belonging to a certain evolutionary lineage (Losos, 2008; Revell et al., 2008). Phylogenetic signal has been used at the scale of broad phylogenetic clades to explore extinction risks across mammals (Fritz and Purvis, 2010), trends in niche breadth in bats (Peixoto et al., 2017), behavioral and life history traits in primates (Kamilar and Cooper, 2013), and the relative invasiveness of species belonging to the *Acacia* and *Eucalyptus* genera (Miller et al., 2017). Within a community context, tests of phylogenetic signal have been used to determine if the phenology of subalpine plants is shifting with abiotic conditions (CaraDonna and Inouye, 2015), whether closely related plants are more susceptible to similar pathogens (Gilbert et al., 2012), and whether phylogenetic relationships determine the fidelity between mutualistic and parasitic symbionts (Krasnov et al., 2011; Prieto et al., 2017). Incorporating phylogenetic information has become an integral approach to interrogate both evolutionary, clade-based, and ecological, spatially explicit questions.

In the present study, we construct a community phylogeny for a globally critically imperiled ecosystem, the pine rocklands of South Florida in the United States. Pine rockland habitat occurs along the Miami Rock Ridge, an exposed oolitic limestone bedrock remnant from the Pleistocene that stretches from Miami-Dade County into Long Pine Key in Everglades National Park, with

disjunct outcroppings in the Florida Keys and Big Cypress National Preserve (Fig. 1) (Robertson, 1953; Snyder et al., 1990; O'Brien, 1998; Possley et al., 2008; Diamond and Heinen, 2016). This plant community is also found in The Bahamas and the Turks and Caicos Islands, with a slightly different species composition (Robertson, 1953). Pine rockland ranges from open, savannah-like to more densely forested habitat, with a rich plant community defined by an upper canopy of slash pine (*Pinus elliottii* Engelman var. *densa* Little & K. W. Dorman, J. Forest [= *P. elliottii* Engelm.]), a midstory of various palms (e.g., *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.f., *Coccothrinax argentata* (Jacq.) L.H. Bailey, and *Serenoa repens* (W. Bartram) Small) and woody shrubs (e.g., *Lantana involucrata* L., *Miconia bicolor* (Mill.) Triana), and an understory of mostly perennial herbs and grasses that includes many species endemic to the habitat or to South Florida (Possley et al., 2008; Powell and Maschinski, 2012) (Fig. 2). Straddling the Caribbean floristic region to the south and the North American Coastal Plain floristic region to the north (Myers et al., 2000; Mittermeier et al., 2011; Noss et al., 2014), this unique community has long been thought to represent a confluence of tropical and temperate taxa (Robertson, 1953; Loope et al., 1979; Snyder et al., 1990; U.S. Fish and Wildlife Service, 1999). Pine rockland has a diverse understory with an open canopy that has been maintained historically by a fire return interval of two to ten years (Wade et al., 1980; Snyder et al., 1990). It can succeed into a conjugate habitat, rockland hammock, which is comprised of hardwood trees with a closed canopy and dark, humid understory conditions (O'Brien, 1998; Diamond and Heinen, 2016). Explosive expansion of the greater Miami metropolitan area and its associated urban and agricultural development throughout the 20th century has fragmented this system and led to hydrologic changes and significant fire suppression within these fragments (Possley et al., 2008; Diamond and Heinen, 2016). Today, the pine rockland ecosystem occupies less than 920 ha, or 2% of its historical range, outside Everglades National Park (U.S. Fish and Wildlife Service, 1999). This habitat provides a unique opportunity to use community phylogenetic methods to understand the assembly of a geographically well-defined plant assemblage that includes many endemic and native, as well as invasive species, and which is of grave conservation concern.

Here we present a community phylogeny of 538 plant taxa from the pine rockland ecosystem, which represents 92.28% of the total plant species present in this habitat type (Gann et al., 2017). We use this community phylogenetic framework to first determine whether there is phylogenetic signal to invasiveness and endemism of plants in this habitat. We predict that historical environmental filtering will have produced strong phylogenetic signal for endemic species. Invasive species may show phylogenetic signal if they are from a conserved set of evolutionary lineages. If, instead, invasive species originate from a wide array of distantly related clades, we expect to see little or no phylogenetic signal of invasiveness. We next explore the biogeographic affinities of species in the pine rocklands by enumerating the geographic regions of the home ranges of all nonendemic taxa and exploring representation of temperate vs. tropical lineages in this supposed floristic melting pot. Finally, we determine whether invasive species in the pine rocklands have emerged primarily from the New World flora that is well-represented in this habitat, or if invasive species tend to originate from Old World floras, as previous studies on invasive species in eastern North America have found (Fridley, 2008, 2013). Understanding where invasion pressure may originate from for this endangered habitat will provide insight into the nature of future threats under climate change and anthropogenic





**FIGURE 1.** (A) Map of the historical range and remaining fragments of pine rockland habitat in South Florida (Miami-Dade County). The largest extant, contiguous parcel of pine rockland is in Everglades National Park. (B) Photograph of a typical pine rockland with slash pine (*Pinus elliottii* Engelm. var. *densa* Little & K. W. Dorman, J. Forest [= *P. elliottii* Engelm.]) overstory and understory of various palms, shrubs, and forbs. (C) Photograph of a recently burned pine rockland. The oolitic limestone substrate is visible in the foreground. Soil is shallow to nonexistent in this fire-dependent habitat.

movement of species. Our integration of phylogenetic information complements existing species inventories and provides an additional tool for assessment by managers designing conservation strategies for this globally critically imperiled habitat.

## MATERIALS AND METHODS

### Taxon sampling, biogeographic distributions, and species status

Our sampling goal was to include all vascular plant taxa present in the pine rockland ecosystem. We used the list of pine rockland taxa from the Floristic Inventory of South Florida (FISF; Gann et al., 2017) as a guide for our fieldwork and collection efforts, and also collected any novel plant taxa we encountered in pine rockland habitat, even if it was not on the FISF list. This came to a total of 583 taxa, which includes 28 subspecies and varieties. We sampled material from 331 new field collections, 17 herbarium collections at Fairchild Tropical Botanic Garden (FTBG; Miami, Florida, USA)

or the University of Florida (FLAS; Gainesville, Florida, USA), and 58 field-collected plants currently in cultivation at FTBG. All field-based collections were made from pine rockland fragments in Miami-Dade County. To include the greatest number of taxa, we conducted fieldwork over several seasons and stages of habitat succession. We identified all field collections to species level or below and preserved up to 100 g of fresh leaf material with silica gel for DNA extraction; voucher information is included in Appendix S1 (see Supplemental Data with this article). We included 132 additional pine rockland taxa in our analyses (for which we were unable to obtain fresh material) by using sequence data produced by the Flora of Florida project at the University of Florida (Julie Allen et al., unpublished data). For taxa below the species level (e.g., with variety or subspecies rankings) that we were unable to sequence *de novo*, we used sequence data from Julie Allen et al. (unpublished data) at the species level when available (Appendix S1). The total number of taxa included in our data set is 538, which is 92.28% of the 583 total vascular plant taxa in the pine rockland flora.

We determined the native ranges for all taxa using a combination of the *Flora of North America* (Flora of North America





**FIGURE 2.** Photographs of representative pine rockland plant species: (A) *Ipomoea microdactyla* Griseb. (Convolvulaceae); (B) *Passiflora suberosa* L. (Passifloraceae); (C) *Centrosema virginianum* (L.) Benth. (Fabaceae); (D) *Euphorbia cyathophora* Murray (Euphorbiaceae); (E) *Clematis baldwinii* Torr. & A. Gray (Ranunculaceae); (F) *Opuntia humifusa* (Raf.) Raf. (Cactaceae); (G) *Bletia purpurea* (Lam.) DC. (Orchidaceae); (H) *Liatris tenuifolia* Nutt. (Asteraceae); (I) *Schinus terebinthifolia* Raddi (Anacardiaceae); (J) *Pteris bahamensis* (J. Agardh) Fée (Pteridaceae); (K) *Abrus precatorius* L. (Fabaceae); (L) *Euphorbia deltoidea* Engelm. ex Chapm. subsp. *deltoidea* (Euphorbiaceae); (M) *Miconia bicolor* (Mill.) Triana (Melastomataceae); (N) *Agalinis fasciculata* (Elliott) Raf. (Orobanchaceae); (O) *Mosiera longipes* (O. Berg) Small (Myrtaceae); (P) *Asclepias viridis* Walter (Apocynaceae).

Editorial Committee, 1993), *Flora of China* (Flora of China Editorial Committee, 2013), the Centre for Agriculture and Biosciences International's (CABI) *Invasive Species Compendium* (CABI, 2018), the Institute for Regional Conservation's (IRC) *Floristic Inventory of South Florida* (Gann et al., 2017), and the *South Florida Multi-Species*

*Recovery Plan* (U.S. Fish and Wildlife Service, 1999). We divided the globe into 10 geographic regions and scored taxa as being *native* or *not native* in each area. We treated the state of Florida as a separate unit from the rest of North America. We did not include areas where a taxon is considered as naturalized, because the goal was to



focus on native ranges. We calculated the total number of taxa in each region, and the numbers of taxa in all possible intersections/combinations of these regions, using the *UpSetR* package (Lex et al., 2014) in R (R Development Core Team, 2016).

For taxon status, we designated all taxa in the data set as either “invasive” or “not invasive” in Florida, and as either “endemic” or “not endemic” to the pine rocklands. Each taxon thus received two designations, one relating to invasiveness and the other relating to endemism. We determined invasive status from the Florida Exotic Plant Pest Council (FLEPPC) designations, which include both moderately and highly invasive taxa (Florida Exotic Pest Plant Council, 2017). Endemic designations were based on the *Floristic Inventory of South Florida* (Gann et al., 2017), *South Florida Multi-Species Recovery Plan* (U.S. Fish and Wildlife Service, 1999), and Jones and Koptur (2017).

### DNA extraction, amplification, and sequencing

We extracted total genomic DNA using the Qiagen DNeasy Mini Plant Kit (Qiagen, Valencia, California, USA). We followed a modified protocol that reduced the amount of RNAase to 3.5  $\mu$ L, extended the incubation step to 25 min, and reduced the final elution volume to 100  $\mu$ L to maximize DNA yield. Final DNA concentrations were verified with a Qubit fluorometer (ThermoFisher Scientific, Waltham Massachusetts, USA). We amplified three widely used chloroplast barcoding markers: two coding regions (*rbcL*, *matK*) and one intergenic spacer (*psbA-trnH*), following standard protocols (Kress et al., 2009, 2010). Amplification success was confirmed with gel electrophoresis, and Sanger sequencing was performed by Beckman Coulter Genomics (Cambridge, Massachusetts, USA), Genewiz (South Plainfield, New Jersey, USA), or Eurofins Genomics (Louisville, Kentucky, USA).

### Phylogenetic reconstruction

We edited sequences and assembled contigs for individual plastid markers from newly generated and pre-existing sequences in Geneious R9 (Biomatters, Auckland, New Zealand) and constructed alignments using the MAFFT 1.3.5 (Katoh and Standley, 2013) plugin in Geneious. Individual alignments were checked by eye for major irregularities (e.g., lack of reversed complementing) and manually adjusted before concatenating all three loci into a final alignment. The chloroplast genome behaves as a single locus, hence concatenation of loci is appropriate (Maréchal and Brisson, 2010). We determined the optimal model of DNA evolution for each of the three markers, and the best overall partitioning scheme, using PartitionFinder v. 1.1.1 and the Akaike information criterion (AIC) (Lanfear et al., 2012). The optimal partitioning scheme and set of models were used in subsequent maximum likelihood (ML) and Bayesian inference (BI) analyses. All analyses were performed on the HiPerGator 2.0 supercomputing cluster at the University of Florida.

We performed ML analysis using RAxML v. 8.2.8 (Stamatakis, 2006, 2014), completing a search for the ML tree and 1000 rapid bootstrap replicates in a single run (option *-f a*) to determine support for clades. We enforced a topological constraint at the ordinal level, using the classifications in the Angiosperm Phylogeny Group IV (The Angiosperm Phylogeny Group, 2016) for flowering plants and the Pteridophyte Phylogeny Group (PPG I, 2016) for ferns and lycophytes. Based on well-established phylogenetic relationships among vascular plants (e.g., Wickett et al., 2014), all analyses were

rooted with a lycophyte species (*Selaginella armata* Baker var. *eatonii* (Hieron. ex Small) B.F. Hansen & Wunderlin).

We performed a Bayesian molecular dating analysis in BEAST 2.4.6 (Bouckaert et al., 2014), and used the ML tree as the starting tree for this analysis after calibrating it to align with BEAST fossil constraints using the *chronos* function in the R package *ape* (Paradis et al., 2004). In addition to the order-level constraints from the ML analysis, we also included nine fossil constraints and further constrained several superclades sensu APG IV (i.e., Monocots, Commelinids, Superasterids, Superrosids, Fabids, Malvids, Campanulids, and Lamiids). Fossil constraints were selected from previous molecular dating studies of pteridophytes and seed plants (Schuettpelz and Pryer, 2009; Bell et al., 2010; Magallón et al., 2013). All fossils were modeled with gamma prior distributions, with the bulk of the distribution situated at slightly older than the estimated age of the fossil (see Appendix S2 for hyperprior parameters). We used the nucleotide substitution models and partitioning scheme identified by PartitionFinder and an uncorrelated, lognormal relaxed clock model and a birth-death speciation prior, with clock and tree models linked across all data partitions. We ran four separate analyses for 50,000,000 generations each, to more effectively search tree space. Trees were sampled every 5000 generations and all other parameters were sampled every 500 generations. We combined the four runs using LogCombiner v. 2.4.6 (Bouckaert et al., 2014) and assessed estimated sample size (ESS) values for the combined results in Tracer v. 1.6 (Rambaut et al., 2014). We determined that the analysis had run long enough when ESS values were over 200. We used TreeAnnotator 2.4.6 (Bouckaert et al., 2014) to discard 25% of trees sampled as burn-in and generated a maximum clade credibility (MCC) chronogram from the post burn-in trees. Alignments and trees are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gd86rn1> (Trotta et al., 2018).

### Phylogenetic signal

We calculated phylogenetic signal for invasiveness and endemism using phylogenetic generalized linear mixed models (PGLMM) (Ives and Helmus, 2011; Ives and Garland, 2014). When the observed variable is binary (as both of these traits are), PGLMM assumes that an underlying, unobserved continuous trait evolves along the phylogeny according to a Brownian Motion evolutionary process; this unobserved trait then determines the probability of the observed variable taking values 0 or 1. In PGLMMs, the unobserved traits are modeled as a Gaussian random variable with a covariance matrix,  $\sigma^2C$ , derived from the phylogeny. Without any independent variables (predictors),  $\sigma^2$  can be used to detect phylogenetic signal of the observed variable with relatively high statistical power and lower relative computational burden (Ives and Helmus, 2011; Ives and Garland, 2014). An estimate of  $\sigma^2$  that is significantly larger than zero under a likelihood ratio test suggests strong phylogenetic signal (for more technical details, see Ives and Garland, 2014). Values of  $\sigma^2$  that do not significantly differ from 0 in our analyses indicate that there is no phylogenetic signal for invasiveness or endemism, while values of  $\sigma^2$  near 1 indicate strong phylogenetic signal for the trait in question (i.e., invasive or endemic taxa, respectively, are more closely related to one another than would be expected by chance). We conducted all statistical tests using the function *binaryPGLMM* from the *ape* package (Paradis et al., 2004) in R. All R code for analyses and figures is available on GitHub (<https://doi.org/10.5281/zenodo.1313784>).

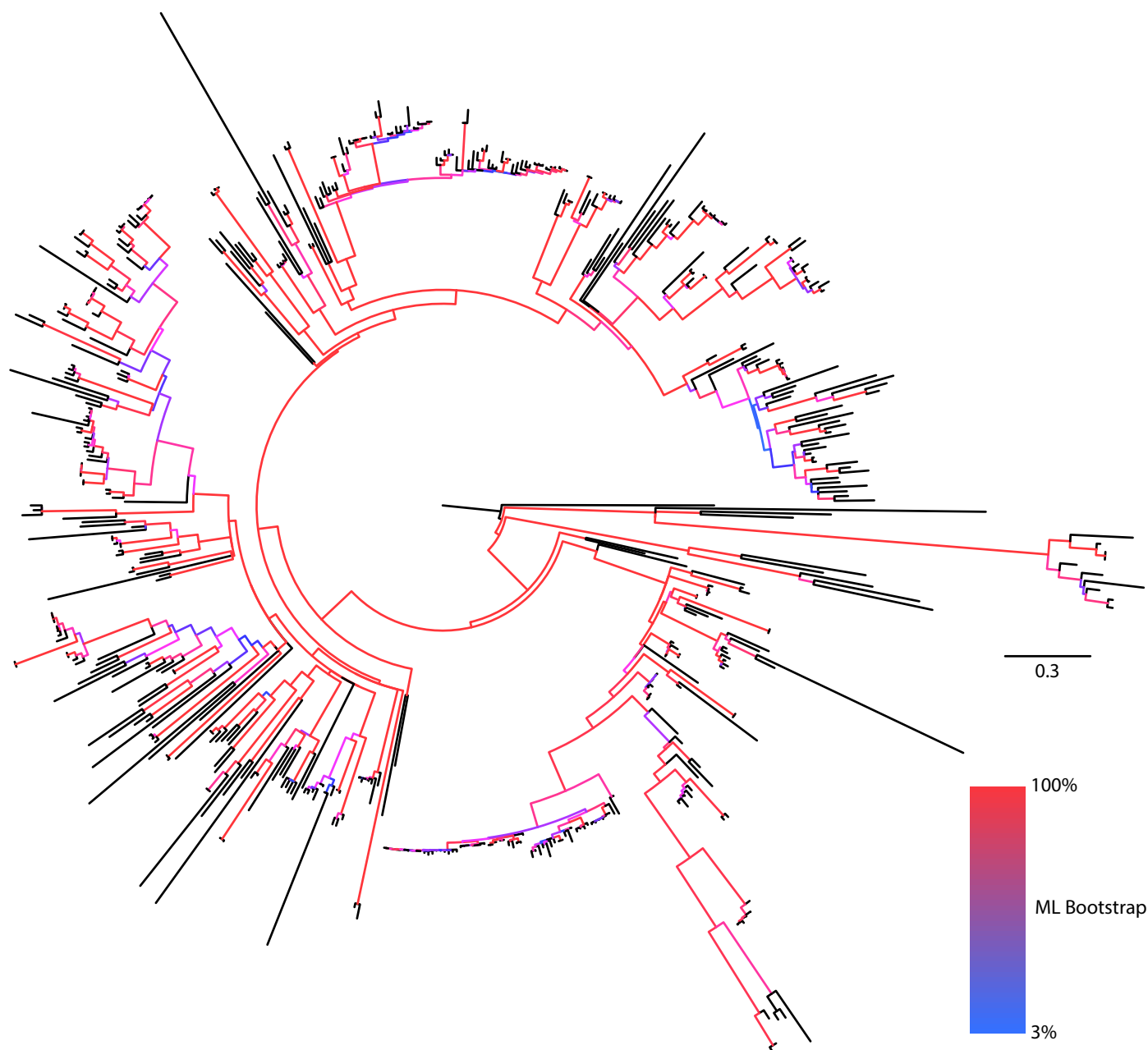
## RESULTS

### Phylogeny, phylogenetic signal, and biogeography

The final data set included 538 taxa belonging to 102 vascular plant families. The aligned, concatenated DNA matrix of sequences from three plastid regions was 4287 base pairs long. We included sequences of *rbcL* for 473 taxa (337 sequenced *de novo*, 136 pre-existing), *matK* for 381 taxa (253 *de novo*, 128 pre-existing), and *psbA-trnH* for 426 taxa (394 *de novo*, 32 pre-existing) (Appendix S1). PartitionFinder identified GTR+ $\Gamma$ +I as the best model of nucleotide evolution for *rbcL* and *matK*, and GTR+ $\Gamma$  for *psbA-trnH*. Because RAxML can only accept a single model of evolution, we

used GTR+ $\Gamma$ +I for all loci while maintaining individual partitions for each, while in BEAST, we used the recommended model for each partition.

The maximum likelihood tree had a score of  $-154,673.47$ . The tree had 536 internal nodes, 50 of which were constrained. Average bootstrap (BS) support across the 486 unconstrained internal nodes was 75.28%. Ninety unconstrained clades received 100% support and a total of 321 unconstrained clades had bootstrap support  $\geq 70\%$ . Relationships along the backbone of the phylogeny consistently received maximum support (BS = 100%), while support generally decreased tipwards (Fig. 3). BEAST recovered a phylogeny generally in agreement with the ML phylogeny and with dates congruent with those in recent studies (Bell



**FIGURE 3.** Maximum likelihood phylogeny of 538 pine rockland species. Branches are colored by maximum likelihood bootstrap value according to the heatmap. Scale bar = 0.3 substitutions/site.

et al., 2010; Magallón et al., 2013; Rothfels et al., 2015) (Fig. 4, Appendices S2, S3).

Twelve taxa are considered to be endemic to the pine rockland ecosystem, and there was strong phylogenetic signal for this trait ( $\sigma^2 = 0.1317$ ,  $P < 0.001$ ) (Fig. 4, Appendix S4). Nine of these taxa are superrosids and three are superasterids. Of the superrosids, five taxa belong to the family Euphorbiaceae, three to Fabaceae, and one to Linaceae; of the three superasterid taxa, Asteraceae, Rubiaceae, and Verbenaceae have one taxon each (Appendix S1). There was no phylogenetic signal to invasiveness ( $\sigma^2 = 0.0286$ ,  $P = 0.14$ ), and the 50 FLEPPC-ranked invasive taxa (Florida Exotic Pest Plant Council, 2017) belong to 26 families from 20 orders across the phylogeny (Fig. 4, Appendix S1). We were unable to include two endemic taxa in our flora and subsequent analyses, but invasive taxa were fully represented (Appendix S5).

Biogeographically, the majority of taxa present in our pine rockland data set (433 of the 538 total) include Florida as part of their native range (Fig. 5), and 47 taxa are endemic to the state of Florida (Fig. 5, Appendix S6). The range intersection with the highest number of native taxa is Florida+North America, with 121 taxa having as their native range the combination of these two areas exclusively (Fig. 5). The next-highest intersection is Florida+Caribbean, with 57 taxa, followed by 48 taxa whose native range includes all of the regions in the New World (Florida, Caribbean, North America, Central America, South America). Various other combinations of New World regions make up most of the next-largest intersections, with Asia and Africa also included in the top 10 largest intersections. The majority of taxa have four or fewer areas in their native range; relatively few taxa have native ranges that encompass five or more of the regions as we designated them.

Asia is the source for the highest number of invasive taxa in the pine rocklands (13), followed by Africa with eight taxa, and then several combinations of New World regions (Fig. 5). Note that of the 28 taxa whose native range is Asia alone, only 13 are considered invasive in the pine rocklands; the remaining 15 have not been designated as invasive in this system. Several other intersections that are the sources of taxa considered invasive in the pine rocklands are also the native ranges of taxa that are not invasive in this habitat (Fig. 5).

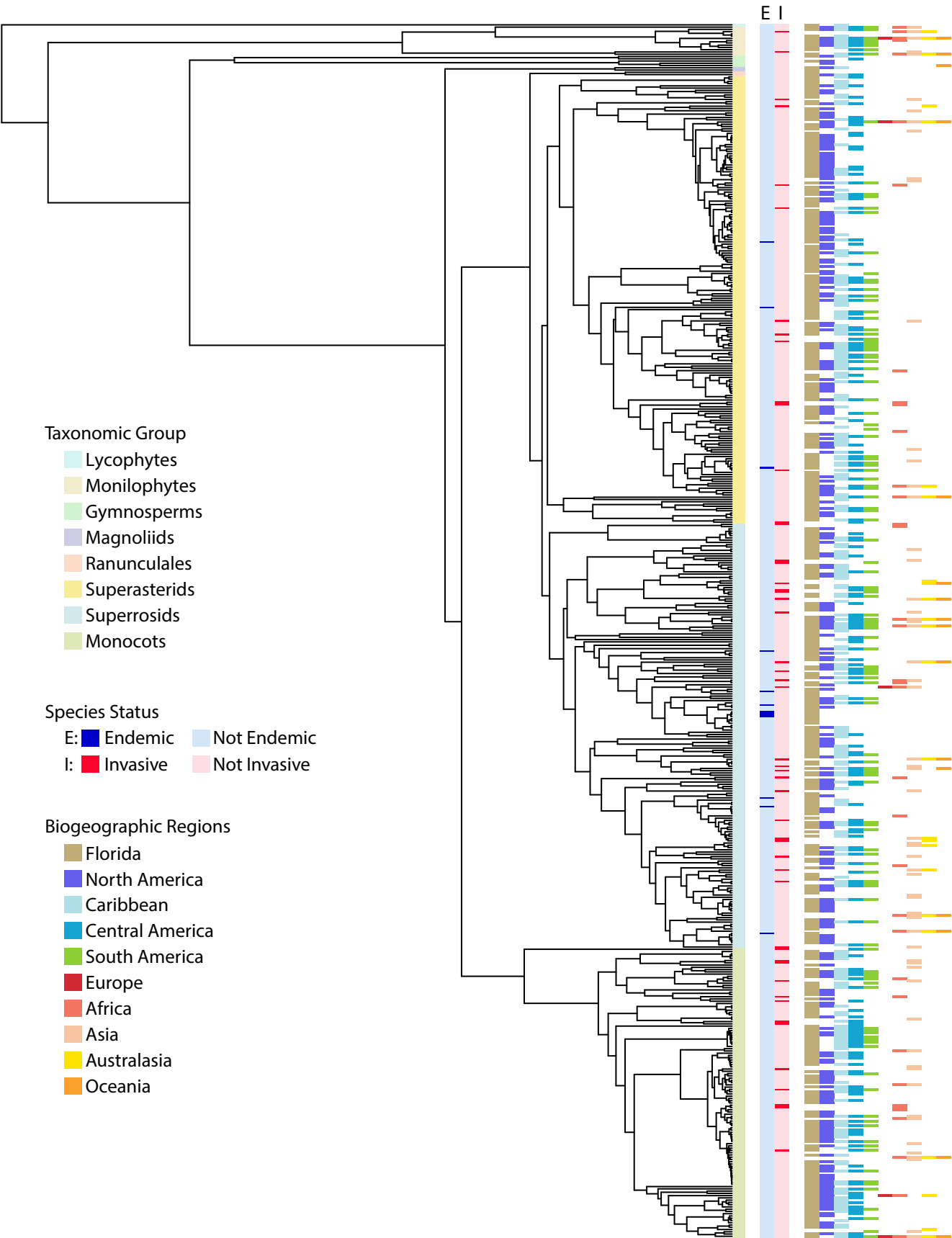
## DISCUSSION

The pine rockland plant community includes members of all the major vascular plant lineages and is an amalgamation of taxa from around the globe (Fig. 4). The vascular flora is dominated by flowering plants, with roughly equal representation of monocots, superrosids, and superasterids, 13 ferns, five gymnosperms and one lycophyte. Taxonomically, the pine rockland assemblage is broadly representative of the larger flora of the state of Florida (Wunderlin et al., 2017). Florida is one of the most floristically diverse states in the United States and has among the highest rates of state endemic plant taxa (Kartesz, 2015). Florida is also unique in the southeastern United States as the only state with rare, southeast-regionally endemic plant taxa present in every county (Estill and Cruzan, 1999). Roughly 9% of the taxa in our pine rockland data set are endemic to the state of Florida (47 of 538), and 12 of those are endemic to the pine rockland ecosystem itself. In total there are around 14 pine rockland endemics (U.S. Fish and Wildlife Service, 1999; Jones and Koptur, 2017). This is a remarkably high number

of endemic taxa considering the relatively small footprint of this habitat, even at its historical maximum (Fig. 1). Our analyses recover strong phylogenetic signal for endemism in the pine rockland flora, with the majority of the endemic taxa belonging to the superrosid clade, including five taxa in Euphorbiaceae and three in Fabaceae (O'Brien, 1998). There are two endemics not sampled in our data set: *Euphorbia deltoidea* Engelm. ex Chapm. subsp. *serpyllum* (Small) Y. Yang (Euphorbiaceae), and *Galactia pinetorum* Small (Fabaceae). Because these taxa both belong to the superrosid clade, and in the case of *E. deltoidea*, multiple subspecies contribute to the phylogenetic signal of endemism we report, we expect that our results for phylogenetic signal would not be substantially different had we been able to include these additional endemic taxa.

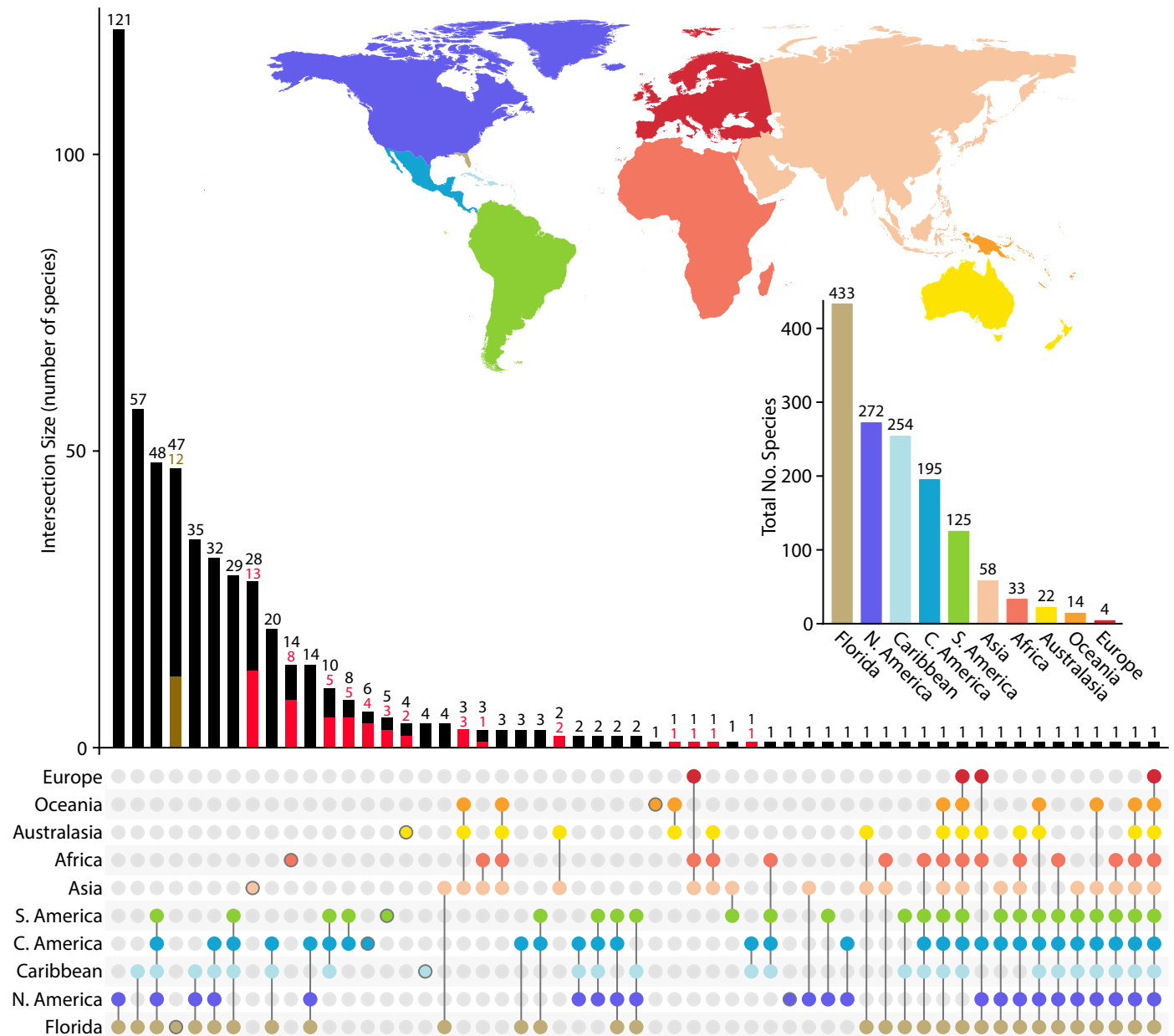
Biogeographically, the pine rockland plant community has long been recognized as representing a confluence between taxa from temperate North America and tropical regions farther south, including the Caribbean, Central America, and northern South America (Robertson, 1953; Loope et al., 1979; Snyder et al., 1990; O'Brien, 1998; U.S. Fish and Wildlife Service, 1999; Diamond and Heinen, 2016). Robertson (1953, p. 20) wrote that the pine rocklands "are often considered to be southern outliers of the extensive longleaf pine forests of the southeastern United States," but noted that they appeared to him to be "more strongly related to pine forest areas of the Bahamas, Cuba, Hispaniola, and parts of Central America" (Robertson, 1953; p. 20). Other authors have also noted this strong connection to the West Indies, particularly for understory components of the flora (shrubs and herbs) (Loope et al., 1979; Snyder et al., 1990). We find that the range intersection Florida+North America is the source of the largest number of pine rockland plant taxa (121), followed by Florida+Caribbean with 57 taxa (Fig. 5). Overall, North America and the Caribbean are part of the native ranges of very similar numbers of taxa: 272 and 254, respectively (Fig. 5, inset graph). It may seem somewhat surprising that temperate, continental North America and the Caribbean should be so nearly equal in their contributions to the pine rockland flora, given that the pine rockland is well within the tropical climate zone that also includes most of the Caribbean (Peel et al., 2007). However, the habitat is not homogeneous from north to south, with more southerly fragments having a higher proportion of tropical taxa, while more northerly fragments are more similar to longleaf pine forests found throughout the southeast (O'Brien, 1998). This reflects the unique mixing of temperate and tropical taxa that is known to be a hallmark of this ecosystem overall, and underscores the connection that Robertson (1953) and others have noted between the pine rockland and other pine-dominated systems to the north in the United States.

Ours is the first study to quantify the native ranges of pine rockland taxa and illustrate the extent of the flora's dominance by New World elements (Fig. 4). Of the 55 range intersections present among the native ranges of the taxa in our data set (Fig. 5), 25 include only New World regions, and these account for 455 of the 538 taxa in the data set (85%). Regions in the Old World—Africa, Asia, Europe, Australasia, and Oceania—are relatively rare sources for pine rockland taxa, either alone or in combination (Fig. 5). Among the New World regions we delineated, the Caribbean is the tropical area that has contributed most to the flora of the pine rocklands. The Caribbean has previously been recognized as a source region for plant (and animal) taxa in Florida as well as Central and northern South America (Kennedy et al., 2016). These movements are facilitated by several generally westward flowing ocean currents





**FIGURE 4.** Maximum clade credibility chronogram of 538 pine rockland species. Major taxonomic groups according to PPG I (2016) and APG IV (The Angiosperm Phylogeny Group, 2016) are shown at the tips of the phylogeny. The first set of vertical bars indicates species status (*endemic* or *not endemic* and *invasive* or *not invasive*). The second set of vertical bars indicates presence or absence in each of ten biogeographic regions (see map in Figure 5). Information on family-level taxonomy and species' endemism and invasiveness designations can be found in Appendix S1.



**FIGURE 5.** Native ranges of all species present in the pine rocklands, shown as intersections (combinations of regions) among ten biogeographic regions depicted in the map at top right. The colored circles and lines illustrate all the intersections of these regions, including single regions (colored circles with grey outline), that are present among the native ranges of the 538 species in our data set. Single intersections (circles with grey outline) indicate taxa that have only a single region in their native range. The black vertical bars indicate the total numbers of species that have a particular intersection as their native range; the brown bar is the 12 endemic pine rockland species as a subset of the Florida native species, and the red bars are pine rockland invasive species as subsets of the total species in a given intersection. The inset vertical bars to the right indicate the total numbers of species that have a particular region as part of their native range. The total number of taxa with a particular region in their native range (for example, 433 taxa include Florida in their native range, brown vertical bar in the inset) can also be determined by summing horizontally across the intersection values for that biogeographic region (i.e., by adding up the values above the black bars for every column where Florida's circle is filled in).

in the region (Kennedy et al., 2016) as well as by migratory birds (Diamond and Heinen, 2016). While exploring the historical biogeography of all the plant taxa in the pine rocklands was outside the focus of the current study, it would be of great interest to reconstruct the historical movements that led to the assembly of this flora, to determine the pathways by which taxa have tended to reach South Florida and how these have changed with time, climate, and sea level fluctuations. Such reconstructions would have value for further understanding the contributions and times of arrival of taxa from various source regions to the pine rocklands and all of South Florida, and for predicting where taxa may arrive from in the future, particularly as climate change alters global wind and ocean current patterns and migratory routes.

While there are relatively few taxa in the pine rockland community whose native range includes the Old World, those regions have served disproportionately as sources for invasive taxa in this habitat. Sixty-four percent of the 50 invasive taxa in the pine rockland have native ranges in the Old World, with Asia acting solely or in combination as the source for 42% of the pine rockland invasives. Our analyses found no evidence of phylogenetic signal to invasiveness, with invasive taxa occurring across the angiosperm phylogeny, plus two species of ferns (*Pteris vittata* L. and *Lygodium japonicum* (Thunb.) Sw.). A potential explanation for the observed lack of phylogenetic signal for invasiveness is propagule pressure. Pine rockland habitat is surrounded by a matrix of residential and agricultural land that can serve as sources of propagules potentially from multiple microhabitats and evolutionary lineages (Holle and Simberloff, 2005; Lockwood et al., 2005, 2009). Alternately, invasive species from distantly related clades may share similar traits due to convergent evolution or plasticity, which could be advantageous in the shifting environmental conditions present in pine rocklands (Richards et al., 2006). Information on functional traits and life history strategy will be critical for further understanding why certain taxa have already become invasive and for evaluating the invasive potential of other taxa.

Given the lack of phylogenetic signal to invasiveness, a more promising strategy to identify nonnative taxa with potential for becoming invasive may be to monitor those taxa whose native ranges have already produced high numbers of invasives in this habitat. Our community phylogeny includes several taxa not considered invasive in the pine rockland, but whose native ranges are exclusively Asia (15 taxa) or Africa (6 taxa)—regions which we have shown to contribute the greatest number of known invasive taxa. These taxa might therefore be considered to have high potential for becoming invasive in the future. Additionally, many recent studies have sought to leverage evolutionary relationships between native communities and their non-native counterparts to determine invasive potential through the lens of Darwin's Naturalization Conundrum (DNC) (Fridley and Sax, 2014; Marx et al., 2016; Gallien and Carboni, 2017). Modern conceptions of the DNC predict that invasive species that are closely related to native communities should share traits that allow them past environmental filters, while invasive species that are distantly related may be able to avoid competition with established species if they differ in traits. Further exploring the relationships between invasive and native species in the context of DNC has the potential to reveal mechanisms structuring pine rockland plant assemblages in the face of anthropogenic change. Finally, the scale of inquiry could shift our interpretation of phylogenetic signal, as has been found previously in other community phylogenetic analyses

(Cavender-Bares et al., 2006; Cadotte et al., 2009; Krasnov et al., 2011). While we did not find phylogenetic signal for invasiveness at the scale of the pine rockland flora, at smaller (e.g., individual habitat fragments) or larger (e.g., the entire flora of Florida) scales, invasive species may in fact be more closely related than recovered by our analyses.

The pine rockland is a globally critically imperiled ecosystem, and preservation of remaining habitat fragments is imperative for retaining and protecting plant and animal biodiversity of South Florida, particularly Miami-Dade and Monroe Counties (Possley et al., 2008; Diamond and Heinen, 2016). The high numbers of endemic taxa in the pine rockland exemplify the unique nature of this habitat, but the traits that have allowed these taxa to succeed historically are unlikely to sustain them unless critical habitat processes are restored and maintained. The Euphorbiaceae endemic taxa in particular exemplify a habit and morphology that are likely adaptations to the historically fire-maintained pine rockland ecosystem: all are small in stature and require precise environmental conditions to flourish. They are fire-dependent epipetric taxa that take advantage of the high-light environment atop the bare limestone substrate that is available after frequent fires (Herndon, 1993). Changes in fire regime, along with fragmentation of the pine rocklands, have increasingly allowed encroachment by fast growing, invasive taxa, which has raised the risk of extinction for the endemic taxa that exhibit these specialized traits. This has led to the pine rockland endemic plant species' perennial membership on Florida state and U.S. federal lists of threatened and endangered taxa (U.S. Fish and Wildlife Service, 1999).

Despite the many threats to the pine rockland and to fragmented natural ecosystems in general, several studies have shown that conserving small fragments of habitat can lead to successful preservation of taxa of interest (Shafer, 1995; Possley et al., 2008, 2014; Diamond and Heinen, 2016). Incorporating phylogenetic information into our current treatment of endangered taxa and communities provides a novel means to identify conservation priorities and assess success of restoration practices that can complement traditional approaches (Winter et al., 2013; Forest et al., 2015; Hipp et al., 2015; Laity et al., 2015). Taxa of greatest conservation concern are often those that are endemic and heavily dependent on historical ecosystem processes. These taxa often require the most intensive management practices to maintain suitable habitat conditions (e.g., prescribed burning, invasive species removal, mowing, etc.). The fact that endemic taxa tend also to be highly threatened and/or endangered, and that we found strong phylogenetic signal for endemism in the pine rockland flora, suggests that we can use information about phylogenetic relationships and the structure of fragmented communities to identify taxa of concern and the spatial areas or fragments in which they occur. Armed with this information, we can then act to preserve the greatest amount of evolutionary history and potentially the greatest amount of ecosystem function (Devictor et al., 2010; Rosauer and Mooers, 2013; Winter et al., 2013). Incorporating phylogenetic information should facilitate assessment of both the potential impact of proposed management efforts, and the success of already-implemented actions (Hipp et al., 2015). Community phylogenetics thus represents a critical framework that can aid our understanding of how communities assembled historically, how we might best maintain them currently, and how we can most effectively conserve biodiversity in the future.



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## DATA ACCESSIBILITY

GenBank accession numbers for newly generated sequences are available in Appendix S1. The sequence alignment, the XML file used for our BEAST analysis, and the resulting maximum clade credibility phylogeny are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gd86rn1> (Trotta et al., 2018). R code used for all analyses and figures is available on GitHub (<https://doi.org/10.5281/zenodo.1313784>).

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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