The role of phylogenetic scale in Darwin's naturalization conundrum in the critically imperilled pine rockland ecosystem

Lauren B. Trotta1 | Zachary A. Siders2 | Emily B. Sessa3 | Benjamin Baiser1

1Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA
2Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA
3Department of Biology, University of Florida, Gainesville, FL, USA

Abstract

Aim: We expand on community phylogenetic approaches to Darwin's Naturalization Conundrum by considering phylogenetic scale, comprised of phylogenetic grain and extent. We assess relatedness between invasive, non-native and native plant species at multiple depths in the phylogeny (i.e. phylogenetic grain) and across multiple clades (i.e. phylogenetic extents) at regional and local spatial scales in the highly fragmented, critically imperilled pine rockland ecosystem.

Location: Miami-Dade County, Florida, USA.

Methods: We used two metrics differing in phylogenetic grain to determine whether invasive or non-native species were more closely related to native species in the regional pool and at 33 habitat fragments. At both spatial scales, we altered phylogenetic extent from all vascular plants to four smaller phylogenetic domains (Monilophyte, Gymnosperm, Monocotyledon and Dicotyledon) and assessed whether the interpretation of relatedness changed.

Results: For the regional pool and at a broad phylogenetic grain, non-native species were more closely related to the native community than invasive species were for all phylogenetic extents (i.e. support for Darwin's Naturalization Hypothesis, DNH), and at a fine phylogenetic grain for only two phylogenetic extents. At the local scale, there was limited support for DNH across all phylogenetic extents. In Monocotyledons, support for DNH was more prevalent at the fine phylogenetic grain, while Dicotyledons showed support for DNH at the broad phylogenetic grain.

Main conclusions: In the pine rockland flora, we found either support for DNH or no difference in relatedness between non-native-to-native and invasive-to-native species. However, patterns of relatedness varied across spatial and phylogenetic grain and, critically, this variability is highly dependent on the phylogenetic extent considered. By explicitly assessing the interactions between spatial scale and phylogenetic scale, we show that support for DNH was context dependent, and findings at smaller phylogenetic extents rarely agreed with findings at the larger phylogenetic extent.

Keywords

biological invasions, community phylogenetics, Darwin's Naturalization Conundrum, Darwin's Naturalization Hypothesis, phylogenetic extent, phylogenetic grain, phylogenetic scale, pine rocklands, spatial scale
Darwin’s Naturalization Conundrum (DNC) is composed of two paradoxical hypotheses: Darwin’s Naturalization Hypothesis and the Pre-Adaptation Hypothesis (Daehler, 2001; Mack, 2003; Rejmanek & Richardson, 1996). Darwin’s Naturalization Hypothesis (DNH) predicts that for a non-indigenous species to establish, it should be distantly related to the indigenous community allowing it to exploit under-utilized resources and, avoid competitive exclusion (Daehler, 2001; Darwin, 1859; Rejmanek & Richardson, 1996). Alternately, the Pre-Adaptation Hypothesis (PAH) predicts that a non-indigenous species should be closely related to the indigenous community, so it shares evolutionary history and traits allowing this species to pass through environmental filters and establish (Mack, 2003). Support for one of these hypotheses over the other may be influenced by idiosyncrasies of the study system, such as invasion stage, spatial scale and phylogenetic scale (Cadotte et al., 2018; Thuiller et al., 2010). To untangle how these system-specific features influence our view of the mechanisms shaping communities in the face of species invasion, they must be accounted for simultaneously.

Community phylogenetics seeks to understand mechanisms (e.g. environmental filtering, competition, facilitation) that structure ecological communities using phylogenetic relationships (Cavender-Bares et al., 2009). From the perspective of invasion ecology, community phylogenetics leverages evolutionary information through the framework of DNC to explore the mechanisms by which non-indigenous species invade communities (Diez et al., 2008; Thuiller et al., 2010). However, observed patterns of phylogenetic relatedness are inconsistent across both invasion stage (sensu, Cadotte et al., 2018; Li et al., 2015; Lockwood et al., 2013) and spatial scale, diminishing our ability to synthesize findings across studies of DNC (Cadotte et al., 2009, 2018; Lim et al., 2014; Ma et al., 2016). Further, phylogenetic scale, or the nested relationships between clades in a phylogeny, may be important to consider when assessing communities that represent a broad array of evolutionary lineages (Graham et al., 2018). An integrative, community phylogenetic approach is required to understand how invasion stage, spatial scale and phylogenetic scale influence interpretations of DNC.

Mounting evidence suggests that invasion stage can influence the role of evolutionary relatedness in establishment of non-indigenous species (Cadotte et al., 2018; Li et al., 2015). Following transport to novel environments, non-indigenous species can progress through stages of invasion from introduction, to establishment/naturalization, and finally to spread/impact (Blackburn et al., 2011; Kolar & Lodge, 2001; Li et al., 2015; Pyšek et al., 2004; Richardson et al., 2000; Seastedt & Pyšek, 2011). It is often difficult to evaluate which stage non-indigenous species fall into. As a result, invasion spread or proxies for the impact of non-indigenous species on indigenous communities are commonly considered in studies of DNC (Cadotte et al., 2018). In this study, we focus on two levels of invasion impact: non-native (i.e. naturalized sensu Richardson et al., 2000) and invasive. Non-native species have minimal impacts on the indigenous community because, while they can establish and sustain a population, their spread to new habitat patches is limited. Invasive species can establish, sustain a population and spread, greatly altering the indigenous community structure.

In a community predominantly structured by competition (DNH), we expect non-indigenous species considered invasive to be more distantly related to the indigenous community than those considered non-native are. Under DNH, invasive species that share less evolutionary history with indigenous species avoid competition by occupying empty niches and using different resources. In contrast, in a community where environmental filtering determines invasion impact (PAH), we expect non-indigenous species considered invasive to be more closely related to the indigenous community than those considered non-native are. Under PAH, invasive species that share a large amount of evolutionary history with indigenous species will have diverged more recently and share more similar features leading to greater niche overlap, increased competition, and potentially detrimental impacts on the indigenous community if the invasive species is a strong competitor.

Spatial scale plays an important role in mediating mechanisms responsible for shaping ecological assemblages (Levin, 1992; Swenson et al., 2006; Wiens, 1989). At small spatial scales (i.e. local communities), indigenous and non-indigenous species are thought to compete directly such that phylogenetic relatedness between these groups should reflect the struggle for co-existence (i.e. DNH) (Cadotte et al., 2018; Park et al., 2020; Thuiller et al., 2010). At larger spatial scales (e.g. the regional pool), indigenous and non-indigenous species merely co-occur, a process likely governed by the strength of the environmental filter and habitat heterogeneity (i.e. PAH) (Cadotte et al., 2018; Thuiller et al., 2010). As a result, the mechanisms driving observed species relatedness may be incongruent across different spatial scales (Park et al., 2020; Thuiller et al., 2010).

Phylogenies have been increasingly incorporated into community ecological questions, like DNC, because of their power to account for the evolutionary non-independence of co-occurring species (Faith, 1992; Felsenstein, 1985; Li & Ives, 2017; Webb, 2000). However, the optimal methodology to represent and query phylogenetic information in relation to community data is an active topic of debate (Cavender-Bares et al., 2004; Swenson et al., 2006). Recently, Graham et al. (2018) proposed a systematic framework for incorporating phylogenetic scale comprised of two facets, phylogenetic extent and phylogenetic grain, into community phylogenetic analyses. Phylogenetic extent refers to the tips and subtending branches selected for an analysis. By varying phylogenetic extent in an analysis, the size of phylogeny considered can range from including all species in a phylogeny or be limited to a smaller clade. Phylogenetic grain refers to the node depth within a phylogeny considered in an analysis. When phylogenetic grain is varied, analyses can include only closely related species (i.e. fine grain measures such as distance to the nearest native species, nearest taxon distance and nearest taxon index) or distantly related taxa (i.e. broad grain measures such as mean distance to a native species, mean pairwise distance and net relatedness index) (Graham et al., 2018). Phylogenetic scale has repeatedly been proposed as an important
facet to incorporate into analyses of DNC (Godoy et al., 2014; Graham et al., 2018; Park et al., 2020; Procheş et al., 2007; Thuiller et al., 2010). While few studies have considered phylogenetic scale by name (Ng et al., 2018), multiple studies have queried different phylogenetic grains (Bezeng et al., 2013; Carboni, Münkemüller, et al., 2013; Lim et al., 2014; Maitner et al., 2012; Marx et al., 2016; Parker et al., 2012; Ricotta et al., 2010; Schaefer et al., 2011), and no previous studies of DNC have considered phylogenetic extent. Concurrently accounting for phylogenetic grain and extent in DNC may alter our understanding of mechanisms driving invasion in communities, especially in cases where invaders arise non-randomly across the phylogeny (e.g. predominately in a single lineage).

Here, we explore the role of phylogenetic grain and phylogenetic extent on DNC across two spatial scales using our previously published community phylogeny of the pine rockland flora (Trotta et al., 2018). The savanna-like pine rockland ecosystem is found along the Miami Rock Ridge in Miami-Dade County with allied habitats found in the Florida Keys and The Bahamas. The plant community is a confluence of tropical Caribbean and temperate North American taxa, resulting in an indigenous flora of nearly 500 species (Loope et al., 1979; Robertson, 1953; Snyder et al., 1990; Trotta et al., 2018). Pine rockland habitat is defined by a canopy of solely South Florida slash pine (Pinus elliottii var. densa), a midstorey of palms and woody shrubs and a diverse herbaceous understory that includes many endemic, threatened or endangered species. Rapid expansion of the Miami Metropolitan Area has reduced pine rockland habitat outside Everglades National Park to less than 2% of its historic range (U.S. Fish and Wildlife Service, 1999). Remnants of this globally critically imperilled habitat are highly fragmented, isolated “islands” in a matrix of urban development and agricultural land (FNIAI, 2010). Currently, there are 106 species considered to be non-indigenous found in the pine rockland flora (FLEPPC, 2017; Gann, 2019). Pine rocklands are ideal for testing the interactions of invasion impact, spatial scale and phylogenetic scale on DNC due the high diversity of indigenous and non-indigenous species that have been robustly sampled and represented in a well-resolved, species-level community phylogeny (Trotta et al., 2018).

Our goal in this study was to explore the roles of phylogenetic grain and phylogenetic extent across two spatial scales and two levels of invasion impact in the context of DNC using the pine rockland flora. To do this, we had two objectives and associated predictions:

1.1 | Objective 1

To test DNC, we compared phylogenetic relatedness of non-native and invasive to native species using two metrics of phylogenetic grain for Tracheophyta (all vascular plants) across regional and local spatial scales. We predict that we will find support for PAH at the scale of the regional pool (i.e. invasive species are more closely related to native species than non-native species are) and support for DNH at the local scale (i.e. invasive species are more distantly related to native species than non-native species are) (Cadotte et al., 2018; Carboni, Münkemüller, et al., 2013; Park et al., 2020). At the scale of the regional pool, being closely related to native species will allow invasive species to overcome the environmental filter in order to establish and spread. At the local scale, competition for resources will result in impactful, invasive species being distantly related to native species and therefore able to exploit unused resources.

1.2 | Objective 2

To determine whether conclusions about DNC differ across phylogenetic extents, we repeated our analysis of Tracheophyta using four large phylogenetic domains (sensu Graham et al., 2018) represented in our phylogeny: Dicotyledons, Monocotyledons, Gymnosperms and Moniliphytes (i.e. ferns). We predict that patterns of relatedness between invasive and non-native species to the native community in each phylogenetic domain will not match patterns observed across Tracheophyta. Thus, subsuming individual domains into a single, global analysis can obscure important, domain-based inferences.

2 | METHODS

2.1 | Taxon sampling & phylogeny

We used the community phylogeny from Trotta et al. (2018) that includes 538 species from the pine rockland flora and represents 92.28% of the species present in this habitat type (Gann, 2019). This community phylogeny was estimated using sequences of the plastid loci \textit{rbcL}, \textit{matK} and \textit{psbA-trnH} generated from field collections, herbarium vouchers or sequence data from GenBank. Details about collections, DNA extraction, sequencing and phylogenetic reconstruction can be found in Trotta et al. (2018). The product of this analysis was an Maximum Clade Credibility chronogram generated from the posterior distribution of phylogenetic trees produced with the molecular dating software BEAST v. 2.4.2 (Bouckaert et al., 2014) (Figure 1; see Appendix S1). We used a time-dated phylogeny because we are interested in (un)relatedness of species across a regional pool representing roughly 400 my of evolution (Elliott et al., 2018). While we do not expect relatedness to translate to feature diversity evenly across the phylogeny, we generally assume that closely related species will share more similar features than more distantly related species (Elliott et al., 2018; Jantzen et al., 2019; Mooers & Redding, 2009). This chronogram was used for all downstream analyses described below (see Appendix S2).

2.2 | Invasion impact

Species were ranked as either native or non-indigenous based on The Institute for Regional Conservation's (IRC) assessment of South
Florida’s flora (Gann, 2019). The non-indigenous species group was further divided into invasive and non-native species. Invasive species are those ranked as a Category I or Category II invasive species based on the Florida Exotic Plant Pest Council (FLEPPC, 2017). Category I invasive species alter “native plant communities by displacing native species, [or] changing community structures or ecological functions,” while Category II invasive species are less ecologically impactful but “have increased in abundance or frequency” (FLEPPC, 2017). Non-native species are all other non-indigenous species considered “not native” by the IRC (Gann, 2019). Invasion impact groups were mutually exclusive. Of the 538 species in our regional pool, 432 were native, 57 were non-native, and 49 were invasive (Table 1).

### 2.3 Phylogenetic diversity metrics

We determined the phylogenetic cophenetic distance from each invasive species to all native species and did the same for each non-native species to all native species. We then calculated two metrics of phylogenetic diversity: distance to the nearest native species (DNNS) and mean distance to a native species (MDNS). DNNS is the pairwise distance between each invasive or non-native species and its nearest native neighbour (i.e., the shortest branch length) and describes diversity at the tips of the tree (i.e., fine phylogenetic grain). MDNS is the average phylogenetic pairwise distance of each invasive or non-native species to all native species (i.e., the average of
all branch lengths between one invasive or non-native species and all native species) and captures basal diversity in the tree (i.e. broad phylogenetic grain).

2.4 | Statistical tests

We used one-sided Mann–Whitney U tests to determine whether distributions of distances between non-native-to-native and invasive-to-native species differed significantly. We performed a single Mann–Whitney U test for each metric of phylogenetic grain for each instance we were interested in assessing in Objectives 1 and 2 (i.e. scale of the regional pool vs. within fragments; Tracheophyta vs. phylogenetic domains).

2.5 | Objective 1: DNC of Tracheophyta

At the scale of the regional pool, we tested whether invasive or non-native species were more closely related to native species using all Tracheophyta in the community phylogeny for both metrics of phylogenetic grain.

Local-scale analysis similarly tested relatedness of invasive-to-native and non-native-to-native species but was performed on 33 individual pine rockland fragments. These fragments were classified as being composed exclusively of pine rockland habitat by Miami-Dade County Natural Areas Inventory or local experts (MDC Natural Areas Management, 2004, 2010). Detailed species lists for these fragments are available from IRC Floristic Inventory of South Florida (Gann, 2019). For each fragment, we subset the phylogenetic distance matrix to only include taxa that were present at the site and represented in our chronogram.

2.6 | Objective 2: DNC with phylogenetic domains

Any two taxa belonging to distantly related clades share similar pairwise distances because their lineages diverge deep in the phylogeny. Evolutionarily distinct taxa, subtended by disproportionally long branch lengths, have been cited as a statistical issue because they can bias interpretation of phylogenetic community structure (Cadotte, 2014; Graham et al., 2018; Hardy & Senterre, 2007; Swenson et al., 2006) and generally are removed from analyses (Feng et al., 2014; Letcher, 2010; Ndiribe et al., 2013; Purschke et al., 2017). Using an approach that varies phylogenetic extent allows for the inclusion of these taxa in community phylogenetic studies.

To minimize the influence of repeated, large pairwise distances in our analysis, we performed regional and local-scale analyses within four large phylogenetic domains: Dicotyledons, Monocotyledons, Gymnosperms and Monilophytes. Each domain represents a clade (i.e. all species in the domain share a common ancestor). We considered Dicotyledons to be the Eudicot clade (The Angiosperm Phylogeny Group, 2016) (Figure 1). We excluded two native species of Magnoloids from our analysis as they are sister to both the Dicotyledon and Monocotyledon domains (see Appendix S3).

At the scale of the regional pool, we divided Tracheophyta into these four domains and tested whether invasive or non-native species were more closely related to native species using both phylogenetic grains. At the local scale, the flora of each fragment was also subset into domains and relationships between invasive-to-native and non-native-to-native were tested. In fragments where both non-native and invasive species categories included only one or zero species, we did not perform significance tests for either phylogenetic grain. Based on this constraint, we did not perform tests for the Gymnosperm domain at either the regional or local scale and the Monilophyte domain at the local scale. Further, we excluded six fragments from analysis at the local scale for the Monocotyledon domain.

3 | RESULTS

3.1 | Objective 1: Testing DNC in Tracheophyta

3.1.1 | Regional scale

Across all Tracheophyta, we found that the distribution of DNNS for non-native-to-native and invasive-to-native species showed no difference in relatedness \( w = 1586.5, p = .114; \) Figure 2a). When comparing the MDNS distributions, we found that non-native species were more closely related to native species than invasive species were \( w = 1677.5, p = .0372; \) Figure 2b; Table 2).
FIGURE 2  Empirical relative density distributions of distance to nearest native species (DNNS; a, c, e) and mean distance to a native species (MDNS; b, d, f) between invasive and native species (orange) and non-native and native species (blue) at the scale of the regional pool. Rows represent phylogenetic extents: top row shows Tracheophyta (entire regional pool; a, b); middle row shows Dicotyledon (c, d); bottom row shows Monocotyledon (e, f). Monilophyte domains included three or fewer comparisons and so distributions are not shown. Columns represent phylogenetic grain: left column shows fine phylogenetic grain (DNNS); right column shows broad phylogenetic grain (MDNS). DNNS and MDNS values have been log transformed (x axis) to emphasize the separation in significantly different distributions. The empirical relative density distributions were scaled by dividing by the maximum density of the two relevant distributions for ease of comparison. Below the empirical relative density distributions we show the spread of raw DNNS and MDNS values (points) as well as a boxplot summary of the distributions. Outliers have been removed from the boxplots. An asterisk (*) indicates where non-native species are significantly more closely related to native than invasive species are.
3.1.2 | Local scale

We analysed data from 33 urban pine rockland fragments in our local-scale analysis (SI 3). The species lists for these fragments included 455 taxa from our phylogeny including 363 native taxa, 46 non-native taxa and 46 invasive taxa (Table 1; see Appendix S4 and S5).

For Tracheophyta, we found that non-native species were more closely related to native species than invasive species were in four fragments at the fine phylogenetic grain (DNNS) (ranges: \( w = 262.5–450.5; \ p = .002–.025 \)). At the broad phylogenetic grain (MDNS), we also found that non-native species were more closely related to native species than invasive species were in four fragments, though the fragments with significant results differed between phylogenetic grains (ranges: \( w = 21–526; \ p = .003–.049 \)) (Figure 3) (see Appendix S6). In one fragment, invasive species were more closely related to native species than non-native species were at the broad phylogenetic grain (\( w = 21; \ p = .022 \)) (Figure 3). Across the other 29 and 28 fragments, at the fine and broad phylogenetic grains, respectively, there were no differences in relatedness between phylogenetic grains (ranges: \( w = 3–45.5; \ p < .05 \)).

Distance to nearest native species metric for Dicotyledons showed no difference in relatedness between invasive and non-native species to the native community (\( w = 656.5, \ p = .391; \ Figure 2c \)). DNNS for Monocotyledons and Monilophytes showed that non-native species were more closely related to the native community than invasive species were (Monocotyledon: \( w = 145.0, \ p < .001 \); Monilophyte: \( w = 2, \ p = <0.001; \ Figure 2c \)). For MDNS, all three domains analysed showed that non-native species were more closely related to the native community than invasive species were (Dicotyledon: \( w = 961.5, \ p = .001 \); Monocotyledon: \( w = 134.0, \ p = .00467 \); Monilophyte: \( w = 2, \ p = <0.001; \ Figure 2d–f \) (Table 2).

3.2 | Objective 2: Testing DNC in phylogenetic domains

3.2.1 | Regional scale

The Dicotyledon domain was the most speciose, followed by Monocotyledon, Monilophyte and Gymnosperm (Table 1). Pairwise distances between species in each domain were as follows: Monilophytes ranged from 0 to 413.07 my; Gymnosperms from 0 to 623.45 my; Dicotyledons from 0 to 253.14 my; Monocotyledons from 0 to 260.30 my.

| Spatial scale | Phylogenetic extent | Phylogenetic grain | DNNS | MDNS |
|---------------|---------------------|--------------------|------|------|
| **Regional**  | Tracheophyta        | None               | DNH  |      |
|               | Dicotyledon         | None               | DNH  |      |
|               | Monocotyledon       | DNH                | DNH  |      |
|               | Monilophyte         | DNH                | DNH  |      |
| **Local**     | Tracheophyta        | None               | 29   | 28   |
|               | DNH                 | 4                  | 4    |      |
|               | PAH                 | 0                  | 1    |      |
|               | Dicotyledon         | None               | 33   | 19   |
|               | DNH                 | 0                  | 14   |      |
|               | PAH                 | 0                  | 0    |      |
|               | Monocotyledon       | None               | 13   | 22   |
|               | DNH                 | 14                 | 5    |      |
|               | PAH                 | 0                  | 0    |      |

**TABLE 2** Overview of support for Darwin’s Naturalization Hypothesis (DNH), Pre-Adaptation Hypothesis (PAH) or no support for either hypothesis (None) across regional and local spatial scales for metrics of fine phylogenetic grain (DNNS) and broad phylogenetic grain (MDNS) across four phylogenetic extents.

3.2.2 | Local scale

The floras represented in our fragments included 331 Dicotyledons, 107 Monocotyledons, 12 Monilophytes, and four Gymnosperms (Table 1; see Appendix S3). For a full accounting of the number of taxa for each species designation within each fragment, see Appendix S4. When we considered phylogenetic domains independently, we found no difference in relatedness between invasive and non-native to native species for Dicotyledons at the fine phylogenetic grain (Figure 3). However, at the broad phylogenetic grain non-native species were more closely related to native species than invasive species were in 14 fragments for Dicotyledons (ranges: \( w = 18–306; \ p < .05 \)). In 19 fragments, there was no difference in relatedness between invasive and non-native to native species (Figure 3; Table 2).

For Monocotyledons, at the fine phylogenetic grain, we found that non-native species were more closely related to native species than invasive species were in 14 fragments (ranges: \( w = 3–45.5; \ p < .05 \)), while invasive and non-native species were equally related to native species in 13 fragments (Figure 3). At the broad phylogenetic grain, we found that non-native species were more closely related to native species than invasive species were in five fragments,
all of which also showed the same pattern at the fine phylogenetic grain (ranges: $w = 3-44.5$; $p = <.05$). At the broad phylogenetic grain, 22 fragments did not show any difference in relatedness between invasive-to-native and non-native-to-native Monocotyledons (Figure 3) (Table 2). We did not perform tests of either phylogenetic grain in the remaining six fragments because only one or zero non-native or invasive species were reported for the Monocotyledon domain (Figure 3; see Appendix S6).

4 | DISCUSSION

We add to the literature on DNC by contributing evidence of support for DNH or no support for either DNH or PAH in the globally critically imperilled pine rockland ecosystem in Miami, USA. Our findings reaffirm that results are dependent on spatial scale and phylogenetic grain, as others have found. Importantly, our study brings to the forefront the critical role of phylogenetic extent in DNC. We find that spatial scale and phylogenetic grain interact to produce disparate incidences of support for DNH or no support for either hypothesis across different phylogenetic extents.

4.1 | Invasion impact

A fundamental element in studying DNC is the definition of non-indigenous species; here, they are defined by their level of impact as non-native or invasive (Blackburn et al., 2011; Cadotte et al., 2018; Li et al., 2015; Richardson et al., 2000). Other studies that considered multiple levels of invasion impact have also predominantly found support for DNH (Bezeng et al., 2015; Schaefer et al., 2011) or no support for either hypothesis (Lim et al., 2014). In pine rocklands, broad support for DNH may have resulted from the native regional pool assembling under historically harsh environmental filters, such as living...
atop limestone substrate, in high-light conditions, and with frequent fire and locally dynamic hydrology (Snyder et al., 1990). While this flora is very diverse, the majority of species are contained within a few, well-represented lineages (e.g. Asteraceae, Poaceae, Fabaceae) (Trotta et al., 2018) and this phylogenetic clustering has left evolutionary gaps in the community. More distantly related non-indigenous species can be introduced via anthropogenic inputs and become highly impactful invasive species (Gerhold et al., 2015) as they exploit vacant niches and out-compete native species (Schaefer et al., 2011; Strauss et al., 2006). In contrast, the close evolutionary relationships and implied trait similarity between non-native and native species we observed may allow non-native species to successfully establish (Rejmanek & Richardson, 1996) but also prevent them from spreading and becoming highly impactful through competition (Cadotte et al., 2009; Carboni et al., 2013). As the assumption of phylogenetically conserved trait similarity can be problematic (Cavender-Bares et al., 2009; Mayfield & Levine, 2010; Münkemüller et al., 2015), further work is needed to link phylogenetic relationships with an array of functional traits that could influence invasion in the pine rockland flora (Bennett, 2019).

### 4.2 Spatial scale

Recent DNC studies have assessed the role that spatial scale plays in determining whether DNH or PAH is expected to dominate community assembly (Cadotte et al., 2018; Carboni, Münkemüller, et al., 2013; Diez et al., 2008; Park et al., 2020; Procheș et al., 2007; Thuiller et al., 2010). Hypothetically, competition at small spatial scales with indigenous species should exclude phylogenetically similar non-indigenous species resulting in DNH. At larger spatial scales, other factors such as dispersal ability, habitat heterogeneity and environmental filtering should outweigh biotic interactions resulting in PAH (Thuiller et al., 2010). In contrast to this expectation, we found 75% of comparisons support DNH at the regional scale, predominate no support for either hypothesis at the local scale and no support for PAH at either scale. Similarly, synthesis of the DNC literature does not always support this hypothesized continuum (Cadotte et al., 2018; Ma et al., 2016; but see Park et al., 2020). Our findings may result from idiosyncratic assembly of native, non-native and invasive species from the regional pool to naturally and anthropogenically fragmented local communities in the pine rocklands ecosystem. For example, the only instance of support for PAH in this study is in a fragment where invasive species were solely from the Monocotyledon domain, while non-native species were more representative of the regional pool. The idiosyncratic assembly of local communities, as demonstrated in the example above, is influenced by a fragment’s size and location in the urban matrix, source and propagule pressure of non-indigenous species, as well as heterogenous fire, hydrology (Snyder et al., 1990; U.S. Fish and Wildlife Service, 1999) and habitat management (Jones & Koptur, 2017; U.S. Fish and Wildlife Service, 1999). In fragmented ecosystems with considerable anthropogenic pressures, it may be necessary to alter our expectations of support for either DNC hypothesis across spatial scales.

### 4.3 Phylogenetic grain

There is a long tradition of comparing multiple metrics of phylogenetic grain in community phylogenetics, broadly as well as in approaches to DNC (Cadotte et al., 2018; Gallien & Carboni, 2017; Li et al., 2019; Tucker & Cadotte, 2013). In the pine rockland ecosystem, we found little support for either DNH or PAH at the fine phylogenetic grain regardless of spatial scale considered. At the broad phylogenetic grain, we found all comparisons supported DNH at the regional pool and 23/93 comparisons supported DNH at the local scale. While support for DNH, PAH or no support for either hypothesis has been found across previous studies, generally, conclusions about DNC are consistent across phylogenetic grain within these studies (Bezeng et al., 2015; Carboni, Münkemüller et al., 2013; Lim et al., 2014; Maitner et al., 2012; Marx et al., 2016; Parker et al., 2012; Ricotta et al., 2010). However, there is precedent for variation in the strength of support for DNH across phylogenetic grains that we observe in the pine rockland ecosystem (Ng et al., 2018; Schaefer et al., 2011; Strauss et al., 2006).

While indigenous pine rockland plant diversity is primarily contained within a few, highly diverse clades, many of the 106 non-indigenous species are also found within these diverse indigenous clades. This results in close relationships between native species and both non-native and invasive species. When we consider nearest neighbour distance (i.e. fine phylogenetic grain), close relationships between native, invasive and non-native species result in no support for either DNC hypothesis. In contrast, when we consider all pairwise distances (i.e. broad phylogenetic grain), invasive species tend to introduce long branch lengths that are, on average, more distantly related to all native species in the phylogeny than non-natives resulting in stronger support for DNH (see Dicotyledon example below). However, our findings based on phylogenetic grain are dependent on phylogenetic extent.

### 4.4 Phylogenetic extent

Incorporating phylogenetic scale into studies of DNC is important for advancing this research framework (Graham et al., 2018; Procheș et al., 2007; Thuiller et al., 2010), and while many studies have explored phylogenetic grain, our study is the first to account for phylogenetic extent. Assessing ecological communities at a broad phylogenetic extent (e.g. all vascular plants in a community) provides a wide-ranging view of evolutionary relatedness. However, in ecosystems where communities encompass large amounts of evolutionary history, determining how patterns of relatedness compare across different lineages is warranted (Cavender-Bares et al., 2004, 2006; Elliott et al., 2016; Ndiribe et al., 2013; Park et al., 2020; Thuiller et al., 2010). In considering phylogenetic extent, we find that support for DNH varies across spatial scale and phylogenetic grain based on phylogenetic extent, but we still find no support for PAH. Importantly, we show that by examining the Dicotyledon and Monocotyledon domains we uncover variability in support for DNH that was not clear when examining the Tracheophyta domain.
4.5 | Dicotyledon domain

Support for DNH in the Dicotyledon domain varies across phylogenetic grain, but not across spatial scale. Dicotyledons show no support for either hypothesis at a fine phylogenetic grain, and 14/33 comparisons support DNH at broad phylogenetic grain. Non-indigenous Dicotyledon species are distributed across many lineages indigenous to the pine rockland ecosystem. As a result, invasive and non-native species can be equally closely related to their nearest native neighbour leading to no support for either hypothesis at the fine phylogenetic grain. With the broad phylogenetic grain, invasive species are on average more distantly related to the native community than non-native species are. For example, two notable invasive Dicotyledon species with large MDNS values are Brazilian pepper (Schinus terebinthifolius; Anacardiaceae) and Shoebotton ardisia (Ardisia elliptica; Primulaceae). These species are distantly related to the native community (i.e. high MDNS), but relatively closely related to their nearest native neighbour species (i.e. S. terebinthifolius to Winged sumac [Rhus copallinum; Anacardiaceae] and A. elliptica to Marlberry [A. escallonioide; Primulaceae]) resulting in small DNNS values. Both of these species reduce recruitment of native species and increase competition for light (Gordon, 1998; Horvitz et al., 1998). Further, S. terebinthifolius can alter the vertical stand structure and disturbance regime in pine rocklands by lowering fire temperature (Ewel, 1986; Gordon, 1998; Stevens & Beckage, 2009). In the Dicotyledon domain, highly impactful invasive species may be striking a balance of overcoming the harsh environmental filters by originating within lineages native to pine rockland while also avoiding competition by being relatively distantly related to the native community. At the local scale, strength of support for DNH with the broad phylogenetic grain depends on the presence of invasive species with long branch lengths, as well as the dynamics of two highly diverse clades: Asteraceae and Fabaceae. While both of these families contain invasive and non-native species and can have very small MDNS values, Fabaceae has more invasive species than Asteraceae does. We find support for DNH in fragments where non-native species are dominated by closely related Asteraceae and invasive species are dominated by more distantly related Fabaceae. We find no support for either hypothesis in fragments where (a) non-native species like the Weeping bottlebrush (Melaleuca viminalis; Myrtaceae) introduce long MDNS values that match the long MDNS values introduced by invasive species; and (b) Asteraceae and Fabaceae have similar relatedness between native, non-native and invasive species. When DNH is supported at the local scale in Dicotyledons, it appears that invasive Fabaceae are either exploiting new niches or out-competing and extirpating native and non-native Fabaceae. In-depth examination of this phylogenetic extent indicates that the relative number of invasive or non-native species within two diverse clades can have implications for support of DNH and local-scale invasion dynamics, a finding that was obscured in Tracheophyta.

4.6 | Monocotyledon domain

In the Monocotyledon domain, we find the most consistent support for DNH across phylogenetic grains and spatial scales because invasive species within Poales are distantly related to native species within Poales and invasive species within all lineages sister to Poales are extremely distantly related to native species within Poales. Poales (especially, the grass family, Poaceae) define pine rocklands as a grassland, savanna ecosystem (Noss, 2012; Snyder et al., 1990) and this speciose lineage contributes the majority of the native species to the Monocotyledon domain.

This clade has undergone recent, rapid radiation (Bouchenak-Khelladi et al., 2014; Linder et al., 2018), and, as a result, phylogenetic distance from invasive or non-native species to a native species can be very short. All other Monocotyledon lineages sister to Poales (i.e. Asparagaceae, Commelinaceae, Dioscoreaceae, Orchidaceae and Araceae) contain few or no native pine rocklands species and most of the invasive species in the Monocotyledon domain. Non-native and invasive species from these lineages can add very long branch lengths and are distantly related to their nearest native neighbour (i.e. fine phylogenetic grain) as well as the whole native community (i.e. broad phylogenetic grain).

One example of this phenomenon is the invasive species Nephthytis (Syngonium podophyllum; Araceae), which is sister to Poales. This invasive contributes the longest, unshared branch length to the community phylogeny and is the same distance from both its nearest native species and all native species. This long unshared branch length is indicative of potentially extreme functional dissimilarly between the native community and the invasive species. Another example from within Poales is Burma reed (Neyraudia reynaudiana; Poaceae), a highly impactful invasive grass, that is relatively distantly related as well as functionally dissimilar to other native grass species. *Neyraudia reynaudiana* is a tall-statured grass (Canavan et al., 2019) that grows in dense clumps that exclude native species, create high fine fuel loads and increase fire frequency in the pine rockland ecosystem (Fusco et al., 2019; Overholt & Franck, 2017; Platt & Gottschalk, 2001). *Invasive species, such as N. reynaudiana, demonstrate that despite a constrained phylogenetic distance to native species, functional dissimilarity can allow invasive species to occupy unused niches, escaping competition. Further, invasive species like N. reynaudiana can alter ecosystem processes that are essential to maintaining native communities, like fire frequency in pine rocklands, to benefit their own growth and abundance. By considering the Monocotyledon domain independently we uncover a clear signal of DNH due to invasive species belonging to lineages sister to Poales, as well as a more subtle, but notable signal of DNH within Poales, which would have been overlooked across Tracheophyta.

At the local scale, support for DNH weakens in the Monocotyledon domain, likely due to idiosyncratic sorting of native species from the regional pool to the local scale. One striking
example of variable support for DNH hinges on the presence of the native Giant Orchid (Orthochilus ecristatus). In fragments where both this native orchid and the closely related non-native Monk orchid (Oeceoclades maculata) are present, we find support for DNH. In the absence of the native orchid, the non-native orchid contributes long branch lengths similar to those contributed by invasive species resulting in no support for either hypothesis. In Monocotyledons, we see the clearest signal that highly impactful invasive species are avoiding competition with the highly diverse Poales clade by originating in lineages sister to Poales and filling empty or partially filled niches. Invasive species from lineages sister to Poales are introducing unique evolutionary history and potentially novel functions to the pine rocklands ecosystem allowing them to utilize resources that were historically untapped or are only available due to the recent, anthropogenically induced changes in this ecosystem.

4.7 | Departures from Tracheophyta

Confronting DNC at the phylogenetic extent of Tracheophyta shows that DNH was supported at the broad spatial scale and broad phylogenetic grain, while DNH received weak support at both phylogenetic extents at the local scale. In the Dicotyledon and Monocotyledon phylogenetic extents, we find stronger support for DNH at the local scale relative to Tracheophyta. Further, we find that support for DNH at the local scale varies in phylogenetic grain across the smaller phylogenetic extents. The Monocotyledon domain shows greater support for DNH with the fine phylogenetic grain, while the Dicotyledon domain shows greater support for DNH with the broad phylogenetic grain.

5 | CONCLUSION

By subdividing our community phylogeny into domains, we are able to explicitly account for how phylogenetic architecture interacts with metrics that query different depths in the phylogeny (i.e., phylogenetic grains). There is moderate support for DNH and no support for PAH across pine rocklands ecosystem indicating non-indigenous species become invasive when they are distantly related to and thus likely to avoid competition with native species. In the Dicotyledon domain, invasive and non-native species are found throughout lineages native to the pine rockland ecosystem resulting in consistent support for DNH across spatial scale, but not phylogenetic grain. In the Monocotyledon domain, non-native species are primarily found within native lineages while invasive species are found within novel, distantly related lineages resulting in consistent support for DNH across both phylogenetic grain and spatial scale. Differences in relatedness between invasive, non-native and native species indicate that invasion dynamics may differ between domains, a phenomenon that is not apparent when we consider DNC at the level of Tracheophyta.

Future assessments of DNC in the pine rockland ecosystem would benefit from improved information about how non-indigenous species differ in time since introduction; ability to surpass historical and current barriers to invasion; and differences in impact across fragments. Studies of repeated, plot-based community sampling are required to assess whether support for DNH is driven by niche-based processes (e.g., competition, environmental filtering) or idiosyncratic sampling from the regional pool. Finally, linking phylogenetic diversity to functional traits will be essential to interpret mechanisms underlying invasion dynamics. To advance the field of invasion ecology within the DNC framework, our results indicate that studies should continue to consider spatial scale and phylogenetic grain, while also explicitly accounting for phylogenetic extent. Integrating components of spatial and phylogenetic scale into DNC assessments may allow the field to better synthesize findings across disparate ecosystems and hone in on generalizable mechanisms of species invasion.

ACKNOWLEDGEMENTS

We would like to thank Jennifer Possley, Sarah Martin, James Lange, Craig van der Heiden and the Institute for Regional Conservation (especially George Gann), Miami-Dade County Natural Areas Management and Miami-Dade County Environmentally Endangered Lands Program. This work was funded by the Eppley Foundation and the Florida Native Plant Society.

PEER REVIEW

The peer review history for this article is available at https://pubons.com/pubon/10.1111/ddi.13220.

DATA AVAILABILITY STATEMENT

The R code and data used for analyses are available on Dryad at: https://doi.org/10.5061/dryad.6wwpzgmx5. The phylogeny is available on Dryad at: https://doi.org/10.5061/dryad.gd86rn1.

ORCID

Lauren B. Trotta https://orcid.org/0000-0001-7847-2284
Zachary A. Siders https://orcid.org/0000-0002-0798-9515
Emily B. Sessa https://orcid.org/0000-0002-6496-5536
Benjamin Baiser https://orcid.org/0000-0002-3573-1183

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**BIOSKETCH**

Lauren B. Trotta is a PhD Candidate at the University of Florida, and this work was completed as part of her graduate research. She is interested in applying phylogenetic approaches to better characterize and understand drivers of diversity in communities, especially those in imperilled ecosystems like the pine rocklands.

**Author contributions:** L.B.T., Z.A.S. and B.B. conceptualized the study; L.B.T., E.B.S., and B.B. collected the data; L.B.T. and Z.A.S. conducted the analysis; L.B.T. led the writing and all authors contributed to revisions.

**SUPPORTING INFORMATION**

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

**How to cite this article:** Trotta LB, Siders ZA, Sessa EB, Baiser B. The role of phylogenetic scale in Darwin’s naturalization conundrum in the critically imperilled pine rockland ecosystem. *Divers Distrib*. 2021;27:618–631. https://doi.org/10.1111/ddi.13220

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