Endemism, Projected Climate Change, and Identifying Species of Critical Concern in the Scrub Mint Clade (*Lamiaceae*)

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Abstract
Recent studies have revealed that narrow endemics, particularly those native to the North American Coastal Plain, are experiencing range contractions due to human development and anthropogenic-driven climate warming. We model how the projected distributions of a group of scrub-adapted plant species with similar evolutionary histories change in response to warming climates. The Scrub Mint clade (Lamiaceae) (SMC), which comprises 24 species in Dicerandra, Conradina, Stachydeoama, Piloblephis, and Clinopodium, including federally or state-listed threatened and endangered species, occurs in the scrub and sandhill biomes of the North American Coastal Plain. Georeferenced occurrence points were used to develop species distribution models (SDMs) to assess both present and predicted future ranges of all SMC species under future climate change. Future SDMs show that suitable environments for 67% of the SMC species would cover reduced geographical areas than at present. This loss of habitat is most pronounced in species of the Florida peninsula but is also prevalent in species found farther north. We use SDMs to identify the most at-risk species and geographic areas. Narrowly endemic species were more susceptible to habitat loss than those species with wider ranges. Using a large dataset and modeling habitat suitability at this regional scale, we demonstrate that scrub-adapted species are highly vulnerable to habitat reduction as a result of climate change.

KEYWORDS
endangered plants, future climate, Menthinae, North American Coastal Plain, species distribution modeling

1 | INTRODUCTION

When the North American Coastal Plain (NACP) was recognized as a biodiversity hotspot (Noss et al., 2015), it was estimated that 96% of the original pine savanna habitat of this ecoregion had been degraded or converted for anthropogenic purposes. This extreme loss of suitable habitat, coupled with projected changes in climate (Wang et al., 2013), could lead to extinction for species that are endemic to this hotspot. Understanding how climate...
change over the next century will drive species extinction is critical for developing conservation policy regarding the biological costs of human economic development in areas with high species endemism and accelerating rates of climate change (Stocker & Qin, 2013; Urban, 2015).

The use of ecological niche models (ENMs) for conservation purposes has become an important approach for evaluating the potential impacts of climate change on the geographic ranges of plant species (Gaynor et al., 2018; Randin et al., 2009; Stubbs et al., 2018). Projections of ENMs onto geographic space—species distribution models (SDMs)—can be used to compare estimated current distributions with those forecast under a range of climate change scenarios. Although useful, this approach has several methodological limitations, particularly with regard to errors introduced with inaccurate georeferencing and the lack of incorporation of eco-physiological and other biological information that might inform the process of building fundamental/realized niches. Additionally, the scarcity of microclimate data makes SDMs inadequate to model microhabitat heterogeneity (Cotto et al., 2017; Ferrarini et al., 2016; Kearney & Porter, 2009; Lozier et al., 2009). Despite these issues, ENMs and the resulting SDMs built from natural history collections are still of great utility in conservation, providing initial insights into possible future distributions of species and laying the foundation for more focused studies (Ellwood, Soltis, & Klein, 2019; Ferrarini et al., 2016). They have been applied to situations that include assorted species with diverse evolutionary histories, dispersal abilities, and climatic tolerances (Loarie et al., 2008; Randin et al., 2009; Stubbs et al., 2018; Warren et al., 2014). These comparisons of distributional responses to climate change, coupled with our preexisting knowledge of plant dispersal and adaptation, can be applied to conservation strategies for narrowly endemic species.

Analysis of an entire clade that is endemic to increasingly endangered habitats in a biodiversity hotspot may provide critical information for both the species in the clade as well as overall habitat conservation in a fragile ecosystem such as the NACP. Here, we use the Scrub Mint clade (SMC) to understand current spatial patterns of species ranges and model future impacts of climate change on species ranges. The SMC comprises 24 species restricted almost entirely to the NACP hotspot (Figure 1) and includes Dicerandra Bent. (11 species), Conradina Asa Gray (seven species), Piloblephis (Bartram ex Bent.) Raf. (monotypic), Stachydeoma (Chapm. ex A. Gray) Small (monotypic), and the woody, southeastern US species of Clinopodium L. (C. ashei, C. georgianum, C. coccineum, and C. dentatum; Crook, 2000; Prather et al., 2002; Trusty et al., 2004). Many species in the SMC are federally and state-listed endangered, with the highest concentration of endangered species in Dicerandra, with six federally listed species. Many perennial species of Dicerandra are only known from a handful of populations. For example, D. christmanii has an extremely small range and is known from only five populations, all in Highlands County, FL (Huck et al., 1989), while D. cornutissimma is known from only 12 small populations in Marion County, FL (Florida Natural Areas Inventory, 2019). Several members of Conradina are comparably small in range, especially C. etonia and C. cygniflora, which are known only from populations at Etoniah Creek State Forest in Putnam County, FL (Edwards et al., 2009; Kral & McCartney, 1991). SMC species are typically gap specialists in sand pine savannas and scrub, and their habitats have been largely destroyed for logging, agriculture, and urban development. Moreover, the habitats of the more northern species are increasingly affected by warmer and drier climatic conditions, while their southern peninsular relatives face even greater risks from human development and stronger tropical cyclones (Trenberth et al., 2007). What remains of their habitats is largely a patchwork of disconnected habitats, mostly on private land (Christman & Judd, 1990; Kral, 1982; Quintana-Ascencio et al., 2019).

Using ecological niche modeling, we evaluate species of conservation concern of the SMC by assessing the extent to which their ranges are projected to change in the future, and the extent to which their ranges are protected by current conservation reserves (Thornhill et al., 2016), and we recommend new species for conservation action. We asked: 1. Are the amount and geographic distribution of suitable habitat, as predicted by SDMs, expected to change and/or move for the SMC species in a future climate? 2. To what extent are current and future ranges protected by conservation areas? 3. Based on projected future distributions of suitable habitat, what recommendations can be made to protect the most at-risk species?

2 | METHODS

2.1 | Locality record processing

To build our occurrence coordinate dataset, we synthesized available point records from all taxa in this study in major data repositories relevant to the study region via online portals (GBIF, https://www.gbif.org and iDigBio, https://www.idigbio.org). Additional locality data from herbarium specimens not reported to GBIF/iDigBio were collected from vouchedered specimens at the UF (FLAS) herbarium. We also used occurrence data from previous
field-collected GPS records (Andre Naranjo, pers. obs.; Payton et al., 2019) or expert-vetted records (Floyd Griffith, Edwin Bridges, pers. comm.). Duplicate and incorrectly formatted records were removed with the Scrubr package (Chamberlain, 2016). Points outside of known distributions were removed manually by reference to known ranges in the literature (Huck, 2001; Oliveira et al., 2007; Payton et al., 2019). For very narrow ranged species, multiple points were obtained that occur within 1 km of each other, which is closer than the resolution of the climate variables. We therefore retained one point per 1 km grid cell. We did this by rarefying locality points using the “gridSample” function in the dismo R package, rarefying points to 1 km/30 arcsecond), for species with small ranges (current ranges <3000 km²; Hijmans et al., 2017).

To georeference localities of specimens lacking GPS coordinates, we primarily used GeoLocate (Rios & Bart, 2010). GeoLocate uses the latest available satellite imagery from Google Maps, and these images were used to corroborate the localities GeoLocate identified (e.g., a species that occurs usually in a sandy open area had a locality recovered by GeoLocate in a sandy open area). We followed best practices using only unique and unambiguous place names and discarding localities that refer to large metropolitan areas or cultivated records.

2.2 | Ecological predictor assembly

Bioclimatic and elevation data were obtained from Worldclim V.1 (www.worldclim.org) at 30 arcsec ($≈$ 1 km²) resolution (Hijmans et al., 2005). Five soil variables at 30 arcsec resolution (clay percentage, silt percentage, sand percentage, pH, organic carbon content; averaged in QGIS across layers at 2.5-, 10-, 22.5-, and 45-cm core depths) were obtained from ISRC SoilGrids API (Batjes et al., 2019; Hengl et al., 2017). The inclusion of soil data prevents overestimation of suitable habitat based solely on climatological data (Murphy & Lovett-Doust, 2007). All 19 Bioclim layers and five SoilGrid layers were tested for correlation within all areas, and a cutoff of ±0.8 Pearson’s correlation coefficient was used to reduce the number of layers for subsequent analyses. For layers that were correlated with each
other, we chose the ones that best captured the multiple climatic and edaphic aspects relevant to Scrub Mints (Huck et al., 1989; Menges et al., 1999).

We assembled nine variable layers capturing aspects of climate and soil for both present climate and 2070. These comprise four Bioclim temperature and precipitation variables (bio2 [mean diurnal range], bio5 [maximum temperature of warmest month], bio9 [mean temperature of driest quarter], bio12 [annual precipitation]), and the five soil layers listed above. From here on, “environmental variables” refer to both climatic and edaphic variables. Projected climatic data for 2070 at RCP8.5 were also obtained from Worldclim. RCP8.5 was selected because it is the closest approximation of both historical emissions and anticipated outcomes of current global climate policies, tracking within 1% of actual emissions (Schwalm et al., 2020). The RCP8.5 model incorporates large populations, moderate rates of technological change, uncertainties in carbon feedback loops, and an absence of enforceable climate change policies, resulting in high-energy demand and greenhouse gas emissions (Riahi et al., 2011), all factors that are likely given current increasing trends in greenhouse gas emission and surface air temperature (Harris et al., 2014; IPCC, 2021; Olivier & Peters, 2019; Schwalm et al., 2020).

### 2.3 Niche modeling in Maxent

In order to determine the geographical range and training area for each species, we placed a 1-km buffer around each locality point using the “gBuffer” function of the “rgeos” R package (Bivand et al., 2017). Buffer size around each point was based on the dispersal potential and accessible area for species in this clade (Barve et al., 2011; Payton, 2012; Romero-Alvarez et al., 2017). Resultant shapefiles for each species were manually edited to be continuous areas for the final shapefile, per Stubbs et al. (2018). Recent work on narrow-range SDMs utilizing simulated and real-world datasets has shown that the number of environmental variables used in model creation is not one of the factors that increases the “minimum required sample size,” which in narrowly distributed taxa may be as low as three to five points per species (also referred to as the “absolute minimum sample size”; van Proosdij et al., 2016). Therefore, in order to methodologically accommodate the creation of a niche model for a narrow-range species with a small number of locality points, we followed McPherson et al.’s (2004) recommendation to choose a species model training area proportional to the presence area of the assessed species, so that a species’ locality points are present in at least 10% of the training area cells. We verified species prevalence with the virtualspecies R package (Leroy et al., 2016).

ENMs were generated using the R package ENMeval V0.3.0 (Muscarella et al., 2014) in conjunction with MaxEnt V3.4.1k (Phillips et al., 2009). We chose ENMeval because: (1) it produces datasets for k-fold cross-validation using one of several methods for partitioning occurrence data, (2) it builds a series of candidate models using MaxEnt with a variety of user-defined settings, and (3) it provides multiple evaluation metrics to aid in selecting optimal model settings. We used the random k-folds (=bins) method for partitioning data. We also quantified four evaluation metrics using ENMeval, among them: the area under the curve of the receiver-operating characteristic plot for test localities (AUC TEST), the difference between training and testing AUC (AUC DIFF), the delta-Akaike information criterion corrected for small sample sizes, and the Continuous Boyce Index (CBI) calculated using Ecospat V3.1. (Di Cola et al., 2017). After model creation, models were projected back within the training regions for each species. No projections were done over large areas outside of species ranges or over the entire coastal plain. To show model uncertainty and extrapolation into novel habitat, we ran a Multivariate Environmental Similarity Surfaces (MESS; Elith et al., 2010) analysis to identify regions where extrapolation may occur for predicting areas of suitable climate.

### 2.4 Location of suitable habitat

We evaluated changes in suitable habitat for each species by comparing the geographical ranges predicted under both present and future conditions. We calculated overlap in two ways: by comparing changes in the size of suitable geographic area (km²), and by calculating the extent of raster overlap between the present and future areas of suitable habitat using Schoener’s D, which states that 0 equals no similarity and 1 equals complete similarity (Broennimann et al., 2012). We used the 5th and 10th percentile training presence (90pct, 95pct) and minimum training presence (MTP) to omit all regions with habitat suitability lower than the suitability values for the 5%, 10%, and lowest predicted suitability value for an occurrence point. This assumes that 5 or 10% of occurrence records in the least suitable habitat are not occurring in regions that are representative of each species’ overall habitat, and thus should be omitted (Escalante et al., 2013). In the case of MTP, it assumes that the least suitable habitat at which the species is known to occur is the minimum suitability value for the species, ensuring that all occurrence points fall within the area of the binary model (Liu et al., 2016). Using the resulting binary model, the area of each cell of the prediction raster
that was considered suitable habitat was summed using the area and zonal functions of the Raster package in R (Hijmans et al., 2015). The cells’ areas were split into three categories: total suitable area in the present, total suitable area in the future, and the ratio of suitable area in the present to that in the future. To quantify this change by species, we divided the total area of projected suitable habitat in the future by the total area of suitable habitat in the present; this ratio quantifies how much habitat each species is predicted to gain or lose under this climate change scenario. Species were then sorted as either gaining (ratio > 1) or losing (ratio < 1) habitat. We also used these binary models to determine the percent extent of current and future suitable habitat located within conservation lands in the NACP.

Our approach generates the potential distribution of suitable habitat for a species in the future. We considered how much of the current projected habitat will remain suitable, despite predicted climate change, and quantified and compared how much of the current distribution overlaps with the future projected range. This area of overlap represents habitat that will remain suitable from the present into the future. In addition to this possible retention of suitable habitat, additional habitat may also become available in the future, enabling possible range expansion. However, despite the possible availability of new suitable habitat in the future, a species may not be able to disperse and establish there; thus, the possibility of future suitable habitat does not ensure that a species will persist in that area.

3 | RESULTS

3.1 | Occurrence data

Across all species of the SMC, 493 occurrence records were compiled. The number of occurrence points per species ranged from 5 (Dicerandra radfordiana) to 51 (Dicerandra linearifolia), and species are distributed throughout the NACP (Figure 1). Because of the sensitive nature of the occurrence records for certain species in this clade, only the data for species not at-risk are available (Figures S1–S3; Table S1). Furthermore, a supplementary table showing the total number of locality points and unique points (points filtered to one per 1 km²/grid cell) for each narrow-ranged species has been included for reference (Table S2).

3.2 | Ecological niche models

Several different measures were calculated to determine model performance. We used the commonly employed AUC score, in addition to ΔAICc and the CBI. While AUC is a metric to describe how well a model discriminates between occurrence and background points, CBI provides predicted-to-expected ratio curves that offer further insights into the model quality, specifically model robustness, habitat suitability resolution, and deviation from randomness. CBI is a reliable measure of presence-only-based predictions and a complement to the typical methods of evaluation of presence/absence models (Hirzel et al., 2006).

In general, an ENM is said to have satisfactory model performance if AUC > 0.7, ΔAICc <2, and CBI is close to 1. We used ΔAICc to select the best model, because of its ability to differentiate between the AICc of a given model and the AICc of the model with the lowest AICc. The median ΔAICc was 0.86 ± 0.13. The median CBI was 0.9035. Only two species had CBI scores lower than 0.8. The median training AUC from the remaining 20 species was 0.88 ± 0.11. AUC scores should be interpreted carefully, because sampling bias can result in spatial clustering of points and affects model quality by inflating model accuracy (by providing higher AUC scores; Veloz, 2009). MESS outputs for each species indicated that the future climates within the projection region largely resided within the parameters of the training region, demonstrating sufficient reliability for model transferability (Figures S4–S28), with only certain narrow species models (e.g., D. radfordiana) affected to some degree by extrapolation.

3.3 | Changes in distribution breadth

Of the 24 species in the SMC, 16 Scrub Mint species are predicted to lose habitat over time (D. frutescens, D. linearifolia, D. odoratissima, D. thinica, Dicerandra modesta, Dicerandra cornutissima, D. radfordiana, D. immacula, Conradina brevifolia, C. canescens, C. cygniflora, C. grandiflora, C. verticillata, S. graveolens, C. coccineum), and the remaining eight species are predicted to gain habitat as a result of projected climate change, according to our 90 and 95% threshold analyses (Table 1; Table S3). One species, D. modesta (Figure 2c,d), is predicted to undergo a decrease in suitable habitat by 99% from its present to future distribution. Three species, C. etonia, Pilolephlus rigidus, and D. christmanii (Figure 3; Table 1), have the largest potential future increases (up to two times greater) in suitable habitat between now and 2070. Additionally, C. etonia (Table 1) has the largest predicted increase in range when compared to the present range under the projected climate change model used. Results from our MTP analysis uncovered similar numbers, with 15 SMC species predicted to lose and 9 species expected to gain habitat (Table S4). In the interest of simplicity, subsequent discussion will focus on the results of our 90% threshold analysis.
There were no strong discernable trends in directional shifts of future habitat suitability for the SMC. Most narrowly distributed peninsular taxa have no discernable shift northwards or southwards. Rather, what is seen is an expansion in suitable habitat around existing suitable areas for some taxa, such as *P. rigida* (Figure 3c,d), or contraction in suitability to areas around current populations, as in the case of *D. immaculata*. Several more widely distributed species, such as *C. georgianum* and *D. linearifolia*, did have modest shifts northward of suitable habitat, while retaining suitability in areas farther south where populations currently occur. We also calculated how well thresholded suitable habitat in the present and future overlapped with existing conservation areas. We focused specifically on endangered and at-risk taxa and found that most current suitable habitat for all at-risk species falls outside of conservation lands, with the majority of species expected to have close to no suitable habitat located within presently conserved lands by the year 2070 (Figure 4; Tables 2, S5, and S6).

### TABLE 1  
Results from SDMs comparing our present and future models for all Scrub Mint species, calculated with a 90% threshold

| Species (90pct)            | Conservation status (federal/state listed) | Schoener’s D | Current area (in km²) | Future area (in km²) | Future/current |
|----------------------------|-------------------------------------------|--------------|-----------------------|----------------------|----------------|
| Clinopodium ashei          | Not listed                                | 0.469254     | 20,944.32             | 39,951.13            | 1.907492342   |
| Clinopodium coccineum      | Not listed                                | 0.5314       | 28,615.32             | 15,448.81            | 0.539878988   |
| Clinopodium dentatum       | Not listed                                | 0.6648825    | 7088.1                | 10,592.39            | 1.494390598   |
| Clinopodium georgianum     | Not listed                                | 0.7054155    | 388,097.7             | 538,813.7            | 1.388345512   |
| Conrada brevifolia         | Endangered                               | 0            | 659.1302              | 0                    | 0.000000000   |
| Conrada canescens          | Not listed                                | 0.1320553    | 10,357.83             | 1421.19              | 0.137209242   |
| Conrada cymiflora          | Not listed                                | 0            | 172.5465              | 0                    | 0.000000000   |
| Conrada etonia             | Endangered                               | 0.06060606   | 44.6458               | 269.6367             | 6.039463959   |
| Conrada glabra             | Endangered                               | 0.8349593    | 907.9495              | 884.6951             | 0.974388003   |
| Conrada grandiflora        | Not listed                                | 0.1168761    | 7053.858              | 827.3084             | 0.117284527   |
| Conrada verticillata       | Threatened                                | 0.001213592  | 569.171               | 0.6870268            | 0.001207066   |
| Dicerandra christmanii     | Endangered                               | 0.4444444    | 24.28612              | 54.64273             | 2.249957177   |
| Dicerandra cornutissima    | Endangered                               | 0            | 323.9577              | 0                    | 0.000000000   |
| Dicerandra densiflora      | Not listed                                | 0.8456902    | 11,357.25             | 13,065.64            | 1.150428258   |
| Dicerandra frutescens      | Endangered                               | 0.3004695    | 161.9974              | 53.23252             | 0.328601076   |
| Dicerandra fumella         | Not Listed                                | 0.6577605    | 12,671.58             | 19,257.66            | 1.519752075   |
| Dicerandra immaculata      | Endangered                               | 0.006944444  | 109.2921              | 0.7580974            | 0.006936434   |
| Dicerandra linearifolia    | Not listed                                | 0.4076949    | 116.6041              | 54.699.27            | 0.469102459   |
| Dicerandra modesta         | Not listed                                | 0            | 9.815296              | 0                    | 0.000000000   |
| Dicerandra odoratissima    | Not listed                                | 0.7          | 38.69031              | 24,659.54            | 0.637367002   |
| Dicerandra radfordiana     | Endangered (GA)                          | 0.6475629    | 65.6416               | 45.94997             | 0.700012949   |
| Dicerandra thinicola       | Not listed                                | 0.01824818   | 205.775               | 4.511229             | 0.021923115   |
| Piloblephis rigida         | Not listed                                | 0.4742625    | 27.164.27             | 56.547.79            | 2.081697391   |
| Stachydeoma graveolens     | Not listed                                | 0.02196436   | 178.86                | 45.82777             | 0.025690228   |

Abbreviation: SDM, species distribution model.
narrow endemics, with some of these species functionally losing all suitable habitat (Table 1) within their ranges by 2070. Ten of fifteen species of Scrub mints that occur in peninsular Florida are predicted to lose habitat, while six of nine species that occur in the remainder of the NACP are predicted to lose habitat as a result of predicted climate change.

Eight of the twelve species of the SMC that occur exclusively in the Florida peninsula are predicted to lose habitat under future climate change models, whereas four are predicted to experience increases in their total amount of habitat. The four species that are predicted to have an increase in habitat, *C. etonia*, *D. christmanii*, *P. rigida*, and *D. densiflora* (Figure 3; Table 1), vary in their present distribution sizes, ranging from narrow endemics to more broad distributions. When looking at all SMC taxa, the species with the largest predicted km² increase in suitable area, *Clinopodium georganum*, has the largest present range of any species in this analysis, and its range overlaps considerably with that of *D. linearifolia*, the second-most widely distributed species (Table 1). However, the predicted future range for *D. linearifolia* is only one third of its present range. Research has uncovered a positive correlation between niche breadth and range size across taxonomic groups and spatial scales, suggesting that niche breadth can explain at least some of the variation in geographical range size among species (Slatyer et al., 2013). This explanation is relevant for understanding the potential range expansion of *C. georganum* but cannot explain the collapse in suitable habitat for *D. linearifolia* despite its widespread distribution and its corresponding relatively broad ecological niche tolerances.

Habitat fragmentation coupled with projected rapid climate change seen in the Florida peninsula have the potential to overwhelm the capacity for adaptation in plant populations and drastically alter their genetic composition and diversity (Jump & Penuelas, 2005). High levels of genetic diversity within a species are correlated with larger ecological niches, allowing these particular species to better cope with a wider range of climatic changes across their distribution (Theodoridis et al., 2017). Payton et al. (2019) uncovered modest levels of genetic diversity in all *Dicerandra* annuals, including *D. linearifolia*. However, the annual habit, low dispersal capability, and fragmented habitat of these species can contribute to physical and genetic isolation. Additionally, *C. georganum* and *P. rigida* are both woody perennials.

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**Figure 2** Species distribution models for Scrub Mint species with the greatest decrease in range in future climate discussed in the text (using a 90% threshold). White represents suitable habitat only in the present, light blue represents suitable habitat in the present and future, and dark blue represents suitable habitat only in the future. For species with decreases in ranges: (a) *Conradina verticilata*, (b) *Dicerandra thinicola*, (c) *Dicerandra modesta*, (d) *Dicerandra immaculata*, (e) *Dicerandra cornutissima*, and (f) *Conradina brevifolia*. All areas are in the southeastern United States. Letters correspond to species listed in Table 1.
Although we lack genetic data for these species, woody species generally maintain more variation within species and within populations than species with other life forms and have less variation among populations (Hamrick et al., 1992), potentially allowing for these species to occupy larger ecological niches.

The risk of extinction that climate change poses for Scrub Mint taxa can also be extrapolated to the gap specialist species that co-occur with Scrub Mint species. Changes in community composition must be considered in order to best mitigate the risk that climate change may have on the communities in which these plants occur, specifically in Florida scrub habitats. The magnitude and direction of species responses, particularly biotic ones, vary greatly among taxa, preventing communities from migrating as intact units in response to climate change (Doak & Morris, 2010; Williams & Jackson, 2007). This means that even if SDMs show new areas with suitable habitat for gap specialists in a future climate, colonization by other plants, particularly tall, woody species, might interfere with the successful establishment of these low-growing taxa (Richardson et al., 2013). Complicating modeling future habitat further is the impact of human development on natural areas. Using current conserved lands as a proxy for measuring the extent of future suitable habitat protected for at-risk taxa reveals that the total percentage of suitable habitat protected by conservation lands will decrease for almost all at-risk species (species with ranges >3000 km²; Tables 2, S5, and S6). Furthermore, increased fragmentation of scrub ecosystems from residential and commercial development, particularly in peninsular Florida, will make it difficult for Scrub Mints and co-occurring gap specialists to migrate effectively. The effects on species in the community that depend on Scrub Mints for pollen, larval food, and habitat might also be pronounced. Several arthropod species (such as Exprosopa spp., Halictidae wasps, and Pyrausta moths) depend on Scrub Mints for pollen, nectar, and larval food (Deyrup & Menges, 1997; Eisner, 1990), and their future is linked to the ability of these Scrub Mints to successfully migrate to new areas with suitable habitat. If these patterns of suitable habitat reduction are similar for other species in the community, and if habitat is moving faster than vascular plants can track it through dispersal and establishment, communities will likely become more homogeneous in species composition.

The members of the SMC that face particularly adverse changes in habitat suitability have two options for survival:
move to an area with greater bioclimatic suitability or adapt to new conditions in their current locations. Movement was a universal response of species to past events such as glacial and interglacial periods, particularly in areas such as Florida during the Pleistocene. The common ancestor of the SMC probably dealt with issues of movement during the late Pliocene and early Pleistocene (Naranjo, 2020). However, the speed required for species to move to a novel area with greater climatic suitability is directly related to the rate at which climate change occurs. Currently, the evidence suggests that many plant species and communities will be unable to keep up with the higher velocities of climate change expected for the remainder of the 21st century (Bertrand et al., 2011; Corlett & Westcott, 2013). The ranges for predicted climate-change and plant-movement velocities broadly overlap, but most plant-movement velocities are likely to be at the lower end of the range and will be exceeded by climate-change velocities in many areas. In the case of the SMC, dispersal capability is thought to be limited, and water after heavy rainfall is thought to be an important dispersal mechanism (Huck, 1987). Limited dispersal is also supported by phylogenetic data, which show a
strong correlation between clades of annual species and the river watershed in which they occur (Oliveira et al., 2007). Furthermore, localized dispersal by water is likely limited to precipitation events of sufficient volume to create sheet flows extending beyond the population perimeter. While precipitation events of this scale do occur, the isolated nature of many populations and their relatively small sizes suggest long-distance seed dispersal is limited (Payton, 2012). This might leave SMC species located along rivers and watersheds (i.e., *D. linearifolia*, *D. odoratissima*, *Conradina verticillata*, among others) with a slight advantage compared to their congeners. Due to the limited dispersal capabilities of SMC taxa, adaptation in situ is likely the more effective strategy for continued survival of at least some SMC species. Several narrowly distributed taxa, such as *D. christmanii* and *C. etonia*, are expected to have an expansion in suitable habitat around current populations, which implies adaptation might not even be necessary for these species to survive as long as suitable habitat is conserved. Other species, such as *D. immaculata*, will see an overall decrease in suitable habitat, but a persistence of high suitability clustered around current populations. Microclimates along the Atlantic coastal ridge, where *D. immaculata* is found, might be more stable than interior peninsular sites, favoring the persistence of favorable conditions for this species (Austin et al., 1987).

### 4.2 Conservation implications

SDMs offer an important perspective for conservation decision-making, helping land-use managers determine which species are at highest risk of suitable habitat loss. Species that are projected to suffer total reductions in range size are at a much greater risk of extinction in the near future (Parmesan, 2006). Within the NACP, we suspect that SMC species are representative of many groups of plants, at least in terms of response to projected climate change. Because the pattern of species distributions of the SMC tends to match that of most other plant taxa (ranging from narrow endemics to widespread species), unless other aspects of the SMC (i.e., dispersal ability) are very different than for other plant taxa, we suspect our results to generalize. To make the point, if the same proportion of the NACP's endemic flora overall is committed to near-extinction (>50 km² total area) as projected for SMC taxa, we can extrapolate that by 2070 around 20% (i.e., ~360 of the NACP’s approximately 1816 endemic vascular plant species) may be at risk of range declines severe enough to threaten their persistence. It is important to stress that given the uncertainties that are intrinsic to the modeling approach we applied, projected impacts should be interpreted with full consideration of the limitations involved and as a first approximation of potential risk rather than a definitive forecast of extinction (Fitzpatrick et al., 2008). We suggest that climate change impacts to the NACP’s flora may be large even under moderate climate change projections and assumptions regarding dispersal abilities of vascular plant species.

Of the four species in most dire risk of losing all suitable habitat in their native ranges, three are endemic to the Lake Wales Ridge, an area undergoing intense human development (Weekley et al., 2008). Of those,

| Species of concern       | Current suitable area (in km²) | Future suitable area (in km²) | Protected current suitable habitat (%) | Protected future suitable habitat (%) |
|--------------------------|-------------------------------|--------------------------------|----------------------------------------|---------------------------------------|
| *Conradina brevifolia*   | 659.1302                      | 0                              | 19                                     | 0                                     |
| *Conradina cygniflora*   | 172.5465                      | 0                              | 3                                      | 0                                     |
| *Conradina etonia*       | 44.6458                       | 269.6367                       | 32                                     | 5                                     |
| *Conradina glabra*       | 907.9495                      | 884.6951                       | 44                                     | 48                                    |
| *Conradina verticillata* | 569.171                       | 0.6870268                      | 17                                     | 100                                   |
| *Dicerandra christmanii* | 24.28612                      | 54.64273                       | 25                                     | 26                                    |
| *Dicerandra cornutissima*| 323.9577                      | 0                              | 13                                     | 0                                     |
| *Dicerandra frutescens*  | 161.9974                      | 53.23252                       | 8                                      | 13                                    |
| *Dicerandra immaculata*  | 109.2921                      | 0.7580974                      | 18                                     | 0                                     |
| *Dicerandra modesta*     | 9.815296                      | 0                              | 23                                     | 0                                     |
| *Dicerandra radfordiana* | 65.6416                       | 45.94997                       | 71                                     | 68                                    |
| *Dicerandra thinicola*   | 205.775                       | 4.511229                       | 15                                     | 0                                     |
| *Stachydeoma graveolens* | 1783.86                       | 45.8277723                     | 37                                     | 10                                    |
D. modesta is projected to have the worst fate, with no suitable habitat remaining by 2070 (Figure 2c,d; Table 1). It is one of the few perennial Dicerandra species not currently listed as threatened or endangered at either the state or federal level. It is also not currently represented in ex situ botanical garden collections. In the wild, currently, there is only one population of D. modesta on public lands and possibly only one small population remaining on private lands (Ward et al., 2009). D. modesta occurs on the Horseshoe Creek Scrub Tract of the Lake Marion Creek Wildlife Management Area in Polk County, FL. This population was likely impacted by the installation of the Sabal Trail pipeline, which was completed in 2017. Our SDMs indicate that 23% of present suitable habitat for this species is located within preserved areas, and efforts should be undertaken to ensure that conservation lands be extended to cover all remaining populations (Table 2). This species requires urgent conservation efforts and should be listed as endangered promptly in order to mitigate any further loss of populations and suitable habitat.

C. brevifolia is the second-most at-risk SMC species, with a projected range area collapse from 662 to 12 km² (Figure 2a,b; Table 1), although there are 30 currently known extant populations. The species is particularly sensitive to disturbance and shading (Florida Natural Areas Inventory, 2019), so extra efforts are needed to ensure existing protected sites are being maintained appropriately. Several populations lie within state refuges such as Lake Arbuckle State Park, Saddle Blanket Lakes Preserve, and Bull Creek Wildlife Management Area. Given the possibility of suitable habitat being absent from these areas in the future based on our projections, efforts to protect and properly manage remaining vulnerable scrub habitat on the Lake Wales Ridge should be taken to allow for future reintroduction from extirpated areas.

D. cornutissima is a close relative of D. modesta that is also at great risk of losing almost all suitable habitat by 2070 (Figure 2e,f; Table 1). In the case of D. cornutissima, the largest and only publicly protected population occurs on the Marjorie Harris Carr Cross Florida Greenway in Marion County, FL. This population was also impacted by recent construction of an access road. The Florida Native Plant Society (FNPS) was recently given funds from Duke Energy, a local utility company, to monitor remaining populations and remediate sites. Only 13% of its current suitable habitat is located within conservation areas, plummeting to near 0% by 2070 (Table 2). Despite the status of D. cornutissima as a federally listed endangered species, more efforts should be undertaken to increase surveillance of remaining population numbers and to increase percentage of suitable habitat covered by conservation areas.

The designation of protected areas is an inherently political process, and conservation concerning threatened species and endemism has historically not been the primary driver of the establishment of protected areas (Loucks et al., 2008). Conservation methods to date have left some threatened species, such as D. cornutissima, with only 5 of its 12 populations included in any protected area, while not taking into account the broader protection of endangered species and local biodiversity (Loucks et al., 2008). Funding allocation to conservation stakeholders, such as FNPS, is an important part of protecting biodiversity, but its benefits might be limited unless a structured systematic approach to conservation planning is used (Sarkar & Illoldi-Rangel, 2010). Bok Tower Gardens currently has eight SMC species in its National Collection, where threatened and endangered species are seed-banked and cultivated to help preserve genetic diversity within populations. Efforts such as these at Bok Tower should be augmented to make sure that all threatened species, particularly those endemic to the Florida peninsula, are included in such collections. Furthermore, efforts should be taken to sample populations of at-risk SMC species to check for individual numbers, habitat condition, and other measures. Acquisition and proper management of remaining unprotected scrub habitat will also be critical to preserve remaining populations and allow for future reintroduction from areas where species were extirpated or into areas where they may thrive in the future based on climate change (McLachlan et al., 2007; Vitt et al., 2009).

4.3 Future directions and applications

In prioritizing areas for conservation and protection, taxon richness (specifically species richness) is a routinely accepted measure. However, understanding future habitat suitability may be of crucial importance when determining species populations in need of preservation and/or restoration. Florida has the most extensive public land system in the SE US, comprising 26% of the state’s land area, and identifying the significant areas that lie outside of these reserves is an effective way of prioritizing conservation efforts in a state with one of the fastest growing populations in the country (U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 2018; Bureau of Land Management, 2019). Members of the SMC, such as D. frutescens and D. cornutissima, have considerable current suitable habitat outside of protected lands (Table 2), and an emphasis should be placed on identifying remaining pockets of scrub habitat that are outside of any protected lands for conservation management.
In a broader sense, understanding phylogenetic patterns and ecological modeling of future distributions will be critical when prioritizing areas in need of preservation and restoration in the Anthropocene. Previous results show that endemism “hotspot” areas with low numbers of species from the SMC can still contain significant relative phylogenetic endemism while also face grave danger from the risks presented by climate change and human development, particularly in unprotected habitat sites (Naranjo, 2020). Biodiversity-based land conservation that combines SDMs with spatial phylogenetic analyses will be crucial to the conservation of species during an era of global change.

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CONFLICT OF INTEREST
The authors declare no potential conflicts of interest.

AUTHOR CONTRIBUTIONS
Andre A. Naranjo conceived and designed the study with input from Pamela S. Soltis and Douglas E. Soltis. Andre A. Naranjo collected the locality and climatic data. Andre A. Naranjo wrote the manuscript. All authors input from Pamela S. Soltis and Douglas E. Soltis. Andre A. Naranjo wrote the manuscript. All authors reviewed and edited the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT
Raw climatic and soil data used in this study are publicly available on WorldClim (https://www.worldclim.org) and SoilGrids (https://soilgrids.org). Raw locality data used in this study are publicly available on iDigBio (https://www.idigbio.org/portal), and is included here in the supplements. Some locality data are excluded from public access due to their sensitive nature (i.e., locations of threatened species that are vulnerable to poaching) but can be requested from the authors. The R code used for the analysis is available at https://github.com/aemelton/EA_ENA_ENM.

ETHICS STATEMENT
All data were collected from online databases and literature following research ethics. No ethical approval was required for this study.

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