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NICHE CONSERVATISM OR DIVERGENCE: INSIGHTS INTO THE EVOLUTIONARY HISTORIES OF Pinus taeda, Pinus rigida, AND Pinus pungens

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NICHE CONSERVATISM OR DIVERGENCE: INSIGHTS INTO THE EVOLUTIONARY HISTORIES OF *Pinus taeda, Pinus rigida,* AND *Pinus pungens*

A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Science at Virginia Commonwealth University.

by

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Abstract

NICHE CONSERVATISM OR DIVERGENCE: INSIGHTS INTO THE EVOLUTIONARY HISTORIES OF *Pinus taeda*, *Pinus rigida*, AND *Pinus pungens*

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Environmentally related selective pressures and community interactions are well-documented drivers for niche differentiation, as natural selection acts on adaptive traits best fit for survival. Here, we investigated niche evolution between and within *Pinus taeda*, *Pinus rigida*, and *Pinus pungens* and sought to identify which climate variables contributed to species divergence. We also sought to describe niche differentiation across genetic groupings previously identified for *P. taeda* and *P. rigida*. Ecological niche models were produced using Maximum Entropy followed by statistical testing based on a measure of niche overlap, Schoener's *D*. Both niche conservatism and niche divergence were detected, thus leading us to conclude that directional or disruptive selection drove divergence of the *P. taeda* lineage from its ancestor with *P. rigida* and *P. pungens*, while stabilizing selection was associated with the divergence of *P. rigida* and *P. pungens*. The latter implies that factors beyond climate are important drivers of speciation within *Pinus*.

INTRODUCTION

The geographical distribution of a species is limited in its extent by certain environmental variables (e.g. climate) and community interactions (e.g. competition); and when considered together, they characterize the niche (Grinnell, 1917; Elton, 1927; Hutchinson, 1957). The definition of niche has varied over the last century, from one that focuses on the influence of abiotic factors alone (Grinnell, 1917) to one that focuses solely on biotic interactions (Elton, 1927). By the mid-twentieth century, however, a definition that recognizes the influence of both factors was proposed by G. Evelyn Hutchinson and is now widely accepted and applied to ecological and evolutionary studies (Hutchinson, 1957). He theorized that there exist two kinds of niches, the realized and the fundamental, and argued that certain geographic barriers or biotic interactions limit the ability of a species to fully occupy the fundamental niche. As a result, species are restricted to where their occurrence can be observed, within the realized niche.

Niches are ultimately defined by the traits of organisms in relation to the environment (Ackerly, 2003). Traits evolve in response to selective pressures generated by environmental change or environmental heterogeneity. There are several forms of natural selection that matter. For example, niche conservatism is the maintenance of the ancestral niche in two descendent lineages due to stabilizing selection. Niche divergence in contrast is driven by positive, directional selection in at least one descendant lineage (McCormack *et al.*, 2010). Because niche conservatism and niche divergence have differing effects on ecological and evolutionary processes, great attention has been given towards identifying mechanisms that promote or inhibit niche evolution within and among species (Emery & Ackerly, 2014). There are two known mechanisms that drive trait differentiation across species, ecological sorting and character displacement, and thus influence niche evolution. Ecological sorting, the primary driver of niche divergence, explains how trait differences are acquired while species or populations are living in allopatry (MacArthur 1970; Janzen, 1985; Ackerly, 2003). Character displacement, on the other hand, facilitates trait evolution while species are living in sympatry, either via secondary contact post allopatry or from long term evolution in sympatry (Lack, 1947; Crozier, 1974; Schluter, 2000). In this case, trait differences arise from competitive interactions rather than environmentally related selective pressures, and as a result, explain why two closely related species may share similar environmental niches. It can also be the case where both ecological sorting and character displacement cause trait variation between lineages, as recently reported for perennial plants of the genus *Mimulus* (Kooyers *et al*., 2017).

The evolution of realized niches can happen through shifts, contractions or expansions within the dimensions that define the fundamental niche (Pearman *et al*., 2007). Climate change has occurred throughout earth's history, and the variability it causes in the environment has played a central role in the selection of fitness-related traits. Trait differentiation and adaptive divergence occur from exposure to novel climate conditions, colonization into new environments, or the loss of competitors and other natural enemies (Emery & Ackerly, 2014). A framework, or series of schemes, was summarized by Ackerly (2003) to elucidate how certain ecologically based scenarios can lead to adaptation within species. The first scheme addresses evolution on environmental islands (e.g. mountaintops, extreme edaphic habitats, geographic/volcanic islands), where in the absence of competition, populations encounter novel conditions, and in these suboptimal niche spaces, they adapt presumably from standing genetic variation. To be able to colonize these areas, species must have a fundamental niche that encompasses the 'island' conditions in order to successfully establish. Thereafter, adaptation will lead to realized niche shifts toward new optima. The second scheme explains how populations at the trailing edge of a species distribution must either adapt to suboptimal conditions associated with climate change or attempt migration into neighboring communities that have optimal climatic conditions but high competition. For instance, Gugger *et al.* (2011) provided evidence of trailing edge populations of Douglas-fir, now isolated in Mexico, as being both morphologically and genetically distinct from U.S. and Canadian populations. In the third scenario, adaptive traits result from changes along multiple niche dimensions and trade-offs within the relative niche-breadth (Jackson & Overpeck, 2000). For instance, if precipitation (i.e. first dimension) within the realized niche of a species decreases but temperature tolerances (i.e. second dimension) for a species have greater control over its current distribution (hence fitness), then migration (niche conservatism) is inhibited and selection for traits that allows persistence in drier climates (niche divergence) would ensue on standing genetic variation (Ackerly, 2003).

Previous studies on niche evolution span a wide range of taxa (e.g. Knowles *et al.* 2007; McCormack *et al.*, 2010; Schultz *et al.*, 2012, Veloz *et al.*, 2012), but trees in particular provide an extraordinary, yet understudied, system for investigation (Petit & Hampe, 2006). Trees are long-lived and sessile, therefore more likely than other taxa to experience extreme climatic events within their lifetime (Gutschick & BassiriRad, 2003). They often have high genetic diversity while experiencing low speciation rates.

Additionally, there is accumulating evidence of tree populations being locally adapted even amidst extensive gene flow across multiple spatial scales (e.g. Eckert *et al.*, 2010; Budde *et al.*, 2014; Csilléry *et al*, 2014; Eckert *et al.*, 2015; Holliday *et al.*, 2016; Roschanksi *et al.*, 2016; Lind *et al.*, 2017). Of the adaptive traits studied in trees (e.g. water use efficiency, growth form, bud set, serotiny, fire tolerance), either at the level of species or among populations, climate appears as the primary driver of variation across landscapes and through time (e.g. Zhang *et al*., 1994; Rehfeldt *et al*., 2001; St. Clair *et al*., 2005). Because temperature and precipitation tolerances specifically limit geographic distribution or promote local adaptation in trees given their life history characteristics (Petit and Hampe, 2006), climate is often considered the most important environmental variable in assessments of niche evolution (Martinez-Meyer & Peterson, 2006; Aitken *et al*., 2008; Soberón & Nakamura, 2009; Kozak & Wiens, 2010; McKenney *et al.*, 2011; Iverson & McKenzie, 2013).

Estimates of niche evolution are consistent with clade-specific rates, possibly linked to life history characteristics (Knouft *et al.*, 2006; Evans *et al.*, 2009; Crisp *et al.*, 2009; Kozak & Wiens, 2010). For example, Smith & Beaulieu (2009) concluded from a comprehensive comparative study on angiosperms, that climatic niche evolution in woody species was two to twelve times slower than herbaceous relatives, although there was one exception. Herbs of the Apiales order had niche evolution estimates three times slower than woody angiosperms, thus leaving the issue of general trends about rates of niche evolution unresolved (Smith & Beaulieu, 2009; Kozak & Wiens, 2010). For trees, which are known to have low substitution rates, long generation times, low dispersal, and high intra- and interspecific gene flow, niche conservatism is often detected over short time spans (Martinez-Meyer & Peterson, 2006; Huntley *et al*., 1989). Thus, Grinnell's (1924) hypothesis that niche evolution is an extremely slow process may apply more so to trees and other organisms with similar life history characteristics.

Ecological niche models (ENMs) are essential to investigations of niche evolution. These statistical models relate presence and/or absence records of species to environmental information (Elith & Leathwick, 2009), and form the basis of quantitative estimates of niche divergence (Warren *et al*., 2008). One such quantitative measure is Schoener's *D*, where low values of *D* indicate niche dissimilarity and high values indicate niche similarity (Schoener, 1968; Warren, 2008; e.g. Kirchheimer *et al.* 2016). ENMs are also powerful tools used to identify refugial populations during past glaciation events, estimate migration rate after glaciation events, determine if distributions may have expanded or contracted over time, and predict future habitat suitability under various climate scenarios (Ackerly, 2003; Kozak & Wiens, 2006; Bridle & Vines, 2006; Pearman *et al*., 2007; McCormack *et al*., 2010; Soltis *et al*., 2006). Similar to the clade-specific nature of niche evolution rates, distributional shifts over time (i.e. migration rate) are difficult to predict. The geomorphologic structures and their positioning (e.g. mountain ranges positioned east to west versus north to south) differ drastically from continent to continent and thereby affect migration potential (Taberlet *et al*., 1998). For example, distributions of eight North American plants, including five tree species, have been able to track their predicted shifts since the Last Glacial Maximum (LGM; Martinez-Meyer & Peterson, 2006), whereas European tree species had significant lags in migration since the last LGM (Jump & Peñuelas, 2005), potentially due to the east-west orientation of the Alps and Pyrenees Mountain ranges obstructing migration. Local adaptation may also have made distributional shifts unnecessary for these European tree species. Bridle & Vine (2006) summarized data across plant and animals and asserted that selective pressures of the Quaternary period involved shifts in seasonality as opposed to increases in thermal tolerance. As a result, the characteristic warming trends of the mid-Holocene (~ 6,000 years ago) may not have been able to be tracked because adaptation to certain seasonal variation limited the realized niche from tracking a thermal optimum, as described in Jackson & Overpeck (2000).

While climate change within the last century has already driven shifts in the geographical distributions of some species, others are not tracking this change and may face extinction if adaptation to novel conditions does not occur (Thuiller *et al.*, 2006; Aitken *et al*., 2008; Iverson and McKenzie, 2013). Most of the studies supporting these conclusions, however, are based on modeling species as single, panmictic units without geographical structure in fitness-related traits. Ecologists have thus recognized the importance of modeling habitat suitability that accounts for variation in fitness-related traits (Hampe, 2004). Doing so not only addresses local adaptation along environmental gradients, but better predicts how changes in climate will affect certain populations, thus improving strategies for species conservation and ecosystem management (Knowles *et al.*, 2007; Sork *et al.*, 2010; Joyce & Rehfeldt, 2013; Oney *et al*., 2013; Ikeda *et al*, 2016).

In this study, we investigated niche evolution within a clade of eastern North American pine trees, loblolly pine (*Pinus taeda* L.), pitch pine (*Pinus rigida* Mill.), and table mountain pine (*Pinus pungens* Lamb.; Figure 1). The current distribution of each species differs greatly, including differences in longitudinal, latitudinal and altitudinal extents; yet, areas of each distribution still marginally overlap and hybridization in these regions, although infrequent, has been observed (Burns, 1990). Two divergence events define the species within this relatively young clade; one occurred approximately 3 million years ago (mya) which resulted in the lineage of extant *P. taeda* populations and the ancestral lineage of *P. rigida* and *P. pungens*, and the second occurred approximately 1.5 mya which resulted in the extant populations of *P. rigida* and *P. pungens* (Figure 1; Hernandez-Leon *et al.*, 2013). Each species within this clade is characterized by geographic variation in fitness-related traits such as height, growth form, cone serotiny, needle length, and water use efficiency (Zobel, 1969; Burns, 1990; Schultz, 1997; Ledig *et al*., 2015), which are known targets of selection in differing climates (e.g. Davis & Shaw, 2001; Aitken *et al*., 2008; Neale & Ingvarrson, 2008; Alberto *et al*., 2013; Budde *et al.*, 2014). The life history of *P. taeda* differs greatly from *P. rigida* and *P. pungens* by having fast, straight woody growth, long needles, and strictly non-serotinous cones (Schultz, 1997). Because of these traits, *P. taeda* has become the leading commercial timber species in the southeastern United States (Burns, 1990) with resources allocated to managing its habitat and genetic diversity. The potentially negative response of *P. taeda* populations to climate change is of great concern; and as a result, the topic of human-assisted migration for *P. taeda* populations northward has been much debated (Koralewski *et al*., 2015). The characteristically low tolerance to cold temperatures of *P. taeda* has delayed decision making, but in the meantime, has inspired hybrid breeding experiments with *P. rigida*, a sister species known for greater cold tolerance (Hyun & Ahn, 1959; Knezick *et al*., 1985a). Populations of *P. rigida* are also characterized as having intermediate heights for an eastern North American pine tree, as well as, short

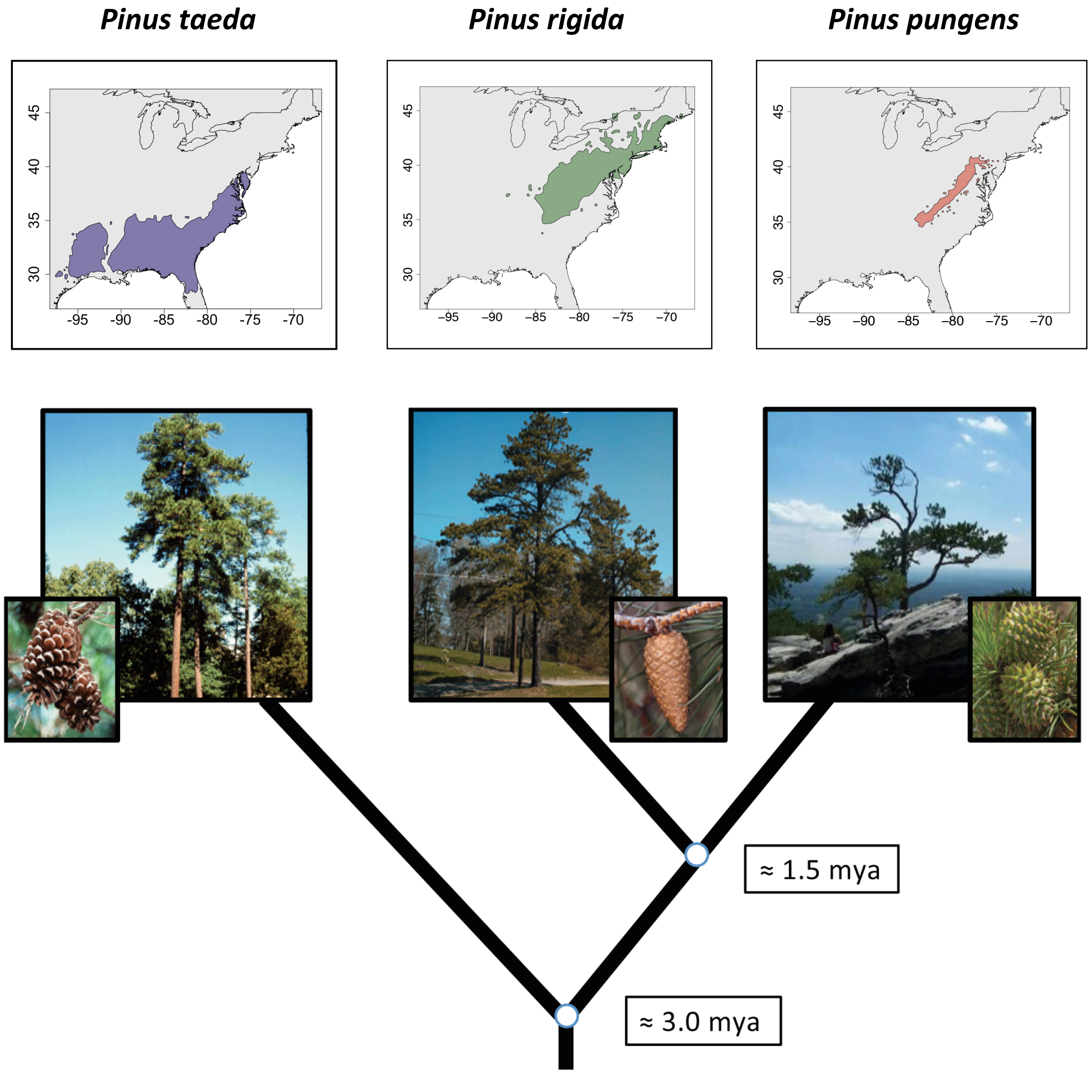


Figure 1. Evolutionary relationships among the three focal taxa reveal that *P. rigida* and *P. pungens* share a common ancestor more recently than either does with *P. taeda*. Estimated time since divergence is labeled at each node (Hernandez-Leon *et al.*, 2013). Examples of tree and cone morphology are provided at each tip along with the geographical distributions for each species (Critchfield & Little, 1966).

needles (i.e. relative to those of *P. taeda*), self-pruning branches, and small, sometimes serotinous, cones. It is important to note that making trait generalizations for *P. rigida* is challenging, as there is remarkable phenotypic variation within its distribution (Ledig *et al*., 2015). For *P. pungens*, traits appear to be more generalizable, although detailed studies of genetic and trait variation are lacking. Isolated populations are distributed along the ridges of the Appalachian Mountains, where a suite of traits related to rapid seedling development, nutrient uptake, and water use efficiencies have allowed populations to persist in low-competition areas with xeric soils (Zobel, 1969). Due to the harsher environmental conditions in these montane regions, certain trade-offs have likely been the cause of their characteristically stunted growth, short needles, and specialized reproductive strategies (e.g. spikey, serotinous cone; Zobel, 1969).

Within the wide, southern distribution of *P. taeda* are two distinct genetic groups divided east and west of the Mississippi River (Eckert *et al*., 2010) - a well-described phylogeographic barrier in southeastern North America (Soltis *et al*., 2006). The landscape of the southeast has variation in aridity, with less precipitation available to populations west of the Mississippi compared to populations of the east (Florence and Rink 1979). As a result, traits adapted for drought tolerance (i.e. deeper stomatal pits, increased root system, shorter needles, and slower growth) are found in the western genetic grouping of *P. taeda* (Shultz, 1997). Existing evidence from transplant experiments suggest niche divergence between east and west genetic groupings as desiccation and plant kill resulted from eastern seed stocks being planted in the western portions of the *P. taeda* distribution (Lambeth *et al*., 1984b).

Within the distribution of *P. rigida*, three genetic groups have been identified from common garden studies - a northern, intermediate, and a southern group arrayed along a latitudinal gradient (Ledig *et al.*, 2015). The northern group of *P. rigida* has earlier reproductive age, greater fecundity, smaller seed size, and resistance to disease compared to the other two groupings. These trait differences along the full distribution of *P. rigida* correlated with latitude, potentially driven by niche shifts involving thermal tolerance and seasonality. It should also be noted that the southern and intermediate groups have greater trait similarities than populations to the north, which could be linked to elevational differences (i.e. near sea level in north) and lack of gene flow to northern populations during the Last Glacial Maximum (Ledig *et al.*, 2015). Southern and intermediate *P. rigida* populations can be found living in sympatry with *P. pungens* along the Appalachian mountain at mid-elevations, although pure stands of *P. pungens* are found at the highest elevations (Zobel, 1969; Burns, 1990).

Describing the evolution of niches and the associated patterns of trait differentiation provide insight into how climate has influenced speciation in these economically and ecologically important tree species. To analyze niche relationships between *P. taeda*, *P. rigida*, and *P. pungens*, we asked the following three questions: (1) Which bioclimatic variables are driving niche divergence in these three species?; (2) Does niche evolution among species accompany known morphological differences?; and (3) Does niche evolution within species, across genetic groupings, accompany known morphological differences? In addressing these questions, we modeled the current geographic distribution of each species and performed pairwise species comparisons based on bioclimatic variable contributions to each niche. Bearing in mind the empirical evidence of local adaptation, that niches evolve over time or across complex landscapes, and that land management agencies have called for ENMs to incorporate population genetic data (Ikeda *et al.*, 2016), we anticipate modeled distributions that consider genetic groupings to illustrate statistically significant niche divergences. The research presented here not only provides unexplored insights into the evolutionary history of this clade of eastern North American pine trees, but in light of rapid climate change, we modeled past and future ecological niches for each species and genetic grouping to provide information pertinent to forest management and conservation.

METHODS

Current habitat suitability models

To compare bioclimatic variable contributions to each ecological niche, modeling of current habitat suitability was performed. Ecological niche models (ENMs) were built using MaxEnt version 3.3.3k (Phillips *et al*., 2006). MaxEnt is a machine-learning program that uses a presence-background algorithm to predict habitat suitability from presence-only data. The predictive power of MaxEnt has ranked well against other niche modeling programs (Elith *et al*., 2006) especially when presence data for a particular species is limited (Pearson *et al*., 2007). Default settings in MaxEnt were utilized, with the exception of 1000 iterations, increased from default of 500, and the removal of clamped pixels by selecting 'fade-by-clamping' (Phillips *et al*., 2006). Models were trained using 10 replications via bootstrap sampling, characterized by random sampling and replacement. To construct a predicted range distribution for each species or genetic cluster, 10,000 background points were sampled. The receiver operating characteristic curve (ROC) was compared to a random prediction curve to evaluate the diagnostic ability (i.e. true positive rate against the false positive rate) of presence and background data during the machine learning process (Phillips *et al.*, 2006). The area under the ROC curve (AUC) scores were used to assess the discriminatory power of each model given the location data. In this study, AUC scores > 0.90 were considered acceptable for further analysis (Swets, 1988; Marmion *et al*., 2009).

Bioclimatic variable contributions to each ENM were observed using MaxEnt jackknife plots. Additionally, we observed climate variable range distributions for each climate variable by extracting the environmental data values associated with presence and background data for each species. We then compared the variable range distributions between the presence and background data.

Habitat suitability by genetic grouping

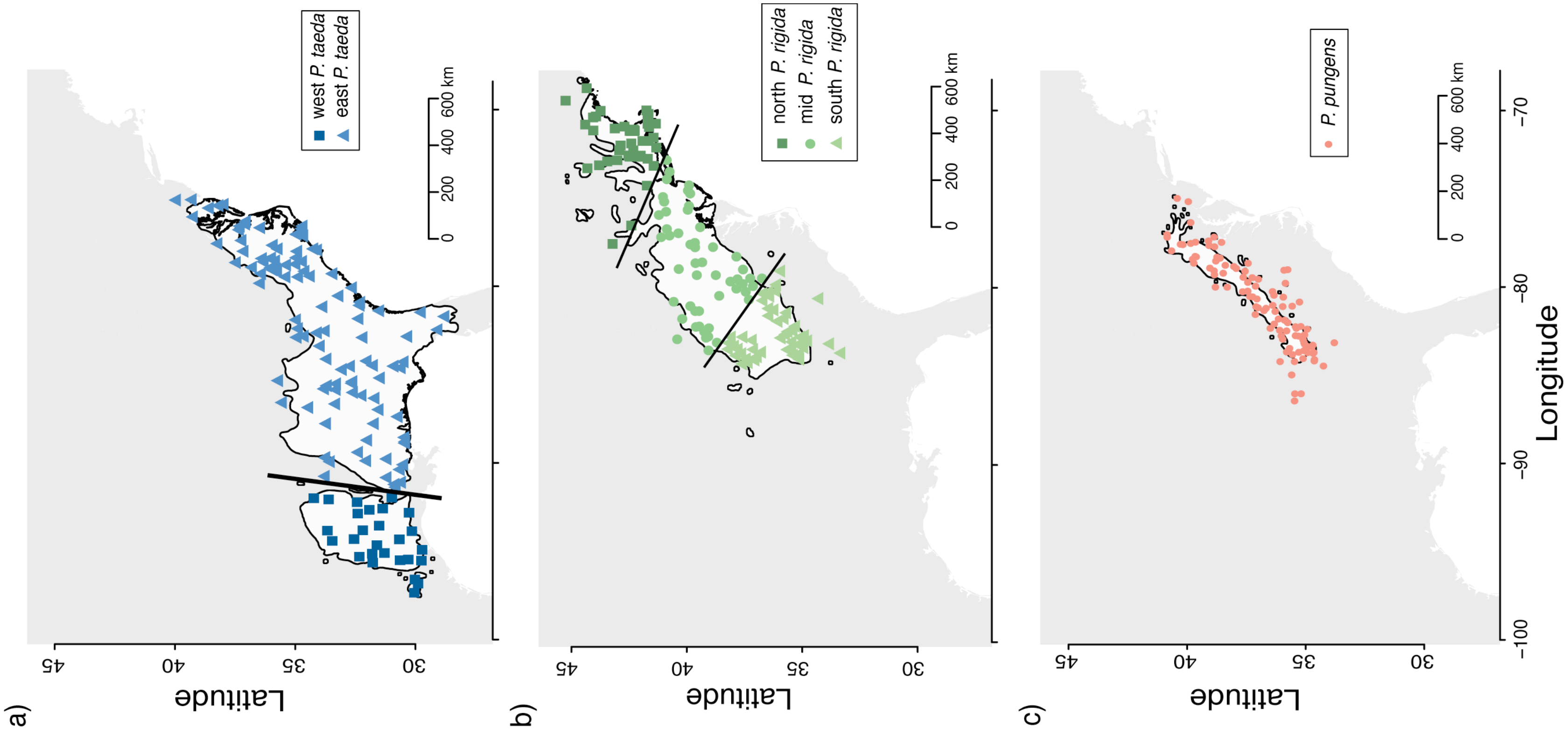
Using genetically informed models, based on STRUCTURE analysis of populations clustered within a full distribution, not only addresses local adaptation, thus niche evolution, but also improves model performance (Alvarado-Serrano *et al.*, 2014; Ikeda *et al.,* 2016). We tested this finding using the distributions of *P. taeda* and *P. rigida*. Full range distributions of *P. taeda* and *P. rigida* were subdivided into genetic groupings; each reduced distribution was determined by previously reported STRUCTURE analysis, and then, modeled independently. From here forward, these habitat suitability models are referred to as reduced models. The location data within the *P. taeda* distribution was divided into two genetic groups, east and west of the Mississippi River (Figure 3; Eckert et al., 2010). This corresponds to a known phylogeographic break across the distribution of this species, as well as others in the southeastern United States (cite Soltis *et al.,* 2006) Likewise, *P. rigida's* distribution was divided into three genetic groups along a latitudinal gradient with a northern, intermediate, and southern group (Figure 3; Ledig *et al*., 2015). Each grouping is suspected to have originated from three refugial populations of the Last Glacial Maximum; distributions have since expanded due to glacial retreat and the subsequent colonization of available land. *Pinus pungens* was excluded from this analysis, as there is currently no literature reporting the identification of genetic groups across its full distribution. Comparisons between the full and reduced models were made qualitatively for AUC scores and contributions of bioclimatic variables.

Location data

Herbarium records were the primary resource for species location data, although 45 geographic coordinates for *P. pungens,* and one for *P. rigida,* were sourced from literature (Appendix A; Jetton *et al.*, 2015; Barden, 1984; Weiner, 1984). Location data spanned the full geographical distribution for each species and limited to one per county, if multiple records were available. Documentation of each occurrence varied in year recorded, but not earlier than that of 1850. Given the long life of pine trees (i.e. hundreds of years without disturbance), it is possible to find an individual in a referenced location 150 years later. Where geographical information on a herbarium record was limited to county name, a representative coordinate near the center of each county was provided using www.latlong.net, which uses the Google Maps Application Programing Interface in referencing locations.

In total, 100 locations for *P. pungens*, 146 locations for *P. rigida*, and 134 locations for *P. taeda* were recorded that span the known geographical distributions for each species following Little and Critchfield (1966). These locations were used in all downstream analyses (Appendix A), including the division of location data into genetic groupings (Table 2). Twenty-seven locations belonged to the west *P. taeda* genetic group and 107 locations belonged to the east *P. taeda* group (Figure 2a). As for *P. rigida* groupings, there were 45, 52, and 49 assigned to the northern, intermediate, and southern (i.e. hereafter referred to as ‘north’, ‘mid’, and ‘south’ *P. rigida*) ranges respectively (Figure 2b).

Figure 2. Occurrence data used to project current habitat suitability (i.e. ENMs) for *P. taeda*, *P. rigida*, and *P. pungens*. **a)** Herbarium records with outline of geographic distribution, where two previously defined genetic groups (east and west, Eckert *et al*. 2010) have been assigned different symbols. **b)** Herbarium records with outline of geographic distribution, where three previously defined genetic groups [north, mid, and south (Ledig *et al.*, 2015)] have been assigned different symbols. The two diagonal lines show geographic separation between each genetic group based on Ledig *et al.* (2015). **c)** Herbarium records with outline of geographic distribution for *P. pungens*



Climate Data

Current environmental data were obtained from the WorldClim website, version 1.4 (Hijmans *et al*., 2005), where 19 bioclimatic variables as well as altitude, were downloaded at 30 x 30 arc second resolutions (~1 km grid cells). Variable extents were then cropped, using the *raster* package in R v.3.2.1 (R Development Core Team, 2015), to include the most northern and eastern extent of *P. rigida*, and the most western and southern extent of *P. taeda.* Environmental variables were examined for correlations across all three species using the *corrplot* package in R v.3.2.1. Twelve bioclimatic variables, as well as altitude, exceeded a correlation threshold (Pearson's $r > |0.80|$) in one or more of the focal species, and thus were eliminated (Appendix B). The remaining seven variables were used for species distribution modeling: mean diurnal range (Bio 2), temperature seasonality (Bio 4), mean temperature of wettest quarter (Bio 8), mean temperature of driest quarter (Bio 9), mean temperature of warmest quarter (Bio 10), precipitation seasonality (Bio 15), and precipitation of driest quarter (Bio 17) (Table 1). Three of these variables represent temperature thresholds, two represent precipitation thresholds, and two represent temperature thresholds during precipitation extremes. Both temperature and precipitation seasonality were included in models as previous research has asserted that changes in seasonality drive speciation, especially in temperate regions (e.g. Dobzansky, 1950; Jump & Penuelas, 2005; Bonebrake & Mastrandea, 2010).

Table 1. Bioclimatic variables selected for niche modeling. The 19 bioclimatic variables available through WorldClim were thinned based on pairwise correlations (Pearson's $r < |0.80|$).

Code	Variable Description
Bio2	Mean Diurnal Range (Mean of monthly (max temp – min temp))
Bio4	Temperature Seasonality (standard deviation *100)
Bio8	Mean Temperature of the Wettest Quarter
Bio9	Mean Temperature of the Driest Quarter
Bio10	Mean Temperature of the Warmest Quarter
Bio15	Precipitation Seasonality (Coefficient of Variation)
Bio17	Precipitation of the Driest Quarter

Estimating niche overlap

To determine how similar or different any two species of this clade are from one another, two measures of niche overlap were estimated; Schoener's D and a modified Hellinger distance, I (Warren *et al*., 2008) where both statistics range from 0 (no overlap between niches) to 1 (niches are identical). Each niche overlap statistic represented a pairwise comparison between two of the three focal species. Niche equivalency and background similarity tests were performed using the *phyloclim* package, v. 0.9-4 (Heibl & Calenge, 2011), in R v.3.2.1. The function *niche.equivalency.test* was used to test the null hypothesis that niche models between two species are equivalent. This test produces null distributions of niche overlap values (n = 100) by comparing presence-only data across the two species. In contrast, the function *bg.similarity.test* was used to test the null hypothesis that niche models are equally divergent compared to background environments. This statistical test produces null distributions, where each distribution represents the first species' niche overlap values from presence data (n = 100) against a randomized background derived from the second species. Thus, this test explicitly acknowledges differences in the local backgrounds of each species being compared. Distributions resulting from the background similarity test in relation to niche overlap statistics of the niche equivalency test were used to evaluate whether two species have experienced niche conservatism or niche divergence over time (McCormack *et al.*, 2010).

Past habitat suitability

We projected historical distributions in order to identify and compare probability of occurrence shifts from the past to present. Here and throughout, we equate the 'probability of occurrence' to 'habitat suitability'. Mid-Holocene (~ 6,000 years ago) and Last Glacial Maximum (~ 22,000 years ago) distribution ensembles were built using two climate models from the Coupled Model Intercomparison Project (CMIP5); one model from the National Center for Atmospheric Research (CCSM4) and one from Max Planck Institute for Meteorology (MPI-ESM-P), downloaded from WorldClim, version 1.4 (Hijmans *et al*., 2005), in 2.5 arc minute resolutions (see Appendix C for model comparisons). Environmental data for the Last Glacial Maximum were unavailable at 30 arc second resolution, hence the decision to project historical distributions in 2.5 arc minute resolution. The MaxEnt settings and parameters applied to hindcasts were the same as those used in modeling current habitat suitability, with model extents being standardized across all species and time periods. The resulting habitat suitability median ASCII files, for each hindcast model (per species, per time period), were then averaged to produce an ensemble model using the *raster* package in R v.3.2.1.

The resulting ensembles were used to calculate changes in habitat suitability (expanding or contracting) by subtracting the current model from the hindcast. Positive values indicated higher suitability in the past, while negative values indicated higher suitability at present. Current ENMs, originally projected in 30 arc second resolution, were needed in 2.5 arc minute resolution in order to calculate change in suitability. Consequently, current models were rerun through MaxEnt using the same aforementioned procedures and settings, but with WorldClim environmental data downloaded in 2.5 arc minute resolutions (see Appendix D for model comparisons of 30 arc second and 2.5 arc minute resolutions). Changes in suitability were performed using the package *raster* in R v.3.2.1 and applied to projections of both full range distribution and distribution by genetic grouping.

Hindcasts of the Last Interglacial period (~120,000 to 140,000 years ago) were also projected, although only one model was available for download from WorldClim (Otto-Bliesner *et al*., 2008) in 30 arc second resolution. As a result, change in suitability was calculated by subtracting current models of 30 arc second resolutions from the non-ensemble models of the Last Interglacial period.

Future habitat suitability

We forecast future distributions in order to identify and compare possible habitat suitability shifts between now, mid-century, and late-century. All forecasts were projected using the same two model types selected for hindcasting the Mid-Holocene and Last Glacial Maximum distributions (CCSM4 and MPI-ESM-LR), and were downloaded from WorldClim, version 1.4, in 2.5 arc minute resolutions (Hijmans *et al*., 2005). See Appendix E for model comparisons. The Maxent settings and parameters applied to forecasts were the same as those used in modeling current habitat suitability. The resulting habitat suitability median ASCII files for each forecast model (per species, time period, and scenario) were then averaged to produce ensemble models in '*raster'*.

Ensembles were built for two times points, years 2050 (average for 2041-2060) and 2070 (average for 2061-2080), under two extreme scenarios. The Representative Concentration Pathway (RCP) of 2.6, one of the chosen scenarios, assumes drastic reductions in greenhouse gas concentrations by 2020 and a continued decrease throughout the 21st century. The other chosen scenario, RCP 8.5, assumes that greenhouse gas concentrations will continue to rise throughout the 21st century (Meinshausen *et al*., 2011).

The resulting ensemble models were used to calculate changes in suitability (expanding or contracting) between the current and future projections, with current distribution models projected in 2.5 arc minute resolution. Changes in suitability were calculated using the package '*raster'* and applied to projections of both full range distribution and distribution by genetic group.

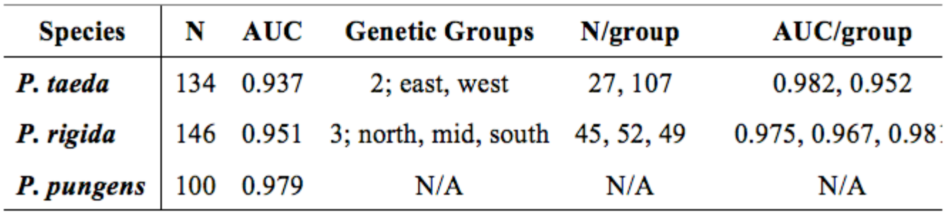
RESULTS

Fit and performance for full models

Full ecological niche models (ENMs), which incorporated all location data to predict habitat suitability within the range distributions for each species, had AUCs > 0.90. This score indicates high discrimative power of the presence data against the background; as a result, model predictions were considered optimal and thus reliable for further analysis (Table 2). Moderate to high habitat suitability predictions (*P*(occurrence) > 0.5) for each species, fell substantially within the geographical ranges defined by Critchfield and Little (1966), although ENMs for *P. taeda* and *P. pungens* had several high suitability regions projected outside their geographical ranges (Figure 3). The ENM of *P. taeda* had highest suitability in the southwest and northeast and lowest suitability in northwest and southeastern portions of the distribution (Figure 3a). The ENM of *P. rigida* had highest suitability in the south, eastern, and northeastern areas of the defined distribution and lowest suitability along the mid-western and northwestern areas (Figure 3b), while the ENM of *P. pungens* had highest suitability in the south and relatively low suitability in the northern portion of its distribution (Figure 3c).

The relative influence of each bioclimatic variable to the modeled distribution of *P. taeda*, *P. rigida*, and *P. pungens* is summarized in Table 3a. Temperature seasonality (Bio4), precipitation of the driest quarter (Bio17), and mean temperature of the warmest quarter (Bio10) had the strongest influence to the ENM of *P. taeda*. In contrast, precipitation seasonality (Bio 15) followed by Bio 10 and Bio 4 (Table 3a) had the strongest influence on ENMs of *P. rigida* and *P. pungens*.

Table 2. Location data sample size (N), model performance (AUC), and genetic group information for full and partial models. Reported AUC values represent the average training AUC for replicate runs. 100% of the test data was used for training the models (bootstrap; random sample and replace).



Species	N	AUC	Genetic Groups	N/group	AUC/group
P. taeda	134	0.937	2; east, west	27, 107	0.982, 0.952
P. rigida	146	0.951	3; north, mid, south	45, 52, 49	0.975, 0.967, 0.98
P. pungens	100	0.979	N/A	N/A	N/A

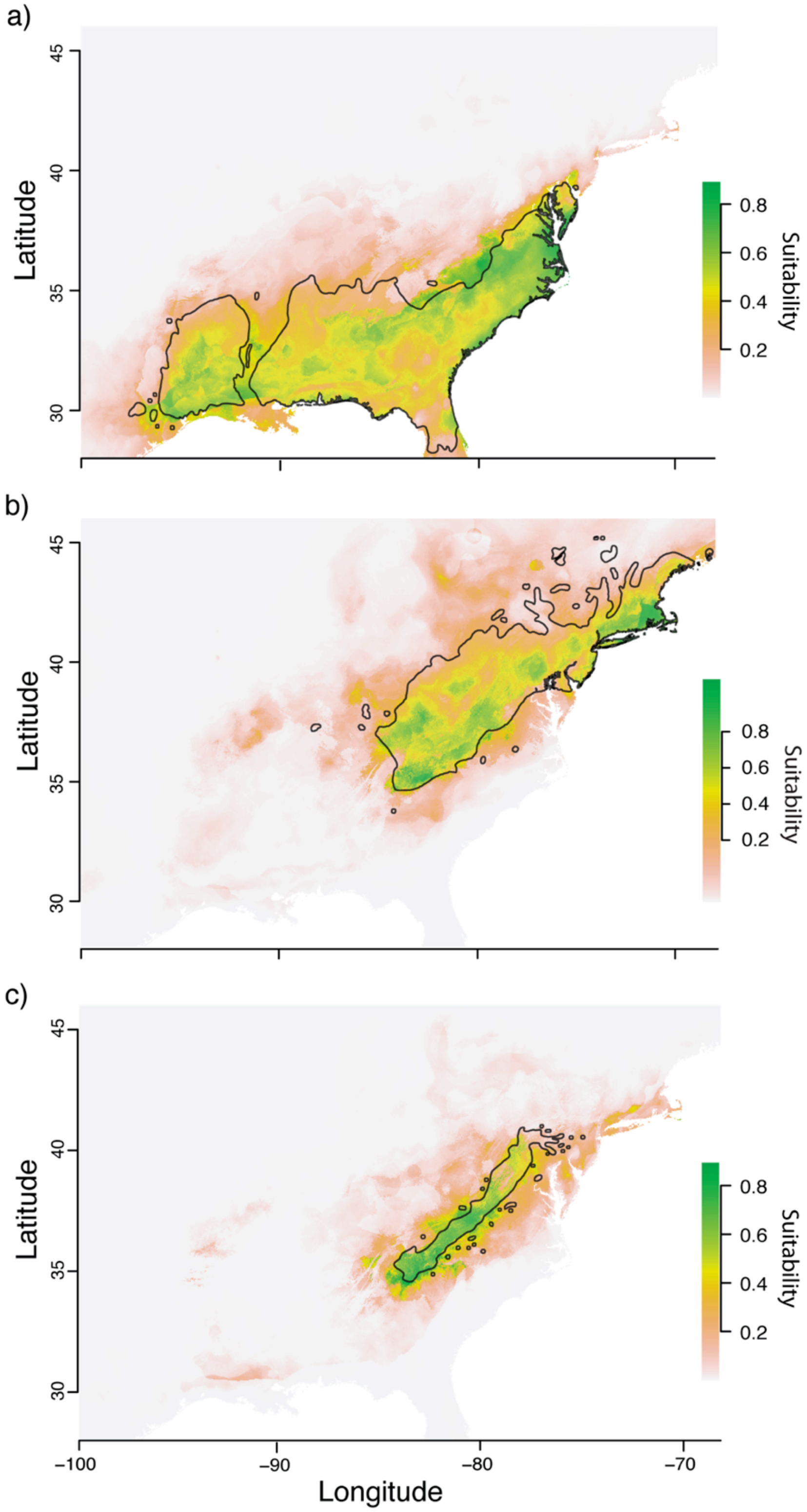


Figure 3. Ecological niche models for each species, **a)** *P. taeda*, **b)** *P. rigida*, **c)** *P. pungens*.

Table 3. Percent contribution of each bioclimatic variable to ENMs of a) *P. taeda, P. rigida,* and *P. pungens* and b) genetic groupings identified within each species.

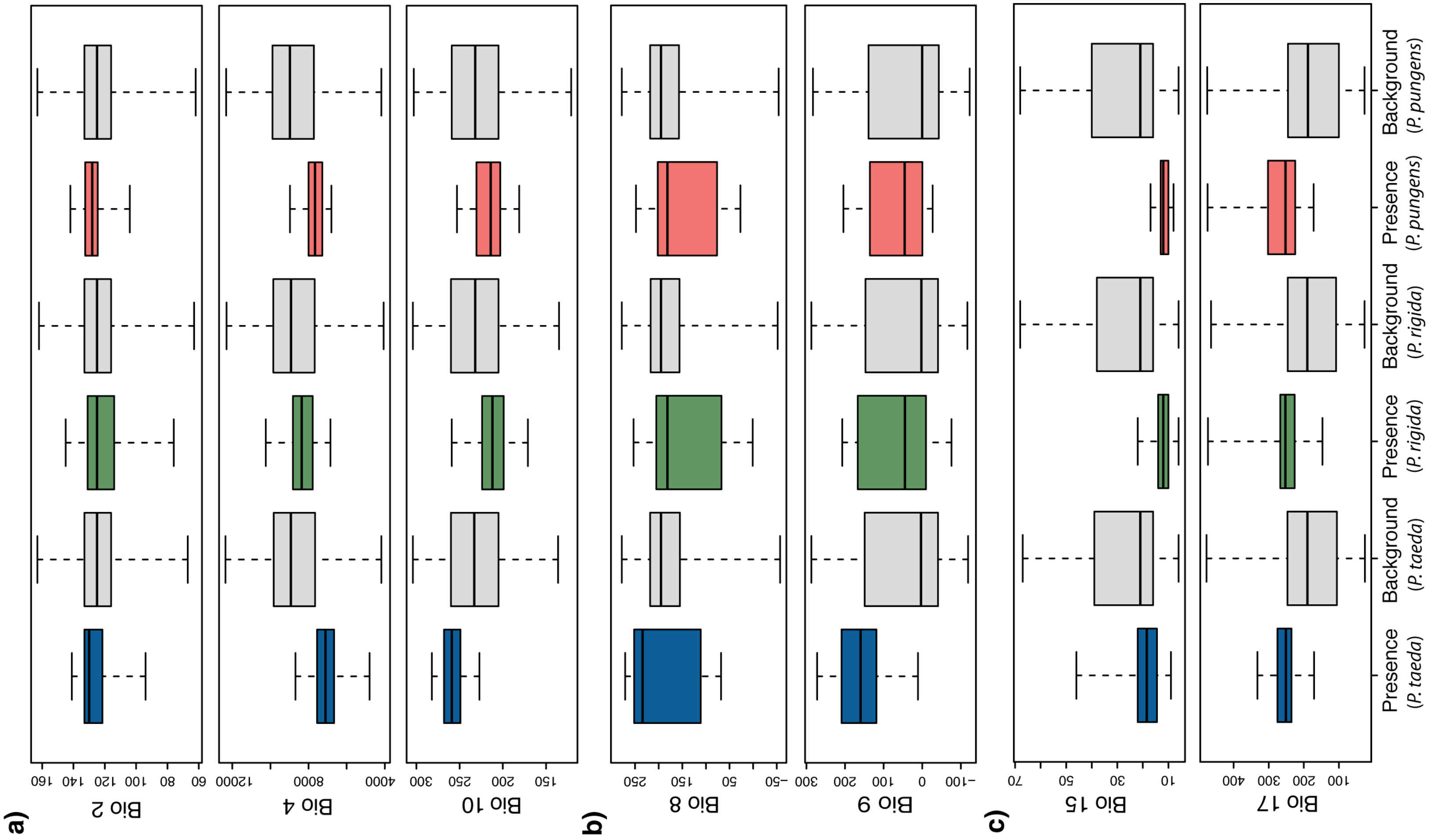
	Variable Contributions (%) to each model						
Model	**Bio 2**	**Bio 4**	**Bio 8**	**Bio 9**	**Bio 10**	**Bio 15**	**Bio 17**
a)							
P. taeda	2.1	**51.3***	6.3	2.5	**13.1**	2.3	**22.4**
P. rigida	1.4	**15.3**	3.5	**15.3**	**21.5**	**49.1***	4.3
P. pungens	2.3	**31.2**	3.2	5.5	**15.2**	**38.6***	3.9
b)							
east *P. taeda*	1.7	**44.3***	7.4	7.5	**17.3**	1.4	**20.3**
west *P. taeda*	1.2	1.4	4.5	**46.3***	**30.5**	10.6	5.5
north *P. rigida*	1.5	0.2	**30**	5.4	**18.1**	**40.4***	4.4
mid *P. rigida*	0.2	**26.9***	1.6	**20.8**	**22.9**	7.6	**20**
south *P. rigida*	8.1	7.2	5.2	**16.9**	13.5	**19.4**	**29.8***

Climatic variable measures associated with presence data were compared to the measures associated with background data to further define the niche profile (i.e. variable range of tolerance) of each species; the greater the deviation between presence and background range distributions, the more influential that particular bioclimatic variable is in defining the niche (Figure 4). For *P. taeda*, ranks of each variable in percent contribution from the jackknife analysis were in line with the observed deviation of presence data from background data; the largest deviations were observed in Bio 4 (51.3% contribution to ENM), Bio 17 (22.4% contribution to ENM), and Bio 10 (13.1% contribution to ENM). Likewise, the deviations of presence data from background data for *P. rigida* and *P. pungens*, were most obvious in Bio 15, Bio 10, and Bio 4, the three variables ranked most influential to ENMs in jackknife analyses.

Similarities and differences in niche profiles among species

Mean temperature of the warmest quarter revealed colder temperatures preferences for *P. rigida* and *P. pungens* compared to *P. taeda*, whose presence value associations were well above the background, indicating preferences for warmer temperatures. The role of temperature and precipitation interactions in niche divergence was further defined by mean temperature of the driest quarter, as range values associated with the niche of *P. taeda* were warmer in comparison to range values associated with the niche of *P. rigida* and *P. pungens*. Both temperature and precipitation seasonality were influential in determining niche distributions for all species of this clade. All three species had lower precipitation seasonality than what was measured in the background, but *P. rigida* and *P. pungens* had a much narrower range. Furthermore, all niches were described as having higher precipitation during the driest quarter than what was measured in the background.

Figure 4. Boxplots comparing bioclimatic variable importance to full ENMs across species. Colors denote variable distributions based on presence of each species (see Figures 3 – 5), while gray denotes variable distributions for background data (n = 10,000/species). a) Variables related to temperature alone. b) Variables related to combined temperature and precipitation measures. c) Variables related to precipitation alone. See Table 1 for description of each variable.



Fit and performance for reduced models

Associated AUC values for each reduced ENM (i.e. ENM for each genetic grouping), was higher than those associated with full ENM AUC scores (Table 2). The AUC for the *P. taeda* ENM was 0.937, while the reduced model AUCs for east and west *P. taeda* were 0.982 and 0.952, respectively. The AUC for the *P. rigida* ENM was 0.951, while the reduced model AUCs for north, mid, and south *P. rigida* were 0.975, 0.967, and 0.98, respectively. Modeled distributions for each genetic grouping all fell within their documented boundaries (Figure 6) with the exception of mid *P. rigida* where high values of habitat suitability were located outside geographical limits of this group (see Methods section, Figure 2).

Temperature seasonality (Bio 4) was the most important variable for the ENM of east *P. taeda* (Table 3b). In contrast, this variable made only a 1.4% contribution to the west *P. taeda* ENM. Bio 10 was important to both east and west *P. taeda* ENMs, but was only moderately important to the west *P. taeda* ENM (13.2% contribution). In contrast to the full ENM, where mean temperature of the driest quarter (Bio 9) had only marginal influence (2.5% contribution), the ENM of west *P. taeda* was most influenced by this variable (46.3% contribution).

For north *P. rigida*, the ENM was most driven by precipitation seasonality (Bio 15, 40.4% contribution), mean temperature of the wettest quarter (Bio 8, 30% contribution), and mean temperature of the warmest quarter (Bio 10, 18.1% contribution). It should be noted that Bio 8 was among the least important variables to the full ENM of *P. rigida* (3.5% contribution). The ENM for mid *P. rigida* was most driven by temperature seasonality (Bio 4, 26.9% contribution), although Bio 9, 10, and 17 were almost as influential. Lastly, the ENM for south *P. rigida*, was most driven by precipitation of the driest quarter (Bio17, 29.8% contribution), with Bio 15 and Bio 9 also providing relatively strong influence to modeled projections (Table 3b). In total, five of the seven bioclimatic variables (Bio 4, 8, 9, 15, and 17) differed greatly in their contribution to one or more reduced models relative to contributions reported in the full ENMs.

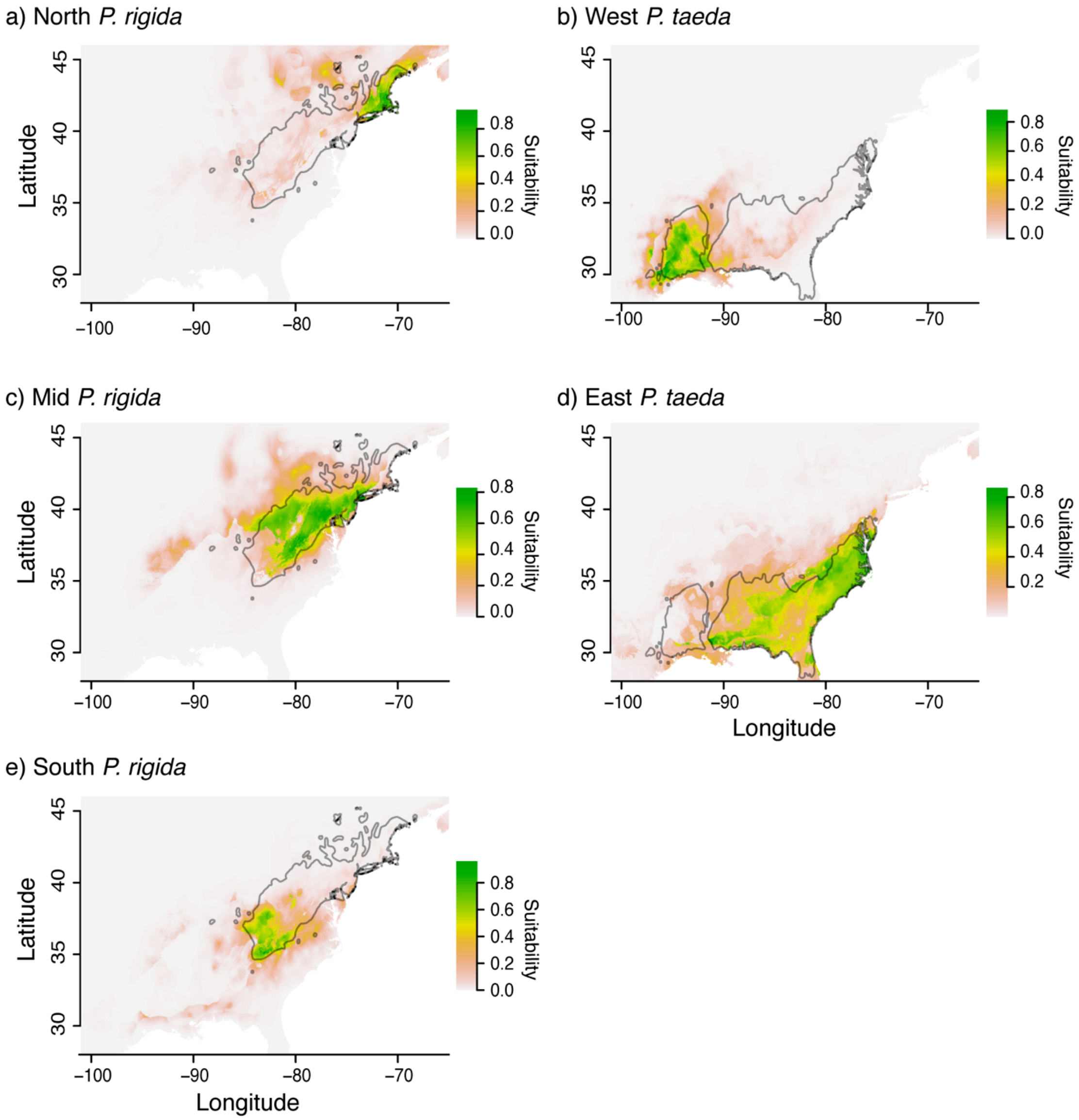


Figure 5. Habitat suitability distributions for each genetic group. The overlay of the full geographic range follows Little (1971). a, c, e) Current projections for *P. rigida* groupings. b, d) Current projections for *P. taeda* groupings.

Figure 6. Boxplots comparing bioclimatic variable importance across genetic groupings for partial models. Colors denote variable distributions based on presence of each species (see Figures 3 – 5), while gray denotes variable distributions for background data (n = 10,000/genetic group). a) Variables related to temperature alone. b) Variables related to combined temperature and precipitation measures. c) Variables related to precipitation alone. See Table 2 for description of each variable.

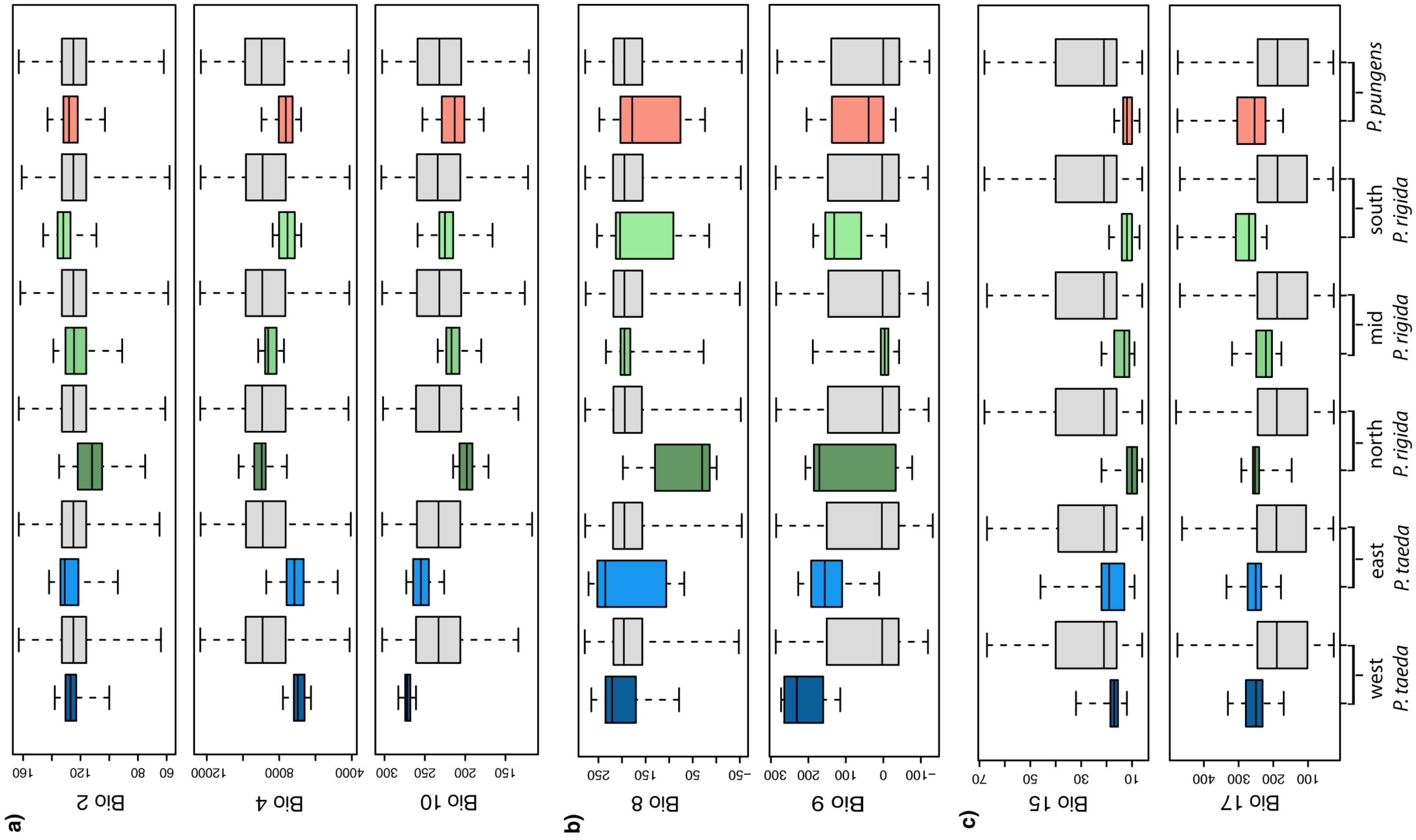


Figure 6 illustrates the range of values (presence versus background) related to each bioclimatic variable of each ENM for west *P. taeda*, east *P. taeda,* north *P. rigida*, mid *P. rigida,* and south *P. rigida*. In order to make comparisons across all species and genetic groupings known to this clade, *P. pungens* was included in Figure 6, though measured ranges for each variable were identical to those presented in Figure 4. When comparing range of values for each bioclimatic variable across genetic groupings, there was an observable gradient that correlated temperature-related variables to the general latitudinal or elevational distribution of each group; Bio 4 was positively correlated (i.e. higher latitude, higher temperature seasonality), while Bio 2 and Bio 10 were negatively correlated (i.e. higher latitude, lower mean temperatures). Variable contributions (in %) to each reduced model were reflected in comparisons of measured range distributions between presence data and background data associations; the higher the percent contribution, the greater the deviation, or narrowness, of presence data from the background. It appears that full model range values were most differing from reduced models in measurements related to temperature. It should also be noted from Figure 6, that there were strong similarities in range distributions, across all bioclimatic variables, between the southern grouping of *P. rigida* and *P. pungens*.

Niche evolution among species

To determine statistical significance in the differences observed between variable influences to the ENM of each species, we used functions within the *phyloclim* package in R to test two null hypotheses. Significant differences (*p*-values $\leq$ 5.78e-20; Table 4) resulted from each pairwise ENM comparison for both one tailed (niche equivalency test) and two tailed (background similarity test) statistical tests. For niche comparisons between *P. taeda* and *P. pungens,* as well as between *P. taeda* and *P. rigida*, we rejected both null hypotheses in support of the alternatives; niches were not identical (niche equivalency test) and niches have diverged (background similarity test). In comparing the niches of *P. rigida* and *P. pungens*, we also rejected both null hypotheses, but in contrast to the other pairwise null distribution analyses, niche conservatism resulted; niches were more similar than what was expected by chance (Figure 7b). Presented in Table 4 are niche overlap estimates in Schoener's *D*; the lowest measure of niche overlap resulted from comparisons in presence data between *P. taeda* and *P. rigida* (*D* = 0.205), and the highest measure niche overlap was estimated between *P. rigida* and *P. pungens* (*D* = 0.595). Niche overlap estimate in terms of *I* provided similar statistical results, though *I* was consistently higher in all comparisons (Appendix F).

Table 4. Schoener's *D* estimates for niche overlap across species. The upper triangular of the matrix reports estimates of *D*. The lower triangular reports the corresponding *p*-value from the *niche.equivalency.test* function in the *phyloclim* package in R v.3.2.1. Significance testing was based on permutations (*n* = 100).

	P. pungens	*P. rigida*	*P. taeda*
P. pungens	-	0.595	0.242
P.rigida	5.78e-20	-	0.205
P. taeda	4.88e-197	2.43e-258	-

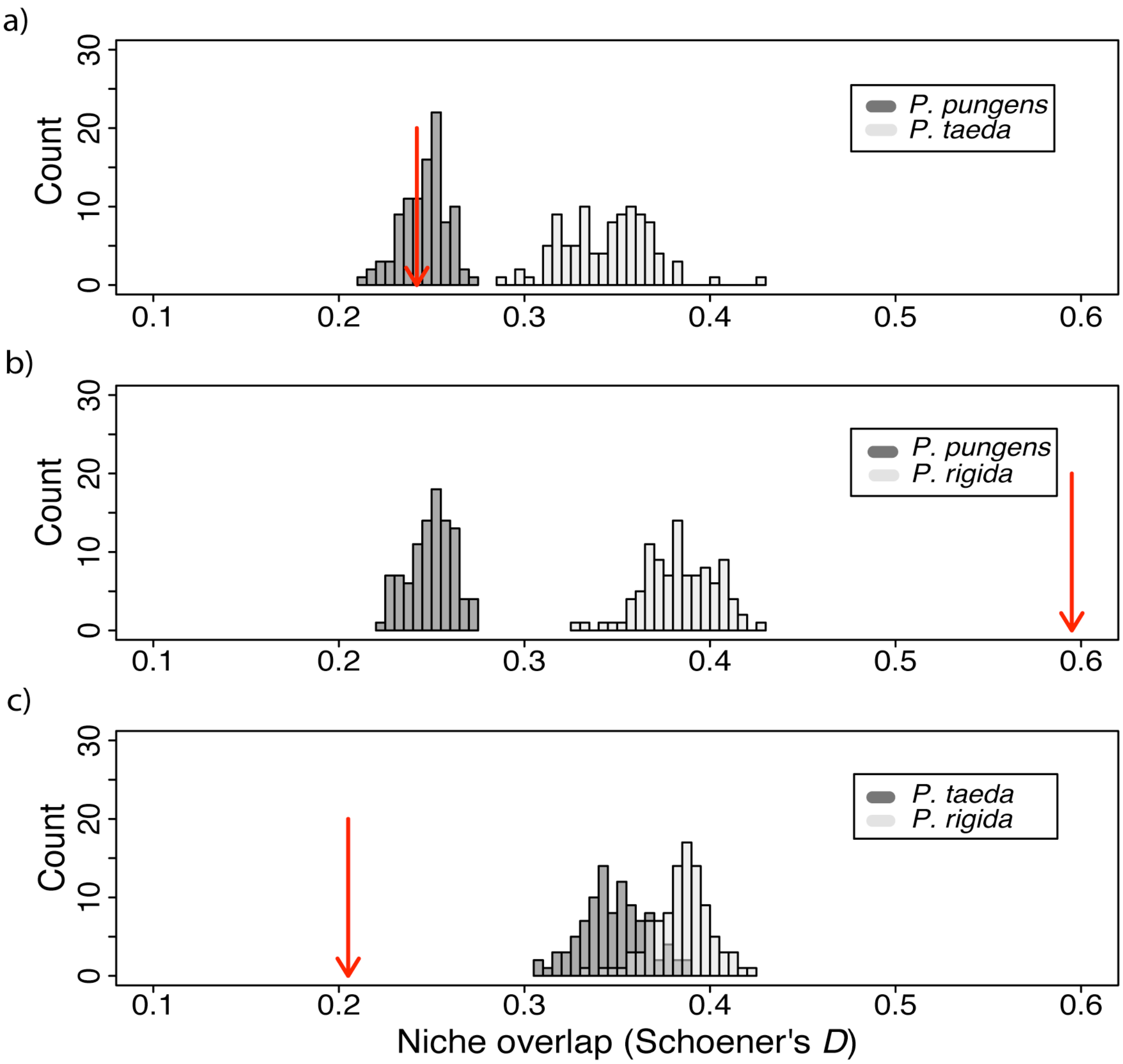


Figure 7. Null distributions and niche overlap results for each pairwise comparison between full models per species. Each distribution represents a species' niche overlap values (n = 100) against a randomized background derived from the second species. Red arrows mark Schoener's *D* estimate, where low values indicate niche dissimilarity and high values indicate niche similarity. a) The *P. pungens* and *P. taeda* comparison is consistent with niche divergence. b) The *P. pungens* and *P. rigida* comparison is consistent with niche conservatism. c) The *P. taeda* and *P. rigida* comparison is consistent with niche divergence.

Niche evolution among genetic groupings

We used statistical tests available in the *phyloclim* package in R to determine if differences we observed for niches between species were significant. Both niche conservatism and niche divergence resulted from comparisons across genetic groupings. The same methods used to test niche evolution across species were used to test niche evolution across genetic groupings. Between east and west *P. taeda* genetic groups, there were significant differences between niches ($D = 0.29$, $p = 9.56e\text{-}62$; Table 5), while the background similarity test indicated niche conservatism for west *P. taeda,* as it is currently distributed in areas west of the Mississippi most similar to those of east *P. taeda* (Figure 8). Similarly, all genetic groups within *P. rigida* had niches that were statistically different (p-values $\leq 1.24e\text{-}39$). Null distributions (background similarity) indicated niche conservatism for geographically neighboring groups, while niche divergence occurred between the non-neighboring groups, north and south *P. rigida* (Figure 9).

Table 5. Schoener's *D* estimates for niche overlap across species' genetic groupings, where '*P.r.*' represents *Pinus rigida*, and '*P.t.*' represents *Pinus taed*a. The upper triangular of the matrix reports estimates of *D*. The lower triangular reports the corresponding *p*-value from the *niche.equivalency.test* function in the *phyloclim* package in R v.3.2.1. Significance testing was based on permutations (*n* = 100).

	P. pungens	**north *P.r.***	**mid *P.r.***	**south *P.r.***	**west *P.t.***	**east *P.t.***
P. pungens	-	0.275	0.576	0.611	0.05	0.273
north *P.r.*	1.48e-72	-	0.323	0.197	0.020	0.084
mid *P.r*	4.43e-11	4.60e-49	-	0.361	0.020	0.151
south *P.r.*	1.58e-10	3.56e-51	1.24e-39	-	0.101	0.358
west *P.t.*	1.16e-106	7.16e-59	1.09e-94	1.71e-56	-	0.290
east *P.t.*	8.39e-124	1.85e-126	1.29e-214	2.21e-64	9.56e-62	-

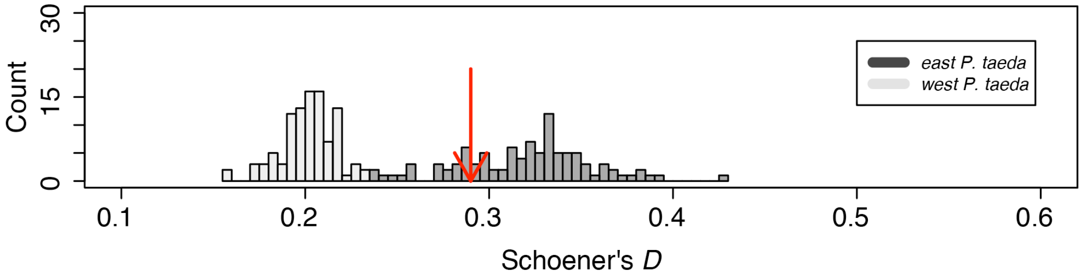


Figure 8. Null distribution and niche overlap results for west *P. taeda* and east *P. taeda* genetic groups. Each distribution represents a species' niche overlap values (*n* = 100) against a randomized background derived from the second species. Red arrow marks Schoener's *D* estimate, where low values indicate niche dissimilarity and high values indicate niche similarity. West *P. taeda's* background distribution relative to that of east *P. taeda* and the niche overlap estimate indicate that the niche of west *P. taeda* was conserved as it sought out through expansions areas similar to east *P. taeda*.

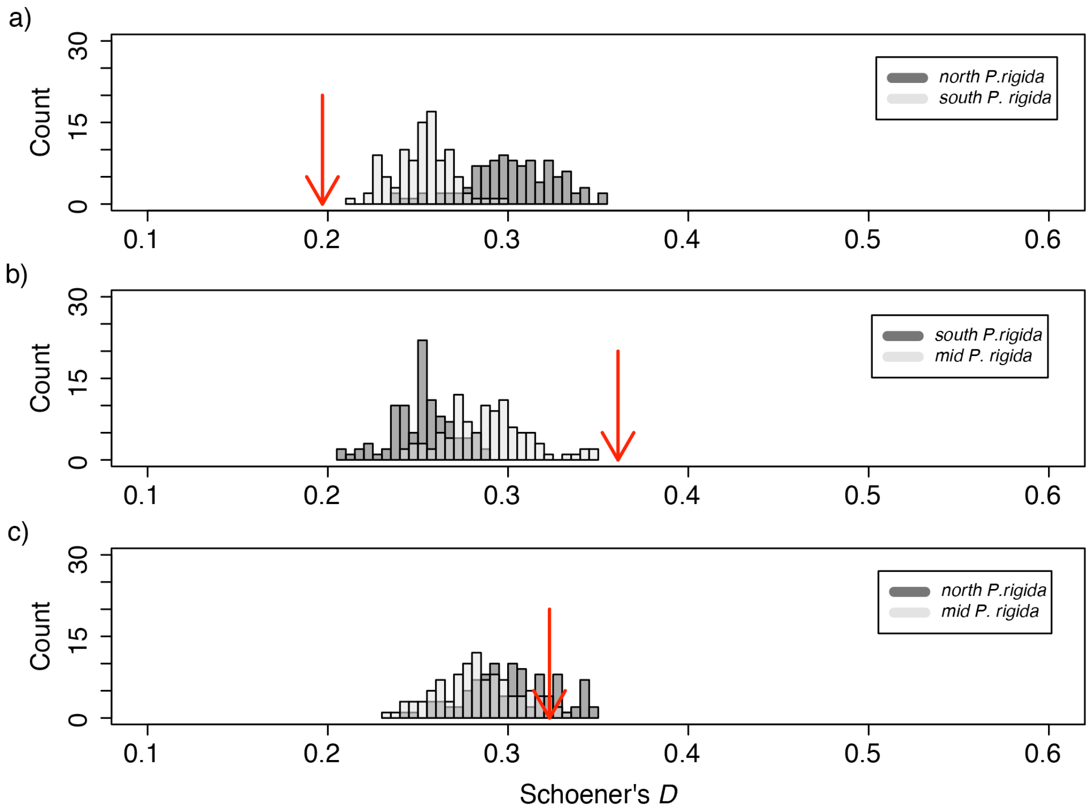


Figure 9. Null distributions and niche overlap results for three *P. rigida* genetic groups. Each distribution represents a species' niche overlap values (*n* = 100) against a randomized background derived from the second species. Red arrow marks Schoener's *D* estimate, where low values indicate niche dissimilarity and high values indicate niche similarity. a) North and south groups indicate niche divergence b) South and mid groups indicate niche conservatism. c) The niche of mid P. rigida indicated niche conservatism in relation to north P. rigida.

Due to the results of niche conservatism found between *P. rigida* and *P. pungens* in full model comparisons and the similar bioclimatic variable range values observed between the presence data of south *P. rigida* and *P. pungens*, niche equivalency and background similarity tests were performed to clarify niche relationships of each genetic group of *P. rigida* to the niche of *P. pungens*. Resulting analyses indicated greater niche overlap for *P. pungens* and south *P. rigida* (*D* = 0.611, *p* = 1.58e-10), as well as for *P. pungens* to mid *P. rigida* (*D* = 0.576, *p* = 4.43e-11), than for niche overlap estimates comparing genetic groups within *P. rigida* (*D* < 0.36, *p* ≤ 1.24e-39) (Table 5).

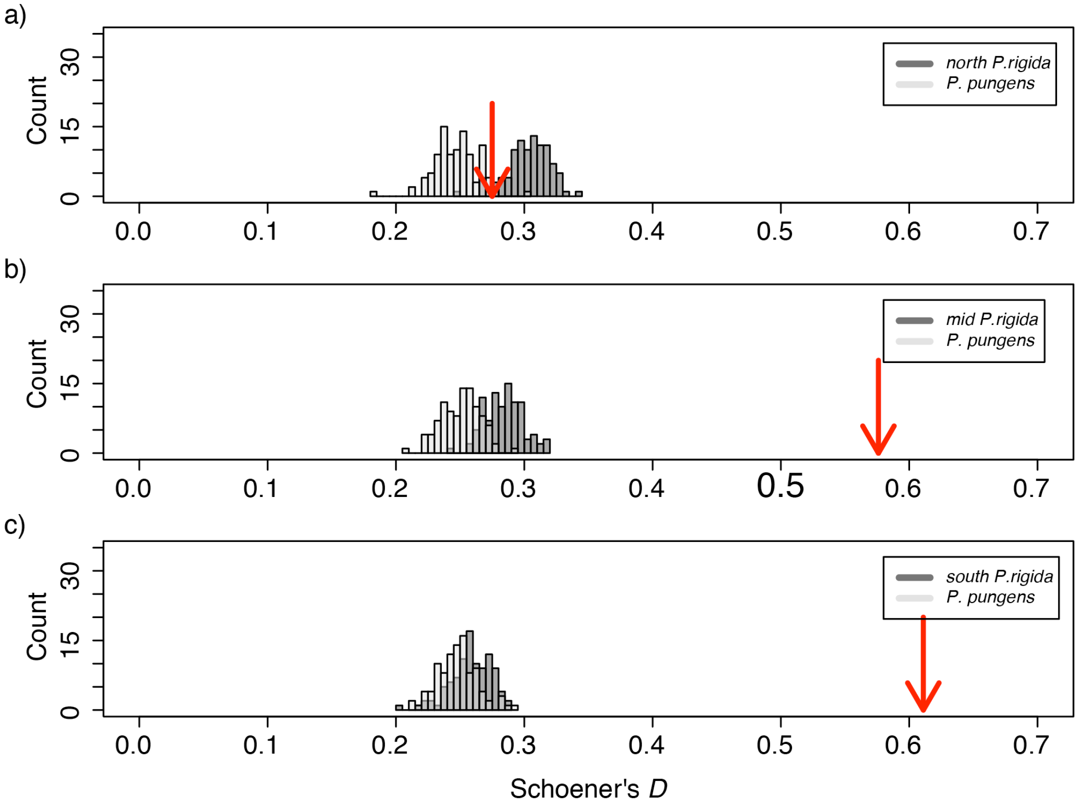


Figure 10. Null distributions and niche overlap results of *P. pungens* to each genetic group of *P. rigida*. Each distribution represents a species' niche overlap values (*n* = 100) against a randomized background derived from the second species. Red arrow marks Schoener's *D* estimate, where low values indicate niche dissimilarity and high values indicate niche similarity a) Niche overlap fell within the 95% confidence interval for null distributions of both species. b, c) A strong indication of niche conservatism exists between *P. pungens* and the genetic groups of the mid and south *P. rigida* distribution.

Past habitat suitability

To estimate and analyze differences in habitat suitability between the past and present ENMs of each species and genetic grouping, ensemble historical distributions for three time periods were created for each species and genetic grouping; we then subtracted the current models from hindcast models to visualize changes in suitability (Figure 11).

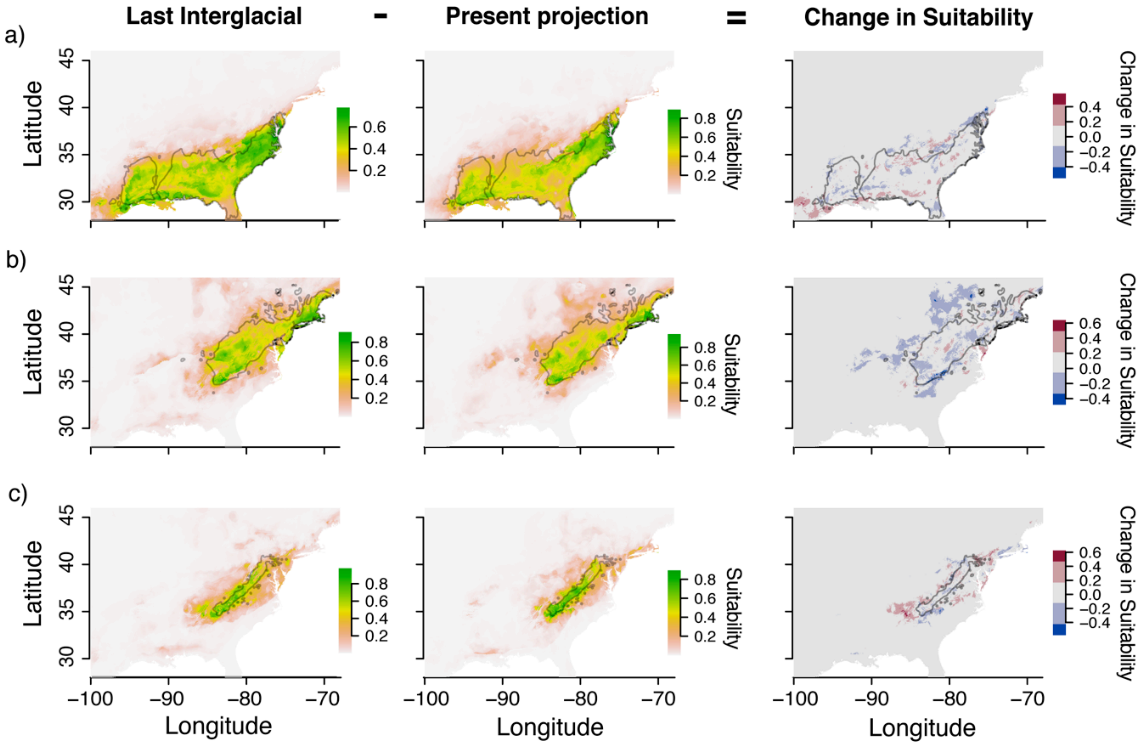


Figure 11. Illustration of how changes in suitability were determined. All changes are quantified as suitability value from the last interglacial period minus those from the current model, where red represents higher suitability in the past and blue represents higher suitability in the present. a) *P. taeda* b) *P. rigida* c) *P. pungens*

Projections for each model type, CCSM4 and MPI-ESM-P, before ensembles were made can be found in Appendix C. Quantitative comparisons of change compared to current

ENMs, via box plot distributions of positive and negative grid cell values, for each species at each time period are provided in Appendix G. Last interglacial (LIG) ensembles showed least change in habitat suitability compared to the Last Glacial Maximum (LGM) and Mid-Holocene (Figure 12). Change in suitability was greatest during the LGM for all species (i.e. boxplots in Appendix G for LGM changes have wider interquartile ranges), and generally was characterized as having suitable habitat losses proportional to the suitable habitat gains during this glacial period. Habitat suitability during the Mid-Holocene showed moderate increases in some areas post-LGM. Ensemble habitat suitability plots for each time period are available in Appendix H. Overall, we observed from ENMs that regions within the current geographical distribution were projected to be relatively stable over time (i.e. since LIG), with fluctuations in suitability ($0.5 \geq$ change in suitability ≥ -0.5) occurring at the margins.

Exceptions to the above generalities include: (1) Change in habitat suitability measures since the LGM revealed an area north of the current geographical distribution of *P. taeda* as having greater habitat suitability during the LGM (Figure 12); (2) Habitat suitability for *P. rigida* has increased since both LGM and mid-Holocene time periods, notably along the southern region of the Appalachian Mountains (Figure 12); (3) For *P. pungens*, habitat suitability of the Last Interglacial period compared to the current model for suitability with the exception of the loss in suitability in the current distribution at most northern and southern regions of the ENM (Figure 12).

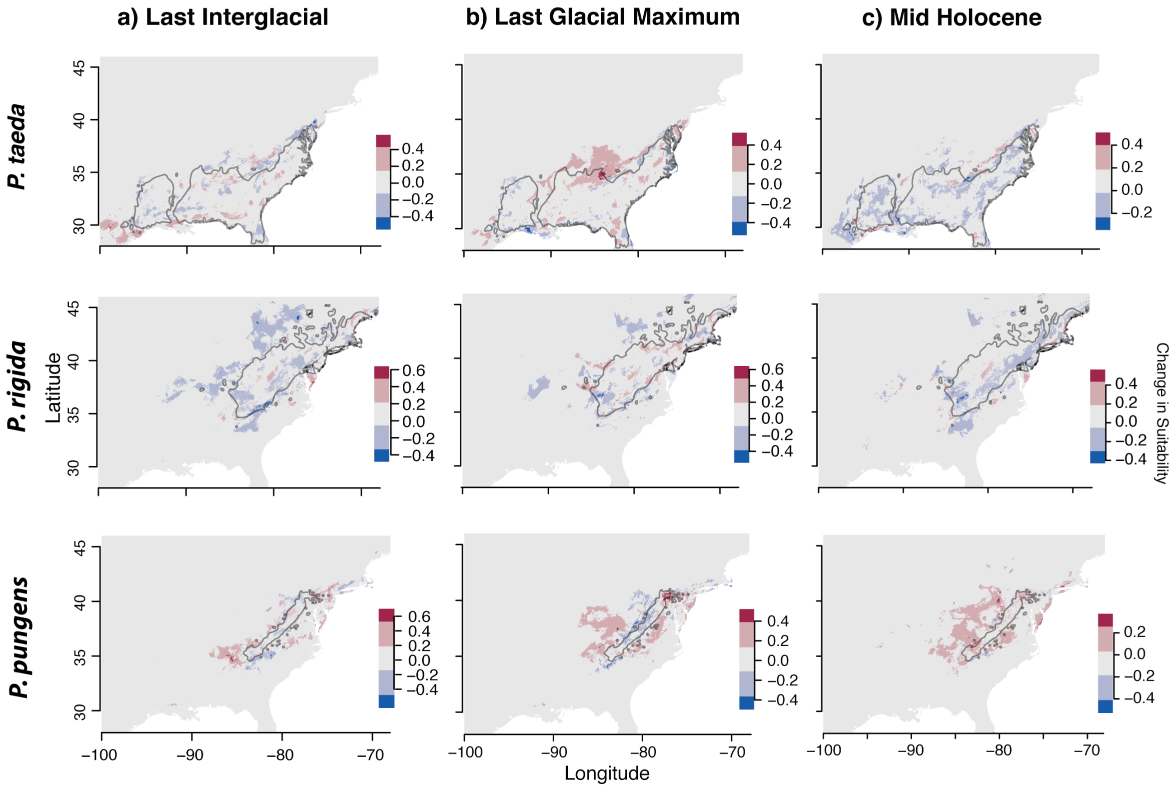


Figure 12. Change in suitability maps for each species, at three time points a) Last Interglacial, b) Last Glacial Maximum, and c) Mid Holocene. Change in suitability was measured as depicted in Figure 11, the difference in the present model from each past ensemble. Red represents higher suitability in the past and blue represents higher suitability at present.

Changes apparent in habitat suitability for each reduced model were often muted in the patterns of change calculated for the full models. For east *P. taeda* LGM projections, a larger region north of the current distribution (location ~ 35°N, 83°W) was modeled to have greater suitability during the LGM than today. For LGM projections specific to north *P. rigida*, there were small, pronounced regions at the southern margin of its current distribution that were more likely to have existed in the past than at present. Likewise, and not apparent in the full models, greater habitat suitability differences, favoring the past, were measured between the LGM and current ENM along the Appalachian Mountains within the distribution of mid *P. rigida*.

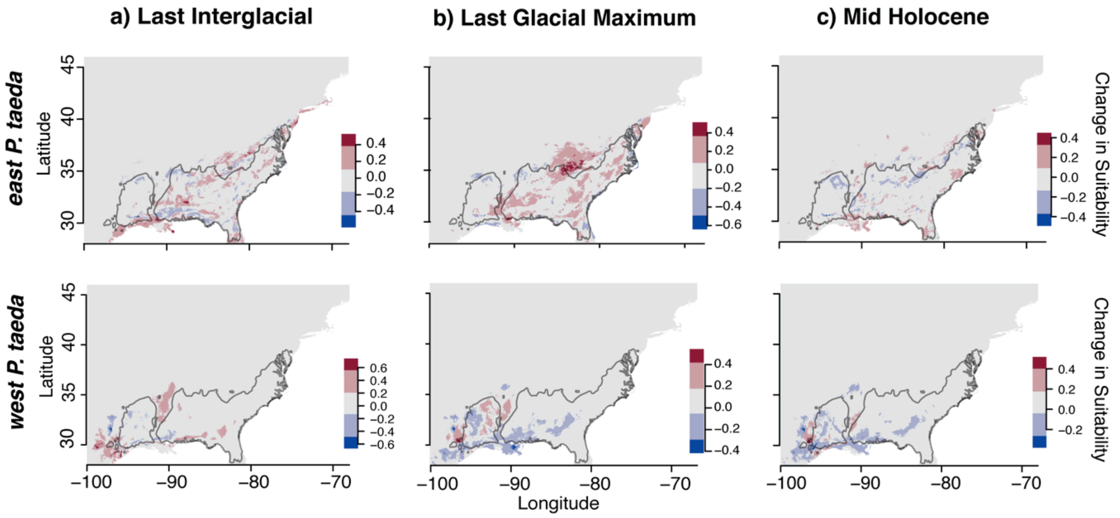


Figure 13. Change in suitability maps for genetic groups within the distribution of *P. taeda*, at three time points a) Last Interglacial, b) Last Glacial Maximum, and c) Mid Holocene. Red represents higher suitability in the past and blue represents higher suitability at present.

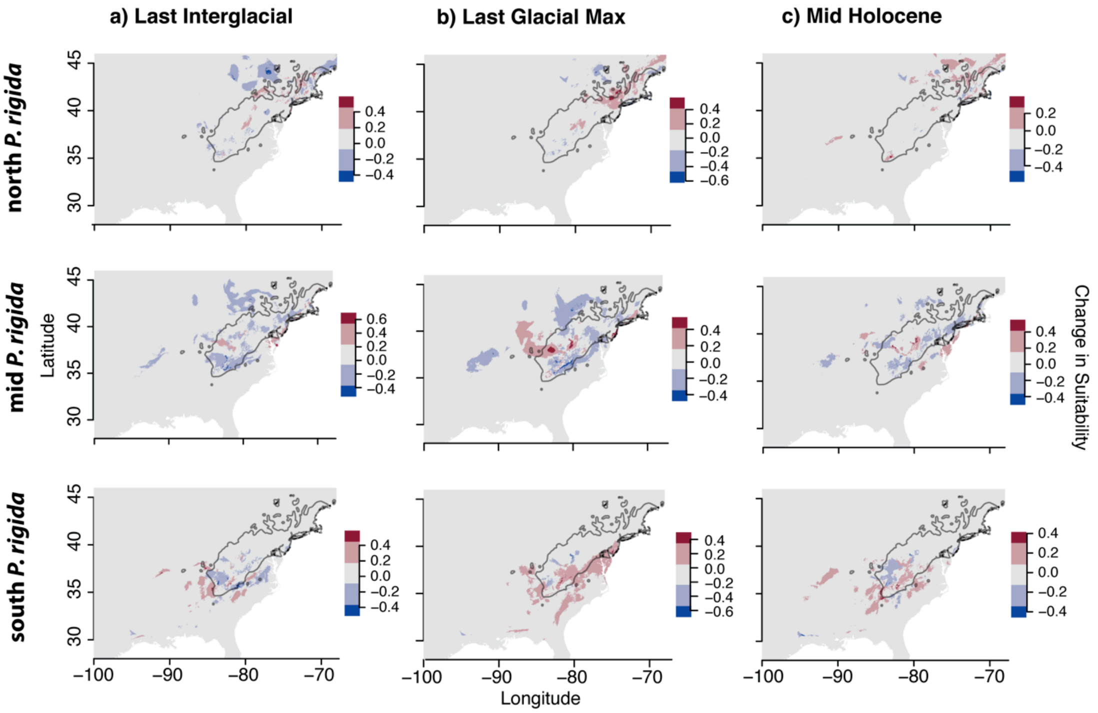


Figure 14. Change in suitability maps for genetic groups within the distribution of *P. rigida*, at three time points a) Last Interglacial, b) Last Glacial Maximum, and c) Mid Holocene. Red represents higher suitability in the past and blue represents higher suitability at present.

Future habitat suitability

Two extreme scenarios, based on the lowest and highest projections for anthropogenic carbon dioxide emissions, were used to forecast future habitat suitability for each species and genetic grouping. Similar to the methods used to analyze historical changes in habitat suitability, we calculated differences in habitat suitability for each species and genetic grouping between present and future ENMs using ensemble forecast distributions across two time points (years 2050 and 2070). In calculating change, we subtracted current models from forecasts to visualize changes in suitability. Projections for each model type (i.e. CCSM4 and MPI-ESM-LR) for each species, under the RCP 8.5

scenario, before ensembles were made, can be found in Appendix C. Quantitative comparisons of change compared to current ENMs, via box plot distributions of positive and negative grid cell values, for each species at each time period are provided in Appendix G. Differences between full and reduced ENMs were evident in future projections as they were in the hindcast ENMs; genetic groupings had distinct shifts (i.e. changes in suitability) in certain regions of their cited distributions that were underrepresented, or undetected, in the full models. Under the RCP 2.6 scenario, ENMs for *P. taeda* models showed slight expansion in habitat suitability by 2050, which carried over into 2070, but in 2070 there was one particular area that may undergo a great reduction in suitability. This reduction was forecast to occur where there is marginal overlap in the distributions of *P. rigida* and *P. pungens*, near or along the Appalachian Mountains in western North Carolina and eastern Tennessee (Figure 15). Habitat suitability of both west *P. taeda* and east *P. taeda* was forecast to increase within their current geographical distribution.

ENMs for *P. taeda* under the RCP 8.5 scenario in both 2050 and 2070 showed little shift in distribution, with the exception of increased suitability at both the most northern and most southern extent of the current distribution (Figure 15). West *P. taeda* was forecast to experience greater increases in suitability under the RCP 8.5 scenario than under a RCP 2.6 scenario at the range margins, specifically in the northeastern corner of the current distribution (Figure 15 and 16). The distribution of east *P. taeda*, under both scenarios, was also forecast to have a net increase in suitability but in no one particular area. Although under the 8.5 scenario, the gains in suitability by 2050 were lost by 2070. (Figure 16).

P. rigida models under the RCP at 2.6 scenario predicted a reduction in habitat suitability at the range margins. Mid *P. rigida* models under the RCP 2.6 scenario predicted minor reduced habitat suitability east and west of the Appalachian Mountains in 2050 and 2070 with an exceptional increase in habitat suitability (Change in suitability ≥ 0.4) along the Appalachian Mountains. South *P. rigida* models were similar in one particular forecast to that of mid *P. rigida*; habitat suitability was predicted to increase along the ridgeline and east of the Appalachian Mountains. Forecasts for south *P. rigida*, unlike mid *P. rigida*, showed an increase in suitability at the northern end of the distribution (Figure 17). Under the RCP 8.5 scenario, by 2070, habitat suitability for *P. rigida* was forecast to moderately increase at the range margins (Figure 18). Under the RCP 8.5 scenario, in 2050, habitat suitability was forecast to increase at the southern margin and continue to increase into 2070, especially along the Appalachian Mountains, Maryland (eastern shore) and New Jersey (Figure 18).

The ENM for *P. pungens*, under the RCP 2.6 scenario, showed niche stability within the current geographic distribution, although an increase outside the current geographic distribution, to the west of the Appalachian Mountains, was observable (Figure 19a). Under the RCP 8.5 scenario, in 2050, the ENM for *P. pungens* forecast specific areas along the current distribution to experience great reductions in habitat suitability (Figure 19b). But unlike the 2050 forecast, the ENM for *P. pungens* under the RCP 8.5 scenario in 2070 predicted little decrease in habitat suitability; instead, expansion in habitat suitability outside the current distribution was forecast (Figure 19b).

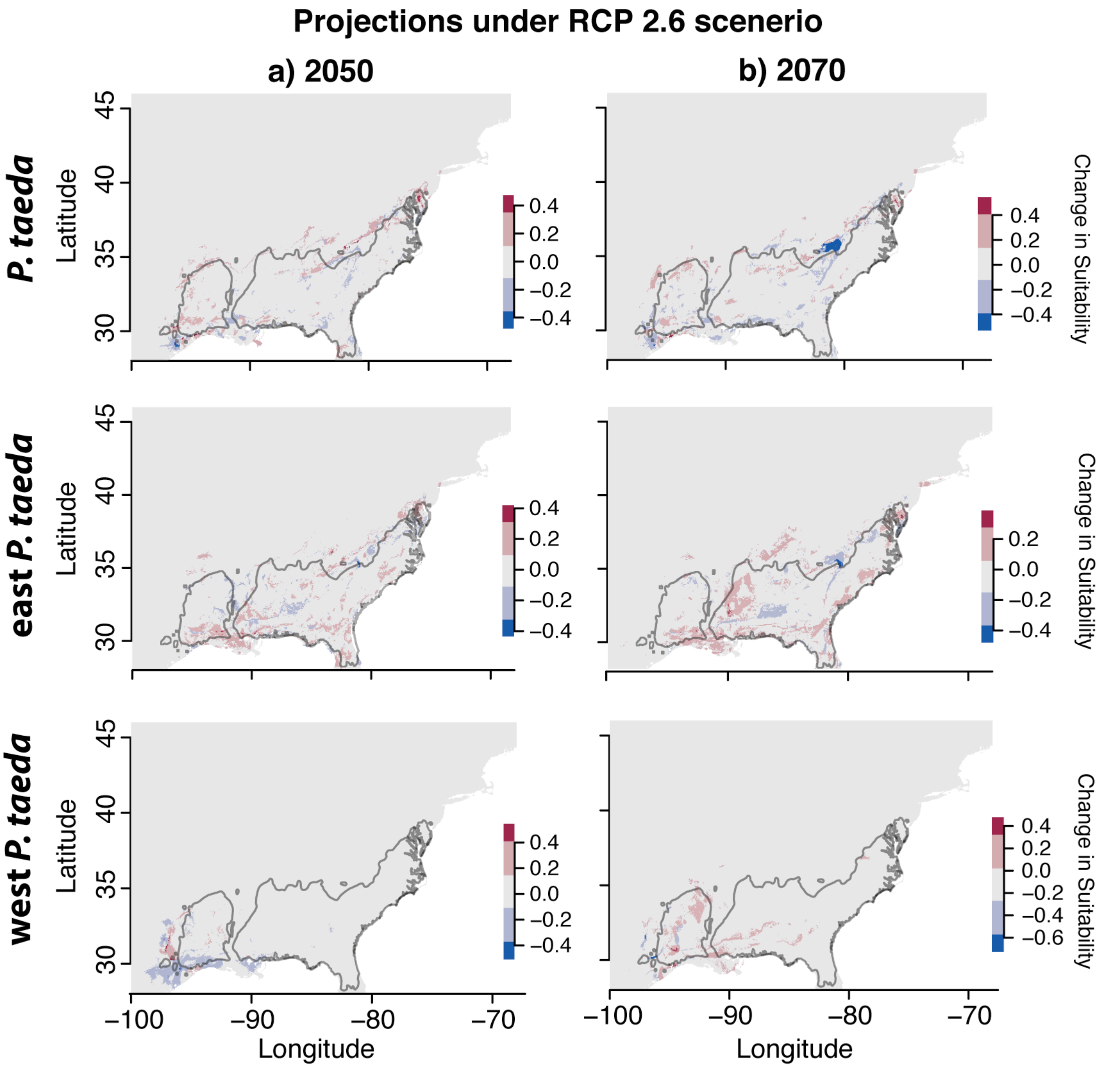


Figure 15. Change in suitability maps for genetic groups within the distribution of *P. taeda*, at two time points in the future, a) 2050 b) 2070, under the RCP 2.6 scenario. Red represents higher suitability in the future and blue represents higher suitability at present.

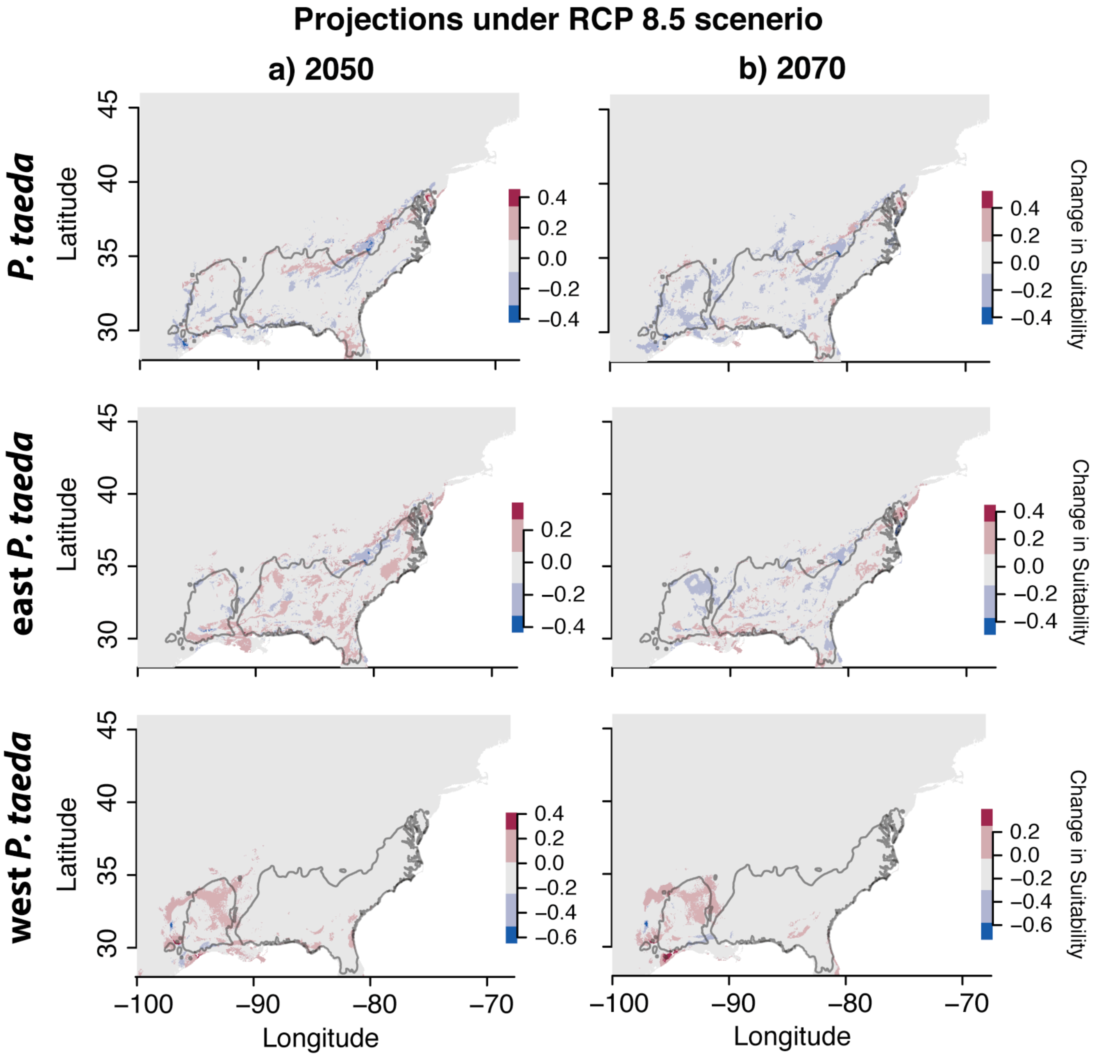


Figure 16. Change in suitability maps for genetic groups within the distribution of *P. taeda*, at two time points in the future, a) 2050 b) 2070, under the RCP 8.5 scenario. Red represents higher suitability in the future and blue represents higher suitability at present.

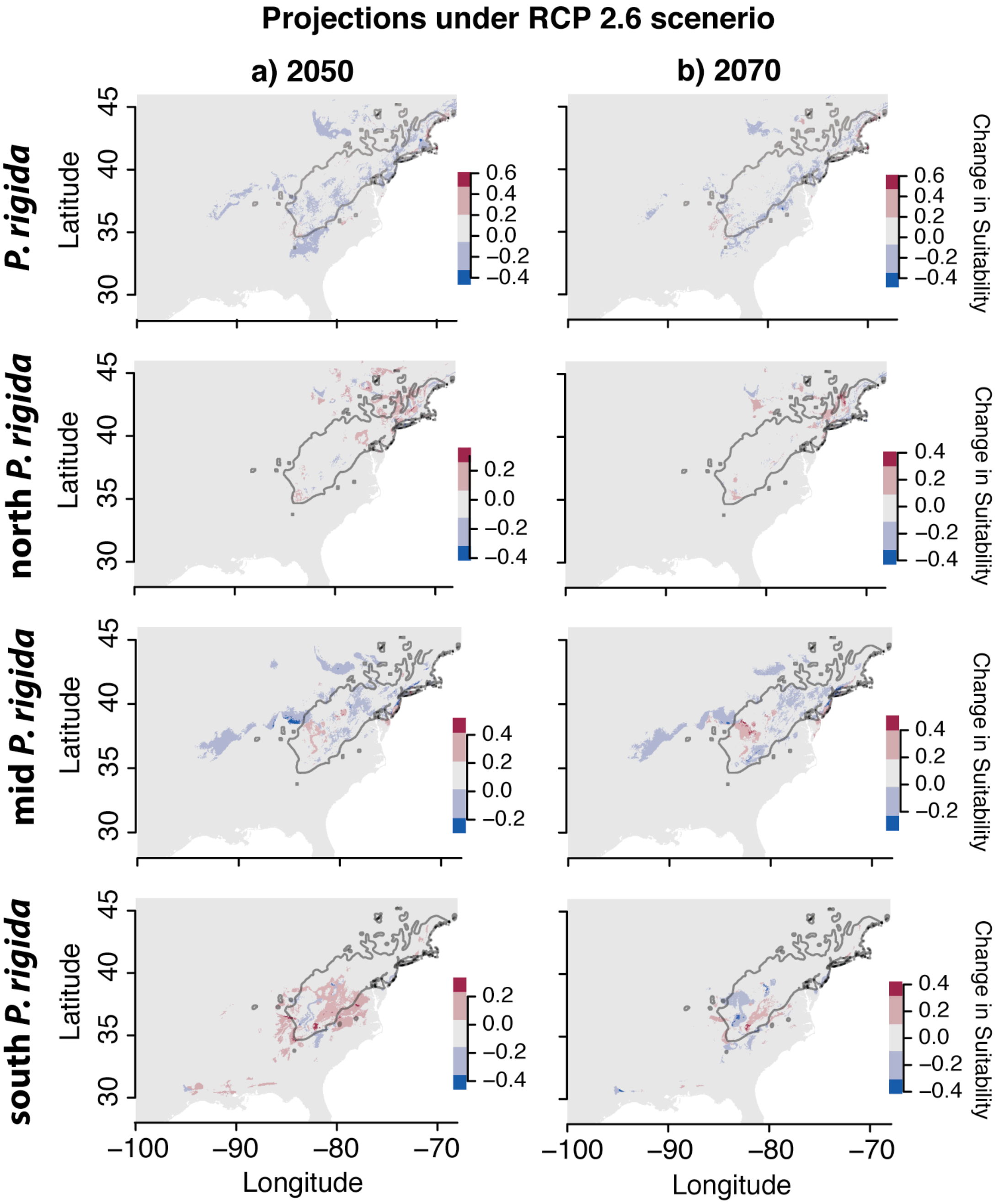


Figure 17. Change in suitability maps for genetic groups within the distribution of *P. rigida*, at two time points in the future, a) 2050 b) 2070, under the RCP 2.6 scenario. Red represents higher suitability in the future and blue represents higher suitability at present.

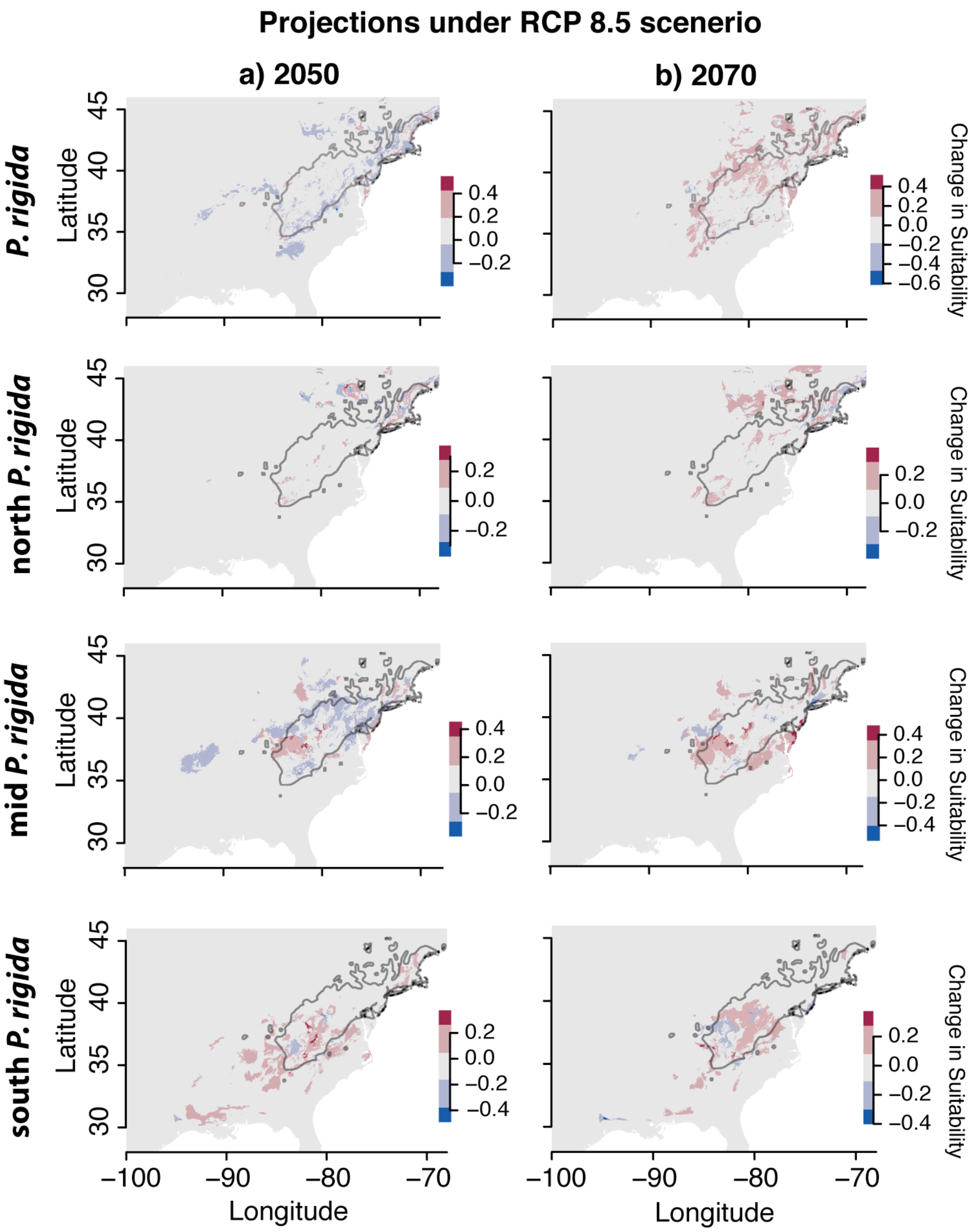
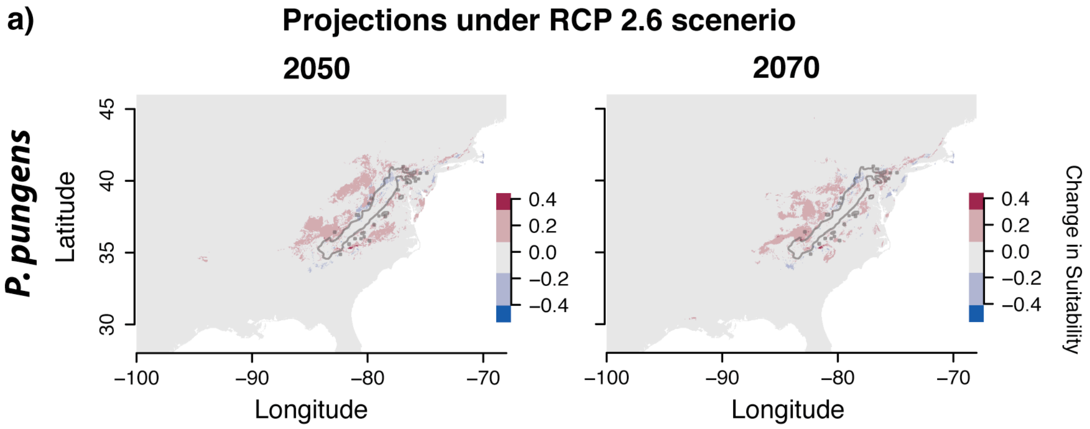


Figure 18. Change in suitability maps for genetic groups within the distribution of *P. rigida*, at two time points in the future, a) 2050 b) 2070, under the RCP 8.5 scenario. Red represents higher suitability in the future and blue represents higher suitability at present.



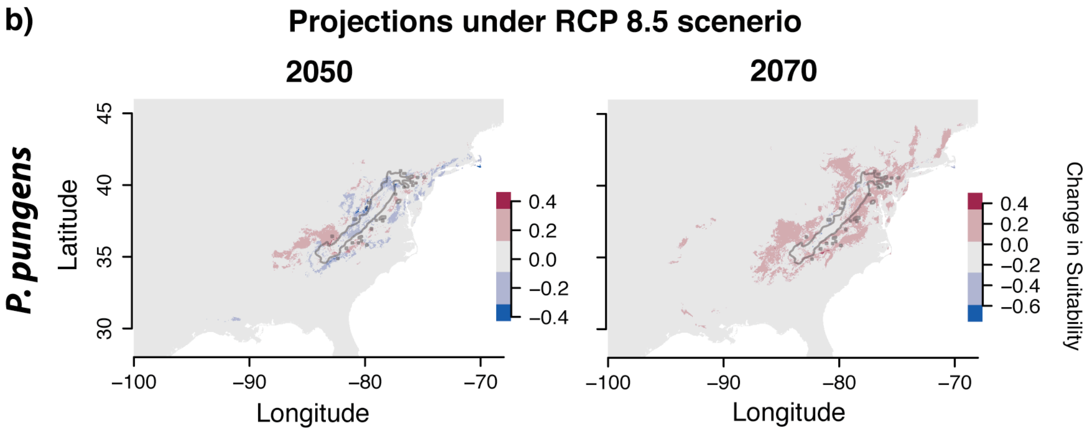


Figure 19. Change in suitability maps for *P. pungens*, at two time points in the future, 2050 and 2070, under a) RCP 2.6 scenario, and b) RCP 8.5 scenario. Red represents higher suitability in the future and blue represents higher suitability at present.

DISCUSSION

Climate contributions to niche differentiation

Temperature seasonality and precipitation seasonality (Bio 4 and Bio 10, respectively) are, given the available data, the two best predictors of niche divergence within this clade of eastern North America pine species. The importance of seasonality in driving adaptive trait variation within and among temperate species has been previously asserted (e.g. Dobzhansky, 1950; Savolainen *et al.*, 2004; Jump & Penuelas, 2005; Williams & Jackson, 2007; Bonebrake & Mastrandea, 2010). For example, temperature seasonality increased dramatically following the Last Glacial Maximum in North America, which could potentially explain the observed changes in community assemblages and adaptive responses to seasonal conditions (Williams & Jackson, 2007). Additionally, phenological and reproductive adaptive traits (e.g. bud set, bud burst, seed production, frost hardiness) observed within species of this geographic region were linked to seasonal variation (Jump & Penuelas, 2005). In support of these previous findings, we conclude that differences in seasonality facilitated differences in traits for each of the focal species of this study, including differences in seed size, reproductive age, timing of pollen release, and rates of seedling establishment and growth (Schultz, 1997; Ledig *et al*., 2016; Zobel, 1969; Burns, 1990).

The geographical distributions of each species are differentiated as far as size, shape and environmental heterogeneity. The distribution of *P. taeda* runs east to west with a rather defining limit to the northern part of the distribution. The distribution of *P. rigida* runs north to south with a defining limit to its eastern (ocean) and western distribution; and in further contrast, *P. pungens* is restricted to mid to high elevations of the

Appalachian Mountains (Critchfield & Little, 1966). The variables that most influence an ENM are affected by geographical range attributes. Likewise, influential variables are considered those that most limit the niche breadth of a species and are presumably associated with certain adaptive traits (Ackerly *et al*., 2006). For instance, adaptations for cold and frost tolerance allow tree populations to persist in the more northern regions of North America (e.g. Sakai & Larcher, 1987; Cavender-Bares *et al*., 2011). Certain phenotypes of *P. taeda* correspond with limited cold tolerance, such as long needles and relatively wide, rounded crown (Burns, 1990; Schultz, 1997) which may explain why temperature seasonality is limiting to the climate niche of *P. taeda* and thus limiting to its geographical distribution. For *P. rigida* and *P. pungens*, phenotypes such as relatively short needles and compact crowns (Zobel, 1969; Burns, 1990) correspond with adaptation to cold tolerance, thus making geographical distributions in the northeastern United States and in the high elevation regions of the Appalachian Mountains feasible. Based on our results, the niches of *P. rigida* and *P. pungens* were most limited by precipitation seasonality, and when compared to the niche of *P. taeda*, they were characterized as having a lower and narrower range of tolerance for precipitation seasonality. This may explain morphological differences in growth form, phenology, and water use efficiency between these three species.

We conclude that niche divergence is congruent with the phylogeny. The earlier divergence of *P. taeda* from the ancestral lineage of *P. rigida* and *P. pungens* (~ 3 mya) is marked by greater climate niche differences than the differences observed from the most recent divergence (~1.5 mya). Schoener's *D* was selected to quantify niche similarity, because this metric has been widely applied and can be statistically assessed

(Warren *et al.*, 2008). When presence data was tested against null models of background environmental differences, we were able to reject the null hypothesis that observed niche overlap between species is explained by regional similarities or differences in available habitat, and further conclude that there is 1) niche divergence between *P. taeda* and *P. rigida*, 2) niche divergence between *P. taeda* and *P. pungens,* and 3) niche conservatism between *P. rigida* and *P. pungens*. With results of niche divergence, it can be reasoned that directional or disruptive selection drove the initial divergence of the ancestral populations of *P. taeda* from the ancestral lineage of *P. rigida* and *P. pungens*. With indication of niche conservatism, neutral evolutionary processes, stabilizing selection or factors beyond climate were likely involved in the divergence of *P. pungens* and *P. rigida*, at least when considering entire ranges of each species. Our results support the hypothesis of Grinnell (1924); niche evolution is a slow process. Aspects of the ancestral niche have remained conserved in both *P. rigida* and *P. pungens*, even after 1.5 million years since divergence. Contingent upon the inferred time of divergence from the most recent common ancestor (Hernandez-Leon *et al*., 2014), we estimate niche divergence to have taken up to a maximum of 3 million years. This may not be surprising since the relevant coalescence time scale is in units of $4N_e$ generations, and with the long generation time and large effect size of pine species, evolution, even under moderately strong selection, could take millions of years to occur (Charlesworth & Charlesworth, 2010).

The accuracy and predictive power of ENMs to draw conclusion related to niche evolution have been questioned (e.g. Soberón & Peterson, 2005; Pearman *et al*., 2007; Warren *et al*., 2008). One concern regards the biases associated with environmental variable selection. In this study, we addressed this concern by selecting climate variables that were not highly correlated (i.e. to reduce overfitting of data in ENM projections) and maintaining those that have been documented as important to temperate tree species (e.g. Sork *et al.*, 2010; Ikeda *et al*., 2017). Although still, some critics might argue that using land variables (e.g. soil or elevation) would have been appropriate to include, we counter this argument by stating that 1) elevational differences noted in previously performed ecological assays of these species are substantially different, 2) mean temperature of the warmest quarter (Bio 10) was highly correlated with altitude in *P. pungens* (Pearson's r = -0.81; Appendix 2), and 3) adding land variables would obscure the primary objective of this study, which sought to determine how climate influenced niche divergence between species of this clade.

Another argument recently echoed in reviews of ENM assumptions and shortcomings relates to the model algorithms, which do not account for local adaptation in projections (e.g. Hampe, 2004; Gotelli & Stanton-Geddes, 2015). The most efficient way to address local adaptation is to reduce a species distribution into regions that reflect genetic grouping or from trait differences observed in common garden studies (e.g. Ikeda *et al.* 2016). Because *P. taeda* and *P. rigida* both have documented genetic groupings within their range distributions, we were able to address this concern through reduced ENM projections. When genetic differences within the geographical distributions of *P. taeda* and *P. rigida* were taken into consideration, niche differentiation between each grouping was detected, and supports the notion that local adaptation at small spatial scales can lead to niche divergence (e.g. Knowles *et al., 2007*; Ikeda *et al*., 2016; Oney *et al.,* 2012). Mean temperature of the driest quarter (Bio 9) was the main differentiating climate variable between the niches of east and west *P. taeda*. With this result, we support previously made statements that the greater aridity within the west *P. taeda* geographical distribution likely resulted in adaptation now lending to the specific drought tolerance, disease resistance, and water use efficiency trait variation observed in each genetic grouping of *P. taeda* (Wells & Wakeley, 1966; Squillace & Wells, 1981; Schmidtling, 2001). It should be noted that in the full ENM of *P. taeda*, Bio 9 went undetected as an important contributor to the ENM projection. This could be explained by the larger distribution of east *P. taeda*, thus larger sample size of occurrence data, which caused greater influence in ENM projections over the smaller area and thus smaller data set of west *P. taeda*. Niche differentiation between east and west *P. taeda* was statistically validated by the niche equivalency test (Table 3). Meanwhile, null distributions from the background similarity test in relation to niche overlap, indicated niche conservatism in west *P. taeda*, whose climate niche was more similar to east *P. taeda* than expected.

For *P. rigida*, trait variation across genetic groupings also accompanied quantitative niche differences. In Ledig *et al.* (2015), some trait values (e.g. growth, seed size, fecundity, disease resistance) were highly correlated with latitude; a similar correlation was observed in the temperature-related (Bio 2, Bio 4, and Bio 10) range tolerances of each genetic group. This result was not surprising given the gradient effects of latitude on temperature (Sakai & Larcher, 1987). More interestingly though, mean temperature of the wettest quarter (Bio 8) and precipitation of the driest quarter (Bio 17) contributed most to niche differentiation across genetic groupings; both Bio 8 and Bio 17 were of low influence to the full ENM of *P. rigida*. In parallel with the greater morphological differences observed in northern group compared to morphology of the southern group, results from niche overlap estimates were lowest between north *P. rigida* and south *P. rigida*, and when tested against null models of background environmental differences, there was indication of niche divergence between these two genetic groupings. Meanwhile, tests of niche overlap against null models of background environmental differences, provided evidence of niche conservatism between mid and south *P. rigida*. Both of these groups are found at mid-elevations along the Appalachian Mountains and have only slight variation in trait values. Several scenarios and/or mechanisms for trait differentiation could explain differences between each of the genetic groups discussed here (Ackerly 2003), but as stated in Ledig *et al*. (2013), it is worth considering the impacts of the Last Glacial Maximum in separating a previously continuous distribution into allopatric populations absent of gene flow (Hua & Wiens, 2013) thus causing further morphological and niche differentiation.

Cycles of glacial and interglacial periods may also explain the divergence of *P. rigida* and *P. pungens* from the ancestral lineage 1.5 million years ago. Based on niche overlap and background similarity tests between mid *P. rigida* and *P. pungens*, as well as between south *P. rigida* and *P. pungens,* which indicated niche conservatism, it could be possible that ecological speciation (e.g. Rundle & Nosil, 2005; Wang *et al.,* 2001) drove divergence within the Appalachian Mountains, a well-documented geographic region for glacial refugia (Hewitt, 2004; Soltis, 2006). In this scenario, southern and mid-*P. rigida* populations may have been the progenitors of *P. pungens*, as observed for other recently evolved sister taxa in the Pinaceae (Jaramillo-Correa & Bousquet, 2003).

ENM projections of the present, past and future

Our location data expanded the range distribution for each species in order to best capture the breadth of the realized climate niche; the power of our data to predict the climate niche of each species was best reflected in high AUC scores for both full and reduced ENMs. We practiced caution in interpreting projections as geographic structures, life history traits, and biotic interactions that may co-regulate occupancy in climatically suitable habitats were unaccounted for in ENM projections. Recognizing these during analyses of ENM predictions is vital. For example, the current ENM of *P. pungens* had several regions measuring high habitat suitability projected outside the geographic distribution. Ecological studies on the distribution of this species describe populations as fragmented and isolated, with reproductively viable seeds only produced in high elevation stands, so even for habitat suitability projected inside its range distribution, we must consider that only a portion of this space is, or can be, occupied. In this example, we were reminded to consider the perspective of G. E. Hutchinson (1957) on how the fundamental and realized niche relate. Biotic interactions such as competition, inhibit species from occupying its broader fundamental niche, and are thus limited to occupancy within the realized niche.

Based on the life history traits common to trees (Petit & Hampe, 2006) and the vast number of studies attributing changes in climate to shifts in geographical distributions (e.g. McKenney *et al.*, 2007; Aitken *et al.*, 2008; Kozak & Wiens, 2010; Iverson & McKenzie, 2013), we projected historical distributions for each species in this study to determine if range shifts since the Last Glacial Maximum (~22,000 years ago) were directional. We also performed hindcast projections for the last interglacial period (LIG), but little attention was given to these results as only one General Circulation Model

(GCM) was available for projections and that this model differed from the two models used for LGM and Mid-Holocene projections (see Methods). Each GCM inherently differs from the next. Varela *et al.* (2015) found that bioclimatic variables were weighted differently across GCMs and were the root cause for variation in ENM projections. To decrease the biasing effects of using one GCM, we averaged the projections for two (i.e. constructed an ensemble model). Main conclusions drawn from comparisons between past and current ENMs include 1) habitat suitability differs most between LGM and current ENMs, 2) changes in habitat suitability cannot be generally categorized as moving poleward with warming trends, 2) changes to habitat suitability may go undetected in full models that do not account for genetic differences; this was specifically evident in the LGM hindcast for mid *P. rigida*. Without accounting for genetic differences, two potential areas for refugial populations during this glacial cycle would not have been detected, and 3) the LGM hindcast of *P. taeda* presented interesting results, which now calls for the previously hypothesized dual refugial model (i.e. situated in Mexico and Florida) to be revisited (Soltis *et al*., 2006). Genetic differences, inferred as admixture, in the middle and northern margins of the current *P. taeda* distribution (Eckert *et al*., 2010), could now potentially be investigated as diversity, based on the historical distributions modeled here. There may have been three refugia during the LGM; the third being situated just north of the current distribution.

In light of the rapid climate change projected to occur within the next century, we forecast distributions for both species and genetic groupings. Based on projections, regardless of the climate change scenario used (RCP 2.6 or RCP 8.5) or year (2050 and 2070), full range ENMs suggested little change. On the contrary, more distributional change was observed in reduced ENM projections. West *P. taeda* and all genetic groups of *P. rigida*, were forecast to have net increases in habitat suitability within their geographic distribution under the RCP 8.5 scenario. In comparing past habitat suitability change (over thousands of years) to future changes (within the next century), we found it alarming that the degree of change predicted for the near future, in most cases, exceeded the changes of the past (see Appendix I). One unwavering assumption of projections across time scales is that ecological niches are conserved, and, although supportive evidence for niche conservatism is widely available across short time spans (e.g. Peterson, 1999; Weins & Graham, 2005; Kozak & Weins, 2010), there is also evidence that local adaptation may cause shifts toward new climate optima within the realized niche (Jackson & Overpeck, 2000; Ackerly, 2003), thus making the accuracy of a hindcast or forecast projection relative to the focal species, which depends on life history and the ability to rapidly adapt under suboptimal conditions (Hampe, 2004; Ackerly, 2006; Aitken *et al*, 2008). To alleviate this concern, ENMs should consider trait differences or genetic groupings within a species range distribution.

ENM predictions assume that species can fully disperse into future suitable habitats (Hampe, 2004). This assumption is greatly compromised by the modern landscape which is characterized by extensive habitat fragmentation from impervious surfaces and land use associated with agriculture (Saunders *et al.*, 1991; Lienert, 2004). This disrupts landscape connectivity needed for migration and furthermore limits gene flow between populations thus limiting genetic diversity. With greater genetic diversity within a species distribution, the more likely the species is to survive and adapt to novel climate conditions (e.g. Aitken, 2008; Pearman, 2008). Another factor that affects dispersal, thus rate of migration, is the dispersal mechanism, dispersal distance, and ability to establish within pre-existing communities amid competition and/or the presence of new enemies (Hampe, 2004). All three pine tree species, *P. taeda*, *P. rigida*, and *P. pungens*, are categorized as pioneer trees who colonize open, low competition areas, where light is plentiful (Burns, 1990), so moving into areas where better competitors exist is unlikely. For example, dispersal was considered in a study of 130 North American trees, in which *P. taeda* was included, where species distributions were forecast under two scenarios, 'no dispersal' and 'full dispersal'. Under the full dispersal scenario, the climate niche of *P. taeda* was predicted to have a 57.2% reduction, but under a no dispersal scenario, the climate niche was predicted to encounter a 79.2% reduction as a response to changes in climate (McKenney *et al.,* 2007).

The conclusions drawn from forecast distributions for *P. taeda* in our study do not align with vast reductions predicted in McKenney *et al.* (2007). Where we avoided annual means in temperature and precipitation and selected seven variables reflecting seasonality and quarterly means, McKenney *et al.* (2007) selected six variables two of which were annual means, none of which included seasonality. In addition, our studies differed in GCM selections. When revisiting their earlier results, McKenney *et al.* (2011) noted differnces in projections with differing GCMs. As a final remark, we used the algorithm of maximum entropy as employed in MaxEnt (Phillips *et al.*, 2006) to project ENMs which differs statistically as compared to the climate envelope method (i.e. ANUCLIM; Busby, 1991) implemented in McKenney *et al*. (2007, 2011).

Aitken *et al.* (2008) stressed that tree species with large distributions and high fecundity are more likely to persist and adapt than species with small, fragmented populations with low fecundity which, without assisted migration, are at risk for extinction. Although future ENM projections for *P. pungens,* based on our methods, predicted negligible changes to habitat suitability under the RCP 2.6 and 8.5 scenarios, *P. pungens* fits the profile of a tree species at risk for extinction. With foresight into the potentially bleak future for *P. pungens*, North Carolina State University's Camcore (International Tree Breeding and Conservation), in collaboration with the U.S. Department of Agriculture, Forest Service, and Southern Regional National Forest System, have collected 390,530 seeds (of 262 mother trees from 38 total populations) for long-term storage, reforestation projects, and research (Jetton *et al.,* 2015). For *P. rigida* and *P. taeda*, we anticipate the high levels of genetic diversity and the large current geographic distribution to help buffer the effects of future climate change and help each species to adapt within suboptimal environmental conditions. But given that future climate models are based off projections of unobserved data and lack the ice core climate data that accompanies historical climate models, general caution must be taken in interpreting projections.

Conclusion

Climate is a primary driver in differentiating niches in this clade of eastern North American pine trees and further elucidates the role of seasonality in niche divergence. Furthermore, our results fit conclusions previously drawn in Ikeda *et al.* (2016); reduced ENMs that acknowledge genetic differences have greater predictive power and are more informative than full ENMs. Based on the strong signals for niche conservatism between *P. pungens* and the southern genetic group of *P. rigida,* we encourage future genetic-based comparative analyses seeking to further elucidate the means for speciation in these two species. Knowing that the distribution of *P. pungens* is nested within the larger distribution of *P. rigida*, that these two species are in sympatry along the Appalachian Mountains, and have similar climatic tolerances influencing their ecological niche, investigations on the role ecological speciation seems warranted.

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APPENDICES

Appendix A-1

Location data collected for *P. taeda*. Reference and year refers to the collector and year cited, respectively, in the herbarium record or author of primary literature article. Source refers to the institution in which the herbarium record was stored.

Species	Longitude	Latitude	Group	General Location	Reference	Year	Source	Extra Info
P. taeda	-84.278	30.458	East	Florida: Leon County	Godfrey	1955	FSU	iDigBio
P. taeda	-84.614	30.580	East	Florida: Gadsden County	Godfrey	1959	FSU	iDigBio
P. taeda	-81.472	29.739	East	Florida: St. Johns	Ward	1960	FSU	iDigBio
P. taeda	-82.843	30.307	East	Florida: Hamilton	Comanor	1961	FSU	iDigBio
P. taeda	-87.380	30.707	East	Florida: Escambia	Ward	1962	FSU	iDigBio
P. taeda	-81.711	28.763	East	Florida: Lake	Ward	1963	FSU	iDigBio
P. taeda	-82.461	29.049	East	Florida: Marion	Brass	1964	ARCH	iDigBio
P. taeda	-81.384	31.475	East	Georgia: McIntosh County	Duncan	1956	VSC	iDigBio
P. taeda	-83.383	33.944	East	Georgia: Clarke County, Lumpkin Hill Campus	Ross	1910	LSU	iDigBio
P. taeda	-84.713	33.029	East	Georgia: Meriwether	Tarrell	1961	KU	iDigBio
P. taeda	-84.522	30.872	East	Georgia: Decatur County	Faircloth	1962	VSC	iDigBio
P. taeda	-84.480	31.737	East	Georgia: Terrell County	Dean	1965	VSC	iDigBio
P. taeda	-84.118	33.665	East	Georgia: DeKalb County, Mt. Arabia.	DE Stone	1973	DUKE	SERNEC
P. taeda	-82.900	32.166	East	Georgia: Columbia County, Elijah Clark State Park	C. Clark	1980	App State	SERNEC
P. taeda	-84.228	31.998	East	Georgia: Sumter County	Parker	1965	VSC	SERNEC
P. taeda	-82.524	33.742	East	Georgia: Lincoln County, Graves Mountain	JH Pyron	1935	DUKE	SERNEC
P. taeda	-89.776	31.171	East	Mississippi: Marion County	Dean	1965	VSC	SERNEC
P. taeda	-88.877	30.407	East	Mississippi: Back Bay	Arzeni	1966	EIU	SERNEC
P. taeda	-88.713	31.974	East	Mississippi: De Soto	Whalen	1974	SDC	SERNEC
P. taeda	-88.797	30.394	East	Gulf Coast Research Laboratory Ocean Springs Mississippi	Ebinger	1971	EIU	SERNEC
P. taeda	-89.399	32.355	East	Mississippi: Wilkinson County, Honochitto	ST Jackson	1993	ASC	SERNEC
P. taeda	-90.759	33.739	East	Mississippi: Bolivar County,Bear Pen Park	B Olivi	2012	DSC	SERNEC
P. taeda	-89.925	33.528	East	Mississippi: Carroll County	JP Key	1987	DSC	SERNEC
P. taeda	-89.698	33.717	East	Mississippi: Grenada County	JR MacDonald	1995	DSC	SERNEC
P. taeda	-88.557	30.428	East	Mississippi: Jackson County	RA Stewart II	1977	DSC	SERNEC
P. taeda	-89.879	32.020	East	Mississippi: Simpson County	RA Stewart II	1986	DSC	SERNEC
P. taeda	-90.829	31.168	East	Mississippi: Amite County	RA Stewart II	1997	DSC	SERNEC
P. taeda	-76.069	39.219	East	Maryland, Kent County	A Harris	1974	EKY	SERNEC
P. taeda	-75.101	39.270	East	Maryland: Worchester County	GF Beaven	1934	DUKE	SERNEC
P. taeda	-75.434	38.158	East	Maryland: Worcester County	Windler	1970	VSC	SERNEC
P. taeda	-85.490	32.608	East	Alabama: Lee County	Carroll	1971	YPM	SERNEC
P. taeda	-75.120	39.926	East	New Jersey: Camden	Kidder	1888	KU	iDigBio
P. taeda	-75.571	38.557	East	Delaware: Sussex County, Laurel	RL Wilbur	1928	DUKE	SERNEC
P. taeda	-85.340	35.679	East	Tennessee: Van Buren County, Fall Creek Fall State Park	C. Fleming	2002	App State	SERNEC
P. taeda	-86.580	35.517	East	Tennessee: Carroll County, Clear Lake Rd	BA Thompson	1970	App State	SERNEC
P. taeda	-81.081	32.287	East	South Carolina: Jasper County, Hardeeville	Bell	1956	KU	iDigBio
P. taeda	-81.901	34.936	East	South Carolina: Spartanburg County	DZ Damrel	2009	CLEMS	SERNEC
P. taeda	-81.833	32.333	East	South Carolina: Aiken County, Silver Bluff Audubon Center & Sancuary	DZ Damrel	2007	CLEMS	SERNEC
P. taeda	-80.909	32.264	East	South Carolina: Beaufort County, Buckwalter Park	D Payne	2004	CLEMS	SERNEC
P. taeda	-82.636	34.066	East	South Carolina: Abbeville, Richard B Russell Dam	JE Fairey	1978	CLEMS	SERNEC
P. taeda	-82.394	34.853	East	South Carolina: Greenville, Pinnacle Mountain	L Zettler	1989	CLEMS	SERNEC
P. taeda	-80.085	32.608	East	South Carolina: Charleston, Kiawah Island	WH Pouch	1978	CLEMS	SERNEC
P. taeda	-82.890	34.908	East	South Carolina: Pickens, 156 Cedar Creek Circle	SR Hill	1992	CLEMS	SERNEC
P. taeda	-82.826	34.612	East	South Carolina: Anderson, Fants Grove game Management Area	SR Hill	1987	CLEMS	SERNEC
P. taeda	-79.425	34.360	East	South Carolina: Dillon County, Welcome Center along I-95	RL Wilbur	2004	DUKE	SERNEC
P. taeda	-80.544	33.168	East	South Carolina: Dorchester County	RL Wilbur	2001	DUKE	SERNEC
P. taeda	-79.290	33.421	East	South Carolina: Georgetown County, Browns Ferry on the Black River	RL Wilbur	2004	DUKE	SERNEC
P. taeda	-81.164	33.836	East	South Carolina: Berkeley County	RL Wilbur	2001	DUKE	SERNEC
P. taeda	-76.325	37.022	East	Virginia: Hampton, Langley Research and Development Park	P Baldwin	1992	WILLI	SERNEC
P. taeda	-78.657	37.432	East	Virginia: Chesterfield, Proctor's Creek VDOT wetland creation site	DA DeBerry	2005	WILLI	SERNEC
P. taeda	-76.803	37.300	East	Virginia: James City, Green Springs National Historic Park	AL Ingram	1997	WILLI	SERNEC
P. taeda	-76.595	37.271	East	Virginia: York County, Colonial Parkway	K Kirkman	1969	WILLI	SERNEC
P. taeda	-77.408	37.197	East	Virginia: Petersburg, Lee Memorial Park	D Ware	1998	WILLI	SERNEC
P. taeda	-78.657	37.432	East	Virginia: Isle of Wight	GM Plunkett	1989	WILLI	SERNEC
P. taeda	-76.479	37.051	East	Virginia: Newport News, The Mariner's Museum	George Mason	1934	WILLI	SERNEC
P. taeda	-77.588	38.198	East	Virginia: Spotsylvania County	T Bradley	1983	GMUF	SERNEC
P. taeda	-78.928	36.766	East	Virginia: Halifax County	E Thomas	1988	DUKE	SERNEC
P. taeda	-78.020	37.115	East	Virginia: Nottoway Co, Camp Pickett	CA Taylor	1943	SDC	iDigBio
P. taeda	-75.362	37.938	East	Virginia: Accomack, Chincoteague Island	Gourley	1967	DEK	iDigBio
P. taeda	-76.740	34.699	East	North Carolina: Carteret County, Atlantic Beach S.	W Fox	1947	KU	iDigBio
P. taeda	-78.566	35.803	East	North Carolina: Wake County	Faircloth	1959	VSC	iDigBio
P. taeda	-79.075	35.910	East	North Carolina: Orange, Cabarro W.	Ahles	1960	KU	iDigBio
P. taeda	-76.687	36.420	East	North Carolina: Gates County	Musselman	1975	VSC	iDigBio
P. taeda	-79.019	35.760	East	North Carolina: Mecklenburg County	Pratt	1964	LSU	iDigBio
P. taeda	-77.882	34.215	East	North Carolina: New Hanover County	Sieren	1975	VSC	iDigBio
P. taeda	-77.948	34.060	East	North Carolina: Brunswick County	SW Leonard	1969	App State	SERNEC
P. taeda	-78.596	34.683	East	North Carolina: Bladen County, Jones Lake State Park	R Power	2011	App State	SERNEC
P. taeda	-76.594	34.661	East	North Carolina: Carteret County, Shackleford Banks	WR Anderson	1962	DUKE	SERNEC
P. taeda	-79.290	36.386	East	North Carolina: Caswell County	JE Mohan	1995	DUKE	SERNEC
P. taeda	-79.178	35.721	East	North Carolina: Chatham County	A Frick	2001	DUKE	SERNEC
P. taeda	-77.056	34.914	East	North Carolina: Craven County, Croatan National Forest	RL Wilbur	1995	DUKE	SERNEC
P. taeda	-78.748	34.954	East	North Carolina: Cumberland County	RL Wilbur	2001	DUKE	SERNEC
P. taeda	-78.943	35.981	East	North Carolina: Durham County, Duke Forest	WJ Kress	1981	DUKE	SERNEC
P. taeda	-78.020	34.884	East	North Carolina: Duplin County	RL Wilbur	1991	DUKE	SERNEC

P. taeda	-77.677	35.902	East	North Carolina: Edgecombe County, Wiggin's Lake	RL Wilbur	1997	DUKE	SERNEC
P. taeda	-78.400	35.969	East	North Carolina: Franklin County, intersection of US 98 and US 401	B Beckage	1995	DUKE	SERNEC
P. taeda	-78.612	36.280	East	North Carolina: Granville County	RL Wilbur	2001	DUKE	SERNEC
P. taeda	-78.793	35.345	East	North Carolina: Harnett County, South Harnett Primary School	RL Wilbur	1990	DUKE	SERNEC
P. taeda	-79.470	35.367	East	North Carolina: Moore County	RL Wilbur	1994	DUKE	SERNEC
P. taeda	-77.149	34.632	East	North Carolina: Onslow County, Bear Island	RL Wilbur	1970	DUKE	SERNEC
P. taeda	-79.148	34.579	East	North Carolina: Robeson County, intersection I-95 and US 301	RL Wilbur	1995	DUKE	SERNEC
P. taeda	-79.830	36.434	East	North Carolina: Rockingham County	J Harrah	1992	DUKE	SERNEC
P. taeda	-78.384	34.920	East	North Carolina: Sampson County	RL Wilbur	1957	DUKE	SERNEC
P. taeda	-79.470	34.845	East	North Carolina: Scotland County, Sandhill Game Land	RL Wilbur	1994	DUKE	SERNEC
P. taeda	-78.430	36.348	East	North Carolina: Vance County, near exit 212 of I-85	RL Wilbur	1992	DUKE	SERNEC
P. taeda	-77.882	35.693	East	North Carolina: Wilson County, South side of Silver Lake	RL Wilbur	1997	DUKE	SERNEC
P. taeda	-91.097	30.569	East	Louisiana: East Baton Rouge Parish	Petersen	1910	LSU	iDigBio
P. taeda	-90.101	30.475	East	Louisiana: St Tammany Parish, Covington	Wurzlow	1914	LSU	iDigBio
P. taeda	-90.375	30.619	East	Louisiana: Tangipahoa Parish	C Brown	1943	LSU	iDigBio
P. taeda	-91.377	30.788	East	Louisiana: West Feliciana County	ST Jackson	1993	ASC	SERNEC
P. taeda	-91.218	30.837	East	Louisiana: Jackson	unknown	unknown	TENN	SERNEC
P. taeda	-84.522	32.689	East	Georgia: Talbot County	JR Diamond	2004	Auburn	SERNEC
P. taeda	-85.396	32.589	East	Alabama: Lee County	CS Walsh	1953	Auburn	SERNEC
P. taeda	-85.808	33.770	East	Alabama: Calhoun County	JM Gregory	1969	Auburn	SERNEC
P. taeda	-86.862	34.424	East	Alabama: Morgan County	TD Atkeson	1969	Auburn	SERNEC
P. taeda	-87.776	33.687	East	Alabama: Fayette County	L Rush	1970	Auburn	SERNEC
P. taeda	-85.630	33.648	East	Alabama: Cleburne	WH Adams	1956	Auburn	SERNEC
P. taeda	-86.012	32.565	East	Alabama: Elmore County	JR Mixner	1971	Auburn	SERNEC
P. taeda	-85.849	33.280	East	Alabama: Clay County	BP Blankinship	1970	Auburn	SERNEC
P. taeda	-86.982	31.502	East	Alabama: Conecuh County	JR Diamond	1985	Auburn	SERNEC
P. taeda	-85.520	33.268	East	Alabama: Randolph County	T Griffin	1983	Auburn	SERNEC
P. taeda	-87.776	31.700	East	Alabama: Clarke County	WK Maddox	1975	Auburn	SERNEC
P. taeda	-86.661	33.304	East	Alabama: Shelby County	AL Webb	1980	Auburn	SERNEC
P. taeda	-86.175	32.208	East	Alabama: Montgomery County	JR Diamond	1989	Auburn	SERNEC
P. taeda	-86.338	31.667	East	Alabama: Crenshaw County	JR Diamond	1996	Auburn	SERNEC
P. taeda	-85.189	31.447	East	Alabama: Henry County	JR Diamond	1992	Auburn	SERNEC
P. taeda	-95.143	31.798	West	Texas: Cherokee County	Joor	1884	LSU	iDigBio
P. taeda	-96.835	29.890	West	Texas: Fayette	Wells	1964	KU	SERNEC
P. taeda	-95.100	31.290	West	Texas, Houston County, Davy Crockett National Forest	Braman	1998	HPC	SERNEC
P. taeda	-94.921	29.726	West	Texas: Chambers County	R Gutierrez	2014	ASU	SERNEC
P. taeda	-92.866	32.400	West	Lousiana: Bienville Parish	Tannahill	1973	LSU	SERNEC
P. taeda	-93.552	31.509	West	Louisiana: Sabine Parish	R Gutierrez	2014	ASU	SERNEC
P. taeda	-91.962	30.984	West	Louisiana: Evangeline Parish, along Bayou Nezpique	JW Thieret	1963	DUKE	SERNEC
P. taeda	-92.224	32.427	West	Louisiana: Ouachita Parish	R & S Thomas	1971	DUKE	SERNEC
P. taeda	-93.815	32.191	West	Louisiana: De Soto Parish	DS Correll	1938	DUKE	SERNEC
P. taeda	-92.818	30.267	West	Louisiana: Jefferson Davis Parish	AW Westling	1968	DUKE	SERNEC
P. taeda	-92.659	31.920	West	Louisiana: Winn	unknown	unknown	TENN	SERNEC
P. taeda	-92.587	31.364	West	Louisiana: Rapides	unknown	unknown	TENN	SERNEC
P. taeda	-96.598	30.022	West	Texas, Shelby	T. Clayton	1961	BYU	SERNEC
P. taeda	-94.655	31.604	West	Texas, Nacogdoches	JA Raines	1978	BYU	SERNEC
P. taeda	-94.315	32.554	West	Texas, Harrison	DS Correll	1956	BYU	SERNEC
P. taeda	-95.646	31.777	West	Texas, Anderson	C Halberg	1973	HPC	SERNEC
P. taeda	-97.352	30.046	West	Texas, Bastrop	A Lievens	1991	LSU	SERNEC
P. taeda	-93.866	30.148	West	Texas, Orange	A Lievens	1989	LSU	SERNEC
P. taeda	-95.310	32.335	West	Texas, Smith County	DL Wilkinson	1971	NY	SERNEC
P. taeda	-94.415	33.460	West	Texas, Bowie County, New Boston	LC Hinckley	1940	NY	SERNEC
P. taeda	-95.510	30.640	West	Texas, Walker County, Sam Houston National Forest	WJ Hess	2001	NY	SERNEC
P. taeda	-95.469	30.298	West	Texas, Montgomery County	MH Nee	2010	NY	SERNEC
P. taeda	-94.330	30.670	West	Texas, Tyler County, Woodville	K Taylor	1984	NY	SERNEC
P. taeda	-95.534	29.753	West	Texas, Harris County, Buffalo Bayou	P Sorensen	2013	DEK	SERNEC
P. taeda	-92.003	34.228	West	Arkansas: Jefferson County, Pine Bluff	Demaree	1943	KU	iDigBio
P. taeda	-92.064	33.613	West	Arkansas: Bradley County, Warren	Demaree	1943	KU	iDigBio
P. taeda	-93.833	33.661	West	Arkansas: Hempstead, Mcnab	Demaree	1959	KU	iDigBio

Appendix A-2

Location data collected for *P. rigida*. Reference and year refers to the collector and year cited, respectively, in the herbarium record or author of primary literature article. Source refers to the institution in which the herbarium record was stored.

Species	Longitude	Latitude	Group	Location details	Reference	Year	Source	Extra Info
P. rigida	-70.790	44.404	North	Maine: Northwest Bethel	A. Wheeler	1938	HUH	Harvard
P. rigida	-68.739	44.342	North	Maine: South Brooksville	RJ Eaton	1961	HUH	Harvard
P. rigida	-70.394	44.061	North	Maine: South Poland	K Furbish	1897	HUH	Harvard
P. rigida	-70.336	43.936	North	Maine: Cumberland County	D. H. Goldman	2006	NYBG	SERNEC
P. rigida	-70.014	43.742	North	Maine: South Harpswell	JM Greenman	1912	HUH	Harvard
P. rigida	-69.445	45.254	North	Maine: Hancock County, Bee Hive Mt. Acadia National Park	S. Wind	1993	EKY	SERNEC
P. rigida	-71.128	44.054	North	New Hampshire: North Conway	FL Steele	1953	HUH	Harvard
P. rigida	-71.970	42.870	North	New Hampshire: Hillsborough County: Peterborough	C.F. Batchelder	1931	HUH	Harvard
P. rigida	-71.012	43.122	North	New Hampshire: Strafford County, Lee	AR Hidgson	1943	HUH	Harvard
P. rigida	-72.236	42.926	North	New Hampshire: Cheshire County	CF Batchelder	1919	HUH	Harvard
P. rigida	-73.261	44.310	North	Vermont: Chittenden County, Charlotte	CG Pringle	1879	HUH	Harvard
P. rigida	-73.088	43.798	North	Vermont: Ruttland County, Brandon	DL Dutton	1924	HUH	Harvard
P. rigida	-72.875	43.450	North	Vermont: East Wallingford	EC Kent	1908	HUH	Harvard
P. rigida	-72.804	43.015	North	Vermont: Windham County	RJ Eaton	1960	HUH	Harvard
P. rigida	-71.138	42.263	North	Massachusetts: Suffolk County, Stony Brook Reservation	Kidder	1922	HUH	Harvard
P. rigida	-70.907	42.705	North	Massachusetts: Essex County	J.R.	1980	HUH	Harvard
P. rigida	-71.156	42.415	North	Massachusetts: Middlesex County, Arlington	BL Robinson	1896	HUH	Harvard
P. rigida	-71.136	42.425	North	Massachusetts: West Medford	CH Morss	1898	HUH	Harvard
P. rigida	-70.321	41.699	North	Massachusetts: Cape Cod	EF Williams	1897	HUH	Harvard
P. rigida	-71.152	42.479	North	Massachusetts: North Woburn	GH Tilton	1902	HUH	Harvard
P. rigida	-71.068	42.302	North	Massachusetts: Dorchester	GG Kennedy	1865	HUH	Harvard
P. rigida	-71.115	42.310	North	Massachusetts: Jamaica Plain	CF Faxon	unknown	HUH	Harvard
P. rigida	-71.163	42.280	North	Massachusetts: West Roxbury	NT Kidder	1886	HUH	Harvard
P. rigida	-71.121	42.332	North	Massachusetts: Norfolk County, Brookline	J.R.	1980	HUH	Harvard
P. rigida	-70.753	41.698	North	Massachusetts: Plymouth County, Marion	SNF Sanford	1914	HUH	Harvard
P. rigida	-70.934	41.636	North	Massachusetts: Bristol County, New Bedford	EW Hervey	1902	HUH	Harvard
P. rigida	-70.300	41.700	North	Massachusetts: Barnstable Town	ML Fernald	1928	HUH	Harvard
P. rigida	-69.991	41.751	North	Massachusetts: South Orleans	J Murdoch, Jr.	1913	HUH	Harvard
P. rigida	-70.185	41.667	North	Massachusetts: South Yarmouth	LL Howe	1921	HUH	Harvard
P. rigida	-70.745	41.343	North	Massachusetts: Dukes County, Chilmark	S Harris	1898	HUH	Harvard
P. rigida	-72.248	42.322	North	Massachusetts: Greenwich	G. Turesson	1938	HUH	Harvard
P. rigida	-71.857	42.410	North	Massachusetts: Worcester County	FW Hunnewell	1914	HUH	Harvard
P. rigida	-72.535	42.536	North	Massachusetts: Franklin County, Montague	LA Wheeler	1912	HUH	Harvard
P. rigida	-72.608	42.477	North	Massachusetts: South Deerfield	EB Harger	1913	HUH	Harvard
P. rigida	-72.544	42.003	North	Massachusetts: Enfield	AS Goodale	1931	HUH	Harvard
P. rigida	-72.615	42.070	North	Massachusetts: Agawam Town	CH Knowlton	1913	HUH	Harvard
P. rigida	-71.715	41.658	North	Rhode Island: Kent	E.J. Palmer	1938	HUH	Harvard
P. rigida	-71.525	41.448	North	Rhode Island: South Kingston	JP Bill, RJ Eaton	1927	HUH	Harvard
P. rigida	-71.716	41.916	North	Rhode Island: Burrillville, near Wallum Lake	E.J. Palmer	1938	HUH	Harvard
P. rigida	-72.723	41.697	North	Connecticut: Hartford County, Newington	C. Wright	1982	HUH	Harvard
P. rigida	-73.117	41.434	North	Connecticut: New Haven County, Oxford	EB Harger	1891	HUH	Harvard
P. rigida	-72.094	41.323	North	Connecticut: New London County	unknown	1980	HUH	Harvard
P. rigida	-74.236	41.729	North	New York: Ulster County, Minnewaska State Park Preserve	Hess	1999	GBIF	GBIF
P. rigida	-73.458	40.746	North	New York, Suffolk County, Farmingdale	Silba	2000	GBIF	GBIF
P. rigida	-77.524	43.218	North	New York: Monroe County, Webster	Goldman	2004	GBIF	GBIF
P. rigida	-76.485	42.407	North	New York: Tompkins County, South Hill, Ithaca	EF Reimschiissel	1952	BRY: V	SERNEC
P. rigida	-74.687	39.856	Mid	New Jersey: Burlington County	PF Maycock	1963	EKY	SERNEC
P. rigida	-74.516	39.950	Mid	New Jersey: Wharton State Park, NJ Pine Barrens	Weiner	1984	publication	lit. cited
P. rigida	-74.876	41.036	Mid	New Jersey: Sussex County, Stillwater	K Barringer	2001	BRY: V	SERNEC
P. rigida	-74.215	39.904	Mid	New Jersey: Ocean County	Atha	2012	GBIF	GBIF
P. rigida	-75.143	40.982	Mid	Delaware Water Gap	F.E. Lloyd	1899	NYBG	SERNEC
P. rigida	-78.945	40.350	Mid	Pennsylvania: Cambria County, Larel Hill	S.G. Shetler	1955	GBIF	GBIF
P. rigida	-79.290	39.568	Mid	Maryland: Garrett County	R Downs	1969	NCU	SERNEC
P. rigida	-77.464	39.653	Mid	Maryland: Frederick, Catoctin Mountain Park	C Hickey II	1972	NCU	SERNEC
P. rigida	-76.585	39.423	Mid	Maryland: Baltimore, Hampton woods sector off Seminary Ave.	D Redman	1973	NCU	SERNEC
P. rigida	-78.612	39.626	Mid	Maryland: Allegany County	R Downs	1968	NCU	SERNEC
P. rigida	-77.720	39.642	Mid	Maryland: Washington County	R Downs	1969	NCU	SERNEC
P. rigida	-80.232	37.447	Mid	Virginia: Craig County, northeast of New Castle	F James	1967	NCU	SERNEC
P. rigida	-79.515	37.806	Mid	Virginia: Rockbridge	R Wyatt	1974	DUKE	SERNEC
P. rigida	-79.470	37.254	Mid	Virginia: Bedford County	R Freer	1947	NCU	SERNEC
P. rigida	-79.785	37.577	Mid	Virginia: Botetourt County	R Freer	1947	NCU	SERNEC
P. rigida	-78.970	37.566	Mid	Virginia: Amherst, Rocky Row Mountain, along US 501	R Freer	1947	NCU	SERNEC
P. rigida	-78.248	37.853	Mid	Virginia: Fluvanna County	F James	1966	NCU	SERNEC
P. rigida	-80.053	37.853	Mid	Virginia: Alleghany County	F James	1967	NCU	SERNEC
P. rigida	-79.650	38.112	Mid	Virginia: Bath County	F James	1967	NCU	SERNEC
P. rigida	-77.706	38.866	Mid	Virginia: Fauquier County, Bull Run Mountains	H.A. Allard	1940	HUH	SERNEC
P. rigida	-75.708	40.898	Mid	Penn: Carbon County, Pocono mountains	KS Erdman	1969	BYU	SERNEC
P. rigida	-76.687	40.867	Mid	Penn: Northumberland County	J Montgomery	1959	DBG:KHD	SERNEC
P. rigida	-77.147	41.111	Mid	Penn: Lycoming County, North White Deer Ridge	EC Earle	1940	NY	SERNEC
P. rigida	-75.605	39.961	Mid	Penn: Westchester	Darlington	unknown	NY	SERNEC
P. rigida	-77.558	39.844	Mid	Penn: Mont Alto	DA Kribs	1935	NY	SERNEC
P. rigida	-77.056	40.751	Mid	Penn: Snyder County	HN Moldenke	1925	NY	SERNEC
P. rigida	-76.925	40.368	Mid	Penn: Dauphin, Stokes State Forest	P Smouse	1967	NCSC	SERNEC
P. rigida	-75.897	41.210	Mid	Penn: Luzerne,	CA Taylor	1934	SDSU: SDC	SERNEC

P. rigida	-75.388	39.908	Mid	Penn: Delaware County	Bayard Long	1921	NC State	SERNEC
P. rigida	-78.566	39.335	Mid	WV: Hampshire County	Robert Downs	1969	UNC	SERNEC
P. rigida	-79.290	38.745	Mid	WV: Pendleton	John Thieret	1993	KNK	SERNEC
P. rigida	-80.455	38.598	Mid	WV: Tucker County, Red Creek Sphagnum Bog	Linda Anderson	1976	NC state	SERNEC
P. rigida	-81.318	39.472	Mid	Ohio: Washington County, Lawrence Twp	EM Herrick	1956	Ohio State	Ohio State
P. rigida	-81.757	40.199	Mid	Ohio: Coshocton County, Linton Twp.	LA Robertson	1931	Ohio State	Ohio State
P. rigida	-82.182	39.462	Mid	Ohio: Athens County, Buchtel	L Stephenson	1925	Ohio State	Ohio State
P. rigida	-82.824	39.169	Mid	Ohio: Pike County, Chimney Rocks	GS Crowl	1938	Ohio State	Ohio State
P. rigida	-81.037	39.848	Mid	Ohio: Monroe County, Beallsville	LA Robertson	1931	Ohio State	Ohio State
P. rigida	-82.280	39.044	Mid	Ohio: Meigs County, Salen Twp.	CH Jones	1935	Ohio State	Ohio State
P. rigida	-80.788	40.571	Mid	Ohio: Jefferson County, Brush Creek	FS Sutton	1927	Ohio State	Ohio State
P. rigida	-82.756	39.075	Mid	Ohio: Jackson County, Liberty Twp.	F Bartley	1935	Ohio State	Ohio State
P. rigida	-83.532	39.063	Mid	Ohio: Highland County, Belfast	KM Roads	1932	Ohio State	Ohio State
P. rigida	-83.094	38.698	Mid	Ohio: Scioto County, Friendship	D Demaree	1934	Ohio State	Ohio State
P. rigida	-82.907	40.417	Mid	Ohio: Ross County, Feightner	GS Crowl	1937	Ohio State	Ohio State
P. rigida	-82.478	39.246	Mid	Ohio: Vinton County, McArthur	GH Jones	1937	Ohio State	Ohio State
P. rigida	-81.318	39.636	Mid	Ohio: Noble County, Elk Twp.	EM Herrick	1956	Ohio State	Ohio State
P. rigida	-82.212	39.605	Mid	Ohio: Perry County, Shawnee	EM Herrick	1956	Ohio State	Ohio State
P. rigida	-72.798	40.873	Mid	New York: Long Island Expressway	D.E. Atha	2011	GBIF	GBIF
P. rigida	-73.880	40.865	Mid	New York: grounds of NY Botanical Gardens	D.E. Atha	2011	GBIF	GBIF
P. rigida	-79.913	37.133	Mid	Virginia: Franklin, near Boone Mill	H Totten	1934	NCU	SERNEC
P. rigida	-80.677	37.313	Mid	Virginia: Giles	JM Fogg, Jr	1940	DUKE	SERNEC
P. rigida	-79.470	36.744	Mid	Virginia: Pittsylvania	DB Zobel	1966	DUKE	SERNEC
P. rigida	-82.707	34.883	South	South Carolina: Pickens	L Rodgers	1942	DUKE	SERNEC
P. rigida	-82.785	35.056	South	South Carolina: Greenville, near Caesars Head	H Totten	1963	NCU	SERNEC
P. rigida	-83.379	34.903	South	Georgia: Rabun	WH Duncan	1941	DUKE	SERNEC
P. rigida	-83.162	33.795	South	Georgia: Stephens	DB Zobel	1965	DUKE	SERNEC
P. rigida	-83.683	33.305	South	Georgia: Monticello	P Gorton	1977	CMC	SERNEC
P. rigida	-83.826	37.838	South	Kentucky: Powell County	TJ Weckman	2005	EKY	SERNEC
P. rigida	-82.959	37.145	South	Kentucky: Letcher, Lilley Cornett Woods Appalachian Ecological Research	J Sole	1978	NCU	SERNEC
P. rigida	-83.635	36.741	South	Kentucky: Bell County	E. Browne Jr.	1996	EKY	SERNEC
P. rigida	-83.485	37.090	South	Kentucky: Leslie County, left fork Elisha Creek	RH Hannan	1979	EKY	SERNEC
P. rigida	-83.464	37.755	South	Kentucky: Wolfe County	P Higgins	1969	NCU	SERNEC
P. rigida	-84.296	37.569	South	Kentucky: Madison County, Indian Fort	J Rozeman	1992	EKY	SERNEC
P. rigida	-83.890	36.926	South	Kentucky: Knox County	J Rozeman	1993	EKY	SERNEC
P. rigida	-84.075	37.025	South	Kentucky: Laurel County, Lily Surface-Mine Experimental Area	RL Thompson	1981	EKY	SERNEC
P. rigida	-83.464	38.177	South	Kentucky: Rowan County	RH Hannan	1979	EKY	SERNEC
P. rigida	-83.720	37.599	South	Kentucky: Lee County	TJ Weckman	1993	EKY	SERNEC
P. rigida	-84.017	37.402	South	Kentucky: Jackson County	TJ Weckman	1996	EKY	SERNEC
P. rigida	-83.293	37.915	South	Kentucky: Morgan County	TJ Weckman	1996	EKY	SERNEC
P. rigida	-84.223	37.320	South	Kentucky: Rockcastle County, Piney Branch Rd.	TJ Weckman	2006	EKY	SERNEC
P. rigida	-82.778	37.546	South	Kentucky: Floyd County	TJ Weckman	2003	EKY	SERNEC
P. rigida	-83.115	38.148	South	Kentucky: Elliott County, Big Caney Creek at junction with Little Sandy River	TJ Weckman	2006	EKY	SERNEC
P. rigida	-82.778	38.053	South	Kentucky: Lawrence County	TJ Weckman	2006	EKY	SERNEC
P. rigida	-83.490	35.612	South	Tennessee: Great Smoky Mountains National Park	H Robinovitz	1982	EMC	SERNEC
P. rigida	-82.993	34.749	South	South Carolina: Oconee County	S.R. Hill	1989	GBIF	GBIF
P. rigida	-80.610	34.260	South	South Carolina: Kershaw County: Camden	McKelvey	1921	HUH	SERNEC
P. rigida	-82.475	35.593	South	North Carolina: Buncombe County	R.C. Dunton	1967	NCU	SERNEC
P. rigida	-82.171	35.269	South	North Carolina: Polk County	RC Clark	1995	EKY	SERNEC
P. rigida	-81.413	35.659	South	North Carolina: Catawba County, Baker's Mountain County Park	T Holdsclaw	2010	NCU	SERNEC
P. rigida	-81.580	36.423	South	North Carolina: Ashe County, Three Top Mountain Game Land Preserve	A Jenkins	2011	NCU	SERNEC
P. rigida	-80.188	36.120	South	North Carolina: Forsyth County	S Leonard	1966	NCU	SERNEC
P. rigida	-82.637	35.699	South	North Carolina, Alexander	C Keever	1940	DUKE	SERNEC
P. rigida	-83.181	35.037	South	North Carolina: Macon County, Fodderstack Mountain	L Schram	1974	NCU	SERNEC
P. rigida	-83.720	35.096	South	North Carolina: Clay County	L Schram	1974	NCU	SERNEC
P. rigida	-81.892	36.028	South	North Carolina: Avery, Pineola	AE Radford	1950	NCU	SERNEC
P. rigida	-81.735	35.762	South	North Carolina: Burke County	L Raubeson	1982	NCU	SERNEC
P. rigida	-83.053	35.424	South	North Carolina: Haywood, Wesner Bald	G Ramseur	1956	NCU	SERNEC
P. rigida	-82.432	35.373	South	North Carolina: Henderson County	D Pittillo	1956	NCU	SERNEC
P. rigida	-80.470	36.387	South	North Carolina: Surry, Pilot Mountain	H Totten	1935	NCU	SERNEC
P. rigida	-83.464	35.433	South	North Carolina: Swain County	G Ramseur	1956	NCU	SERNEC
P. rigida	-79.056	35.913	South	North Carolina: Orange, Arboretum at UNC, ChapelHill	N Reasoner	1917	NCU	SERNEC
P. rigida	-80.232	36.424	South	North Carolina: Stokes County	T Register	1957	NCU	SERNEC
P. rigida	-82.829	35.892	South	North Carolina: Madison, Hot Springs Valley, CR 1303	D Sather	1981	NCU	SERNEC
P. rigida	-81.252	36.203	South	North Carolina: Wilkes County	L Stewart	1936	NCU	SERNEC
P. rigida	-84.035	35.088	South	North Carolina: Cherokee, east of Murphy	H Totten	1962	NCU	SERNEC
P. rigida	-83.203	35.146	South	North Carolina: Jackson, Black Rock Mountain	S Wiser	1990	NCU	SERNEC
P. rigida	-81.170	36.430	South	North Carolina: Alleghany County, Whitehead Township	D Poindexter	2009	NCU	SERNEC
P. rigida	-79.830	36.090	South	North Carolina: Guilford County	L Melvin	1955	NCU	SERNEC
P. rigida	-83.805	35.363	South	North Carolina: Graham County	D Pittillo	1968	NCU	SERNEC
P. rigida	-80.721	36.678	South	Virginia: Carroll	W Cook	1998	DUKE	SERNEC
P. rigida	-80.321	36.689	South	Virginia: Patrick	DB Zobel	1965	DUKE	SERNEC

Appendix A-3

Location data collected for *P. pungens*. Reference and year refers to the collector and year cited, respectively, in the herbarium record or author of primary literature article. Source refers to the institution in which the herbarium record was stored.

Species	Longitude	Latitude	General Location	Reference	Year	Source	Extra info
P. pungens	-75.164	39.952	Penn: Philidephia	W.S. Hall	1892	SDC	IDigBio-
P. pungens	-77.034	40.847	Penn: Snyder County	D. Wade	1940	DEK	IDigBio-
P. pungens	**-77.180**	**40.840**	Penn: Union, Bald Eagle	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.600**	**40.180**	Penn: Cumberland, Blue Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-78.430**	**39.770**	Penn: Bedford, Buchanan	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-76.350**	**39.850**	Penn: Lancaster, Kelly's Run Susquehanna	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.530**	**39.850**	Penn: Franklin, Michaux	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.950**	**40.660**	Penn: Huntingdon, Stone Valley Forest	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.580**	**40.280**	Penn: Perry, Tuscarora	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-74.980**	**40.420**	New Jersey: Hunterson, Abraitys Pine Stand	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	-82.783	35.300	North Carolina: Looking Glass Rock, Great Smokey Mountains	Barden, 1986 paper	1986	literature	
P. pungens	-83.003	35.107	North Carolina: Transylvania, Sapphire near	W.B. Fox	1947	KU	SERNEC
P. pungens	-81.883	35.891	North Carolina: Burke, Table Rock Mountain	F.A. Sargent	1950	KU	SERNEC
P. pungens	-81.388	36.285	North Carolina: Ashe County, At Calloway Gap	Thomas	1969	LSU	SERNEC
P. pungens	**-82.760**	**35.430**	North Carolina: Buncombe, Mount Pisgah	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-83.700**	**35.290**	North Carolina: Graham, Nolton Ridge	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-82.020**	**35.760**	North Carolina: Haywood, Graveyard Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-81.110**	**35.970**	North Carolina: Alexander, Rocky Face	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-82.250**	**35.430**	North Carolina: Rutherford, Chimney Rock	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-80.260**	**36.400**	North Carolina: Stokes, Hanging Rock	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-80.470**	**36.340**	North Carolina: Surry, Pilot Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-81.040**	**36.390**	North Carolina: Wilkes/Alleghany, Stone Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-81.087**	**35.570**	**North Carolina: Catawba County, Caldwell Township**	T Holdsclaw	2010	NCU	SERNEC
P. pungens	-79.019	35.760	North Carolina: Forsyth County	SW Leonard	1966	NCU	SERNEC
P. pungens	-79.789	35.857	North Carolina: Randolph County, 1.2 miles N. of New Salem	L Melvin	1955	NCU	SERNEC
P. pungens	-81.813	36.145	North Carolina: Watauga County, Peak Mountain, ridge top	J Rohrer	1978	NCU	SERNEC
P. pungens	-80.854	35.263	North Carolina: Mecklenburg County	M Mulkey	1947	NCU	SERNEC
P. pungens	-82.238	35.208	North Carolina: Polk County	D Peattie	1921	NCU	SERNEC
P. pungens	-82.341	35.394	North Carolina: Henderson County, East of Edneyville	D Pittillo	1968	NCU	SERNEC
P. pungens	-82.488	35.807	North Carolina: Madison County, Holcombe Branch Olivine Deposity	AE Radford	1946	NCU	SERNEC
P. pungens	-79.049	35.914	North Carolina: Orange County, UNC, Arboretum	N Reasoner	1917	NCU	SERNEC
P. pungens	-83.611	35.075	North Carolina: Clay County, Buck Creek near US 64	AE Radford	1956	NCU	SERNEC
P. pungens	-83.243	35.046	North Carolina: Macon County, On Kettle Rock Mt	S Radford	1940	NCU	SERNEC
P. pungens	-80.577	35.945	North Carolina: Davie County, 1.5 miles S of Cana	H Totten	1932	NCU	SERNEC
P. pungens	-83.167	35.069	North Carolina: Jackson County, Wildcat Cliff	H Totten	1933	NCU	SERNEC
P. pungens	-84.059	35.113	North Carolina: Cherokee County	E Lunsford	1995	NCU	SERNEC
P. pungens	-83.684	35.804	Tennessee: Sevier County, Bluff mountain	B Thompson	1968	KU	SERNEC
P. pungens	**-83.480**	**35.680**	Tennesee: Swain, Cherokee Orchard	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-83.830**	**35.560**	Tennessee: Blount , Cades Cove	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-82.100**	**36.330**	Tennessee: Johnson, Iron Mountain TN	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-82.450**	**36.100**	Tennessee: Unicoi, Cliff Ridge	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-82.960**	**35.970**	Tennessee: Cocke, Meadow Creek	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-82.770**	**36.030**	Tennessee: Greene, Greene Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	-84.228	35.472	Tennessee: Monroe County	D.Zobel	1965	Duke	SERNEC
P. pungens	-82.345	36.493	Tennessee: Sullivan County	unknown	1966	Duke	SERNEC
P. pungens	-86.459	35.470	Tennessee: Bedford County	unknown	not recorded	MTSU	SERNEC
P. pungens	-86.053	35.458	Tennessee: Coffee County	unknown	not recorded	MTSU	SERNEC
P. pungens	-86.053	35.195	Tennessee: Franklin County	unknown	not recorded	MTSU	SERNEC
P. pungens	-84.228	36.081	Tennessee: Anderson County	unknown	not recorded	MTSU	SERNEC
P. pungens	-84.982	35.593	Tennessee: Rhea County	S Edwards	not recorded	MTSU	SERNEC
P. pungens	-81.560	37.125	Virginia: Tazwell County	F James	1968	NCU	SERNEC

P. pungens	-80.677	37.058	Virginia: Pulaski County	F James	1967	NCU	SERNEC
P. pungens	-80.232	37.447	Virginia: Craig County	AM Harvill	1966	NCU	SERNEC
P. pungens	-79.110	37.559	Virginia: Amherst County	R Freer	1947	NCU	SERNEC
P. pungens	-81.208	36.672	Virginia: Grayson County	Faircloth	1982	VSC	SERNEC
P. pungens	-78.364	38.611	Virginia. Stony Man Mountain	E.S. Steele	1901	VSC	SERNEC
P. pungens	-77.171	38.867	Virginia: Fairfax Co. Sleepy Hollow	F.R. Fosberg	1945	VSC	SERNEC
P. pungens	-79.470	37.254	Virginia: Bedford County	A.H. Curtiss	not recorded	KU	SERNEC
P. pungens	**-79.560**	**37.000**	Virginia: Pittsylvania, Smith Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-81.340**	**36.760**	Virginia: Smyth, Snake Den Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-78.950**	**37.930**	Virginia: Augusta, Ravens Roost	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-79.740**	**37.440**	Virginia: Botetourt, Iron Mine Hollow	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-81.180**	**37.010**	Virginia: Wythe, Little Walker Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-78.310**	**38.740**	Virginia: Madison, Shenandoah	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.470**	**38.550**	Virginia: Stafford, Quantico	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-78.770**	**38.390**	Virginia: Rockingham, Massanutten Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.720**	**38.850**	Virginia: Fauquier, Bull Run	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-78.530**	**38.790**	Virginia: Shenandoah, Edinburg Gap	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-79.220**	**38.480**	Virginia: Rockingham, Briery Branch	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-80.560**	**37.240**	Virginia: Montgomery, Brush Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-78.839**	**38.032**	Virginia: Nelson County	RS Freer	1947	NCU	SERNEC
P. pungens	-77.654	39.077	Virginia: Loudoun County	F James	1965	NCU	SERNEC
P. pungens	-81.120	37.092	Virginia: Bland County	F James	1967	NCU	SERNEC
P. pungens	-78.657	37.432	Virginia: Buckingham County (across from Wingina)	C Stevens	1967	NCU	SERNEC
P. pungens	-79.955	37.117	Virginia: Franklin County, near Boone Mill	H Totten	1934	NCU	SERNEC
P. pungens	-79.450	37.634	Virginia: Rockbridge County, Blue Ridge	H Totten	1938	NCU	SERNEC
P. pungens	-80.538	37.355	Virginia: Giles County, near White Pine Lodge, Mountain Lake	H Totten	1936	NCU	SERNEC
P. pungens	-84.480	34.251	Georgia: Cherokee County	Joyner	1971	VSC	SERNEC
P. pungens	-83.720	34.657	Georgia: White County,	Lane	1966	VSC	SERNEC
P. pungens	-83.385	34.918	Georgia: Rabun County, Mountain City (rocky cliffs)	J.H. Miller	1923	LSU	IDigBio-
P. pungens	**-84.120**	**34.630**	Georgia: Lumpkin, Camp Merrill	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-83.760**	**34.690**	Georgia: Habersham, Smithgall Woods	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-83.390**	**34.740**	Georgia: Rabun, Tallulah Gorge	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	-84.192	34.639	Georgia: Fannin County, Springer Mountain	T Govus	2014	NCU	SERNEC
P. pungens	-83.162	33.795	Georgia: Stephens	D.Zobel	1966	Duke	SERNEC
P. pungens	-83.720	34.921	Georgia: Towns	D.Zobel	1965	Duke	SERNEC
P. pungens	**-82.710**	**35.050**	South Carolina: Pickens, Table Rock Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-82.390**	**34.940**	South Carolina: Greenville, Paris Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-83.300**	**34.700**	South Carolina: Oconee, Pine Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.390**	**39.100**	Maryland: Frederick, Sugarloaf Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-78.265**	**39.660**	Maryland: Washington, Tonoloway Ridge	R Downs	1969	NCU	SERNEC
P. pungens	**-78.650**	**39.720**	Maryland: Allegany, Rocky Gap	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-77.460**	**39.650**	Maryland: Frederick, Catoctin Mountain	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	**-79.310**	**38.850**	West Virginia: Pendelton, Smoke Hole	Lawdanski, Tharp	2010-2013	NC State	Camcore
P. pungens	-80.268	37.662	West Virginia: Greenbrier County, Slaty Mountain	unknown	1929	NCU	SERNEC
P. pungens	-78.293	39.620	West Virginia: Morgan County	R Downs	1968	NCU	SERNEC
P. pungens	**-78.929**	**39.042**	West Virginia: Hardy County	M. Brooks	1939	Duke	SERNEC
P. pungens	**-80.009**	**38.310**	West Virginia: Pocahontas County	D. Zobel	1965	Duke	SERNEC
P. pungens	**-80.009**	**38.809**	West Virginia: Randolph County	D. Zobel	1965	Duke	SERNEC
P. pungens	**-79.085**	**38.868**	West Virginia: Grant County, North Fork Mountain	P. Harmon	1986	KNK	SERNEC
Bold coordinates			were those provided by literature or the herbarium record				

Appendix B-1

Bioclimatic variables included in correlation tests.

Code	Variable
Bio1	Annual Mean Temperature
Bio2	Mean Diurnal Range (Mean of monthly (max temp – min temp))
Bio3	Isothermality (BIO2/BIO7) (* 100)
Bio4	Temperature Seasonality (standard deviation *100)
Bio5	Max Temperature of Warmest Month
Bio6	Min Temperature of Coldest Month
Bio7	Temperature Annual Range (BIO5-BIO6)
Bio8	Mean Temperature of Wettest Quarter
Bio9	Mean Temperature of Driest Quarter
Bio10	Mean Temperature of Warmest Quarter
Bio11	Mean Temperature of Coldest Quarter
Bio12	Annual Precipitation
Bio13	Precipitation of Wettest Month
Bio14	Precipitation of Driest Month
Bio15	Precipitation Seasonality (Coefficient of Variation)
Bio16	Precipitation of Wettest Quarter
Bio17	Precipitation of Driest Quarter
Bio18	Precipitation of Warmest Quarter
Bio19	Precipitation of Coldest Quarter
Alt	Altitude

Reference: WORLDCLIM.org

Appendix B-2. Bioclimatic variable correlations to *Pinus taeda* location data.

	Long	Lat	Alt	Bio1	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9
Long	1.000	0.744	-0.101	-0.662	-0.774	-0.576	-0.347	-0.165	-0.017	-0.001	-0.089	-0.280	0.339	-0.422	-0.107	-0.276	0.375	-0.836	-0.541	0.215	0.320	-0.723
Lat	0.744	1.000	0.118	-0.964	-0.906	-0.956	-0.510	-0.572	0.206	-0.485	-0.547	-0.120	-0.273	-0.396	-0.063	-0.671	0.885	-0.782	-0.917	0.715	0.119	-0.608
Alt	-0.101	0.118	1.000	-0.325	-0.333	-0.321	0.054	-0.079	0.199	-0.271	-0.143	0.171	-0.395	0.240	0.476	0.110	0.265	-0.095	-0.390	0.436	-0.567	0.158
Bio1	-0.662	-0.964	-0.325	1.000	0.954	0.989	0.397	0.536	-0.315	0.573	0.530	-0.012	0.344	0.236	-0.081	0.588	-0.900	0.779	0.972	-0.786	0.055	0.527
Bio10	-0.774	-0.906	-0.333	0.954	1.000	0.901	0.298	0.386	-0.318	0.454	0.363	-0.025	0.120	0.207	-0.083	0.436	-0.730	0.885	0.888	-0.622	0.027	0.583
Bio11	-0.576	-0.956	-0.321	0.989	0.901	1.000	0.432	0.592	-0.301	0.612	0.597	-0.004	0.447	0.241	-0.088	0.637	-0.954	0.698	0.985	-0.847	0.071	0.482
Bio12	-0.347	-0.510	0.054	0.397	0.298	0.432	1.000	0.777	0.489	0.085	0.787	0.751	0.474	0.891	0.103	0.454	-0.468	0.135	0.403	-0.430	-0.452	0.498
Bio13	-0.165	-0.572	-0.079	0.536	0.386	0.592	0.777	1.000	0.051	0.635	0.965	0.273	0.711	0.524	0.015	0.540	-0.663	0.154	0.562	-0.619	-0.185	0.403
Bio14	-0.017	0.206	0.199	-0.315	-0.318	-0.301	0.489	0.051	1.000	-0.638	0.055	0.855	-0.021	0.524	0.020	-0.150	0.263	-0.320	-0.284	0.178	-0.377	-0.003
Bio15	-0.001	-0.485	-0.271	0.573	0.454	0.612	0.085	0.635	-0.638	1.000	0.636	-0.526	0.567	-0.181	-0.092	0.433	-0.655	0.270	0.594	-0.594	0.272	0.148
Bio16	-0.089	-0.547	-0.143	0.530	0.363	0.597	0.787	0.965	0.055	0.636	1.000	0.265	0.795	0.507	-0.011	0.552	-0.686	0.105	0.572	-0.658	-0.119	0.347
Bio17	-0.280	-0.120	0.171	-0.012	-0.025	-0.004	0.751	0.273	0.855	-0.526	0.265	1.000	0.078	0.767	0.050	0.054	-0.001	-0.069	-0.005	-0.032	-0.478	0.261
Bio18	0.339	-0.273	-0.395	0.344	0.120	0.447	0.474	0.711	-0.021	0.567	0.795	0.078	1.000	0.105	-0.202	0.394	-0.617	-0.206	0.461	-0.692	0.321	-0.156
Bio19	-0.422	-0.396	0.240	0.236	0.207	0.241	0.891	0.524	0.524	-0.181	0.507	0.767	0.105	1.000	0.288	0.389	-0.231	0.178	0.194	-0.145	-0.710	0.597
Bio2	-0.107	-0.063	0.476	-0.081	-0.083	-0.088	0.103	0.015	0.020	-0.092	-0.011	0.050	-0.202	0.288	1.000	0.631	0.063	0.286	-0.250	0.472	-0.416	0.203
Bio3	-0.276	-0.671	0.110	0.588	0.436	0.637	0.454	0.540	-0.150	0.433	0.552	0.054	0.394	0.389	0.631	1.000	-0.714	0.491	0.517	-0.375	-0.224	0.375
Bio4	0.375	0.885	0.265	-0.900	-0.730	-0.954	-0.468	-0.663	0.263	-0.655	-0.686	-0.001	-0.617	-0.231	0.063	-0.714	1.000	-0.497	-0.936	0.897	-0.092	-0.358
Bio5	-0.836	-0.782	-0.095	0.779	0.885	0.698	0.135	0.154	-0.320	0.270	0.105	-0.069	-0.206	0.178	0.286	0.491	-0.497	1.000	0.631	-0.237	-0.109	0.604
Bio6	-0.541	-0.917	-0.390	0.972	0.888	0.985	0.403	0.562	-0.284	0.594	0.572	-0.005	0.461	0.194	-0.250	0.517	-0.936	0.631	1.000	-0.903	0.129	0.434
Bio7	0.215	0.715	0.436	-0.786	-0.622	-0.847	-0.430	-0.619	0.178	-0.594	-0.658	-0.032	-0.692	-0.145	0.472	-0.375	0.897	-0.237	-0.903	1.000	-0.222	-0.209
Bio8	0.320	0.119	-0.567	0.055	0.027	0.071	-0.452	-0.185	-0.377	0.272	-0.119	-0.478	0.321	-0.710	-0.416	-0.224	-0.092	-0.109	0.129	-0.222	1.000	-0.518
Bio9	-0.723	-0.608	0.158	0.527	0.583	0.482	0.498	0.403	-0.003	0.148	0.347	0.261	-0.156	0.597	0.203	0.375	-0.358	0.604	0.434	-0.209	-0.518	1.000

Appendix B-3. Bioclimatic variable correlations to *Pinus rigida* location data.

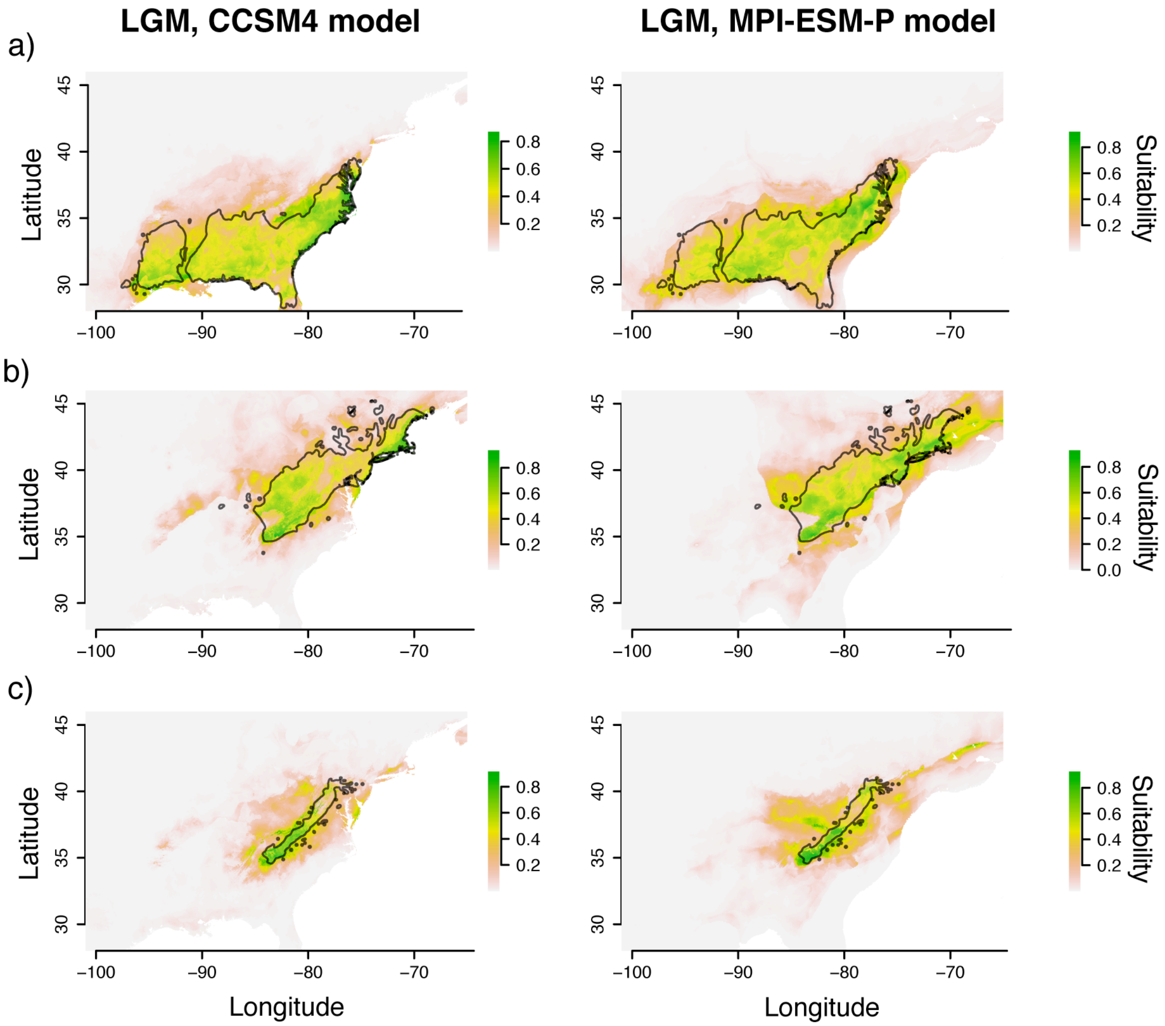
	Long	Lat	Alt	Bio1	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9
Long	1.000	0.860	-0.561	-0.647	-0.465	-0.661	-0.304	-0.400	-0.148	-0.357	-0.400	-0.206	-0.617	-0.143	-0.672	-0.840	0.627	-0.452	-0.570	0.355	-0.573	0.017
Lat	0.860	1.000	-0.560	-0.813	-0.554	-0.888	-0.493	-0.526	-0.404	-0.031	-0.536	-0.427	-0.663	-0.404	-0.543	-0.900	0.898	-0.450	-0.820	0.664	-0.412	-0.195
Alt	-0.561	-0.560	1.000	-0.013	-0.339	0.159	0.653	0.622	0.574	-0.111	0.651	0.575	0.782	0.440	0.274	0.531	-0.565	-0.372	0.110	-0.418	0.110	-0.119
Bio1	-0.647	-0.813	-0.013	1.000	0.920	0.969	0.124	0.181	0.082	0.103	0.172	0.106	0.241	0.157	0.421	0.690	-0.688	0.807	0.937	-0.534	0.434	0.314
Bio10	-0.465	-0.554	-0.339	0.920	1.000	0.800	-0.165	-0.099	-0.182	0.178	-0.118	-0.156	-0.034	-0.097	0.382	0.475	-0.352	0.947	0.774	-0.229	0.469	0.216
Bio11	-0.661	-0.888	0.159	0.969	0.800	1.000	0.290	0.327	0.246	0.013	0.326	0.264	0.361	0.314	0.358	0.732	-0.843	0.647	0.978	-0.707	0.346	0.380
Bio12	-0.304	-0.493	0.653	0.124	-0.165	0.290	1.000	0.952	0.951	-0.425	0.969	0.976	0.863	0.944	0.077	0.402	-0.605	-0.281	0.255	-0.527	-0.318	0.386
Bio13	-0.400	-0.526	0.622	0.181	-0.099	0.327	0.952	1.000	0.856	-0.180	0.989	0.893	0.853	0.907	0.162	0.459	-0.605	-0.204	0.274	-0.492	-0.294	0.449
Bio14	-0.148	-0.404	0.574	0.082	-0.182	0.246	0.951	0.856	1.000	-0.621	0.870	0.982	0.762	0.911	0.011	0.323	-0.552	-0.294	0.224	-0.499	-0.373	0.379
Bio15	-0.357	-0.031	-0.111	0.103	0.178	0.013	-0.425	-0.180	-0.621	1.000	-0.215	-0.574	-0.153	-0.473	0.209	0.072	0.141	0.235	-0.014	0.196	0.360	-0.178
Bio16	-0.400	-0.536	0.651	0.172	-0.118	0.326	0.969	0.989	0.870	-0.215	1.000	0.908	0.872	0.915	0.133	0.450	-0.620	-0.231	0.282	-0.522	-0.284	0.412
Bio17	-0.206	-0.427	0.575	0.106	-0.156	0.264	0.976	0.893	0.982	-0.574	0.908	1.000	0.805	0.936	0.026	0.335	-0.556	-0.273	0.239	-0.502	-0.344	0.406
Bio18	-0.617	-0.663	0.782	0.241	-0.034	0.361	0.863	0.853	0.762	-0.153	0.872	0.805	1.000	0.683	0.360	0.612	-0.604	-0.087	0.291	-0.424	0.124	0.058
Bio19	-0.143	-0.404	0.440	0.157	-0.097	0.314	0.944	0.907	0.911	-0.473	0.915	0.936	0.683	1.000	-0.028	0.304	-0.578	-0.238	0.292	-0.540	-0.508	0.593
Bio2	-0.672	-0.543	0.274	0.421	0.382	0.358	0.077	0.162	0.011	0.209	0.133	0.026	0.360	-0.028	1.000	0.829	-0.243	0.571	0.172	0.224	0.489	-0.148
Bio3	-0.840	-0.900	0.531	0.690	0.475	0.732	0.402	0.459	0.323	0.072	0.450	0.335	0.612	0.304	0.829	1.000	-0.735	0.498	0.596	-0.352	0.426	0.091
Bio4	0.627	0.898	-0.565	-0.688	-0.352	-0.843	-0.605	-0.605	-0.552	0.141	-0.620	-0.556	-0.604	-0.578	-0.243	-0.735	1.000	-0.168	-0.825	0.884	-0.126	-0.393
Bio5	-0.452	-0.450	-0.372	0.807	0.947	0.647	-0.281	-0.204	-0.294	0.235	-0.231	-0.273	-0.087	-0.238	0.571	0.498	-0.168	1.000	0.581	0.049	0.536	0.063
Bio6	-0.570	-0.820	0.110	0.937	0.774	0.978	0.255	0.274	0.224	-0.014	0.282	0.239	0.291	0.292	0.172	0.596	-0.825	0.581	1.000	-0.784	0.301	0.390
Bio7	0.355	0.664	-0.418	-0.534	-0.229	-0.707	-0.527	-0.492	-0.499	0.196	-0.522	-0.502	-0.424	-0.540	0.224	-0.352	0.884	0.049	-0.784	1.000	0.039	-0.431
Bio8	-0.573	-0.412	0.110	0.434	0.469	0.346	-0.318	-0.294	-0.373	0.360	-0.284	-0.344	0.124	-0.508	0.489	0.426	-0.126	0.536	0.301	0.039	1.000	-0.457
Bio9	0.017	-0.195	-0.119	0.314	0.216	0.380	0.386	0.449	0.379	-0.178	0.412	0.406	0.058	0.593	-0.148	0.091	-0.393	0.063	0.390	-0.431	-0.457	1.000

Appendix B-4. Bioclimatic variable correlations to *Pinus pungens* location data.

	Long	Lat	Alt	Bio1	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9
Long	1.000	0.883	-0.365	-0.392	-0.071	-0.596	-0.711	-0.761	-0.606	-0.064	-0.733	-0.645	-0.594	-0.788	-0.575	-0.802	0.806	-0.003	-0.516	0.700	0.700	-0.836
Lat	0.883	1.000	-0.282	-0.586	-0.233	-0.805	-0.716	-0.727	-0.680	0.202	-0.710	-0.701	-0.642	-0.782	-0.593	-0.881	0.925	-0.133	-0.739	0.833	0.578	-0.821
Alt	-0.365	-0.282	1.000	-0.602	-0.855	-0.324	0.496	0.422	0.529	-0.354	0.458	0.501	0.569	0.362	-0.062	0.292	-0.561	-0.902	-0.398	-0.652	-0.398	-0.014
Bio1	-0.392	-0.586	-0.602	1.000	0.921	0.948	0.159	0.219	0.125	0.058	0.172	0.157	0.051	0.317	0.509	0.467	-0.296	0.871	0.964	-0.162	-0.101	0.667
Bio10	-0.071	-0.233	-0.855	0.921	1.000	0.750	-0.140	-0.070	-0.175	0.196	-0.118	-0.144	-0.249	0.023	0.301	0.121	0.098	0.982	0.804	0.204	0.125	0.430
Bio11	-0.596	-0.805	-0.324	0.948	0.750	1.000	0.388	0.429	0.363	-0.080	0.391	0.390	0.294	0.519	0.608	0.691	-0.585	0.678	0.986	-0.447	-0.268	0.775
Bio12	-0.711	-0.716	0.496	0.159	-0.140	0.388	1.000	0.984	0.959	-0.308	0.987	0.984	0.963	0.973	0.181	0.568	-0.750	-0.248	0.348	-0.803	-0.793	0.698
Bio13	-0.761	-0.727	0.422	0.219	-0.070	0.429	0.984	1.000	0.910	-0.165	0.995	0.949	0.918	0.989	0.226	0.578	-0.724	-0.171	0.389	-0.757	-0.836	0.766
Bio14	-0.606	-0.680	0.529	0.125	-0.175	0.363	0.959	0.910	1.000	-0.520	0.916	0.987	0.961	0.894	0.141	0.547	-0.756	-0.282	0.331	-0.826	-0.660	0.571
Bio15	-0.064	0.202	-0.354	0.058	0.196	-0.080	-0.308	-0.165	-0.520	1.000	-0.183	-0.450	-0.431	-0.177	0.077	-0.185	0.364	0.257	-0.088	0.461	-0.072	0.111
Bio16	-0.733	-0.710	0.458	0.172	-0.118	0.391	0.987	0.995	0.916	-0.183	1.000	0.952	0.930	0.982	0.198	0.563	-0.726	-0.219	0.349	-0.767	-0.827	0.728
Bio17	-0.645	-0.701	0.501	0.157	-0.144	0.390	0.984	0.949	0.987	-0.450	0.952	1.000	0.976	0.939	0.169	0.567	-0.758	-0.253	0.355	-0.820	-0.718	0.639
Bio18	-0.594	-0.642	0.569	0.051	-0.249	0.294	0.963	0.918	0.961	-0.431	0.930	0.976	1.000	0.895	0.130	0.532	-0.741	-0.352	0.252	-0.811	-0.679	0.569
Bio19	-0.788	-0.782	0.362	0.317	0.023	0.519	0.973	0.989	0.894	-0.177	0.982	0.939	0.895	1.000	0.279	0.620	-0.746	-0.082	0.480	-0.764	-0.833	0.824
Bio2	-0.575	-0.593	-0.062	0.509	0.301	0.608	0.181	0.226	0.141	0.077	0.198	0.169	0.130	0.279	1.000	0.856	-0.547	0.357	0.488	-0.193	-0.162	0.500
Bio3	-0.802	-0.881	0.292	0.467	0.121	0.691	0.568	0.578	0.547	-0.185	0.563	0.567	0.532	0.620	0.856	1.000	-0.894	0.095	0.579	-0.664	-0.436	0.669
Bio4	0.806	0.925	-0.561	-0.296	0.098	-0.585	-0.750	-0.724	-0.756	0.364	-0.726	-0.758	-0.741	-0.746	-0.547	-0.894	1.000	0.185	-0.497	0.923	0.551	-0.633
Bio5	-0.003	-0.133	-0.902	0.871	0.982	0.678	-0.248	-0.171	-0.282	0.257	-0.219	-0.253	-0.352	-0.082	0.357	0.095	0.185	1.000	0.724	0.337	0.199	0.349
Bio6	-0.516	-0.739	-0.398	0.964	0.804	0.986	0.348	0.389	0.331	-0.088	0.349	0.355	0.252	0.480	0.488	0.579	-0.497	0.724	1.000	-0.406	-0.228	0.744
Bio7	0.700	0.833	-0.652	-0.162	0.204	-0.447	-0.803	-0.757	-0.826	0.461	-0.767	-0.820	-0.811	-0.764	-0.193	-0.664	0.923	0.337	-0.406	1.000	0.575	-0.552
Bio8	0.700	0.578	-0.398	-0.101	0.125	-0.268	-0.793	-0.836	-0.660	-0.072	-0.827	-0.718	-0.679	-0.833	-0.162	-0.436	0.551	0.199	-0.228	0.575	1.000	-0.671
Bio9	-0.836	-0.821	-0.014	0.667	0.430	0.775	0.698	0.766	0.571	0.111	0.728	0.639	0.569	0.824	0.500	0.669	-0.633	0.349	0.744	-0.552	-0.671	1.000

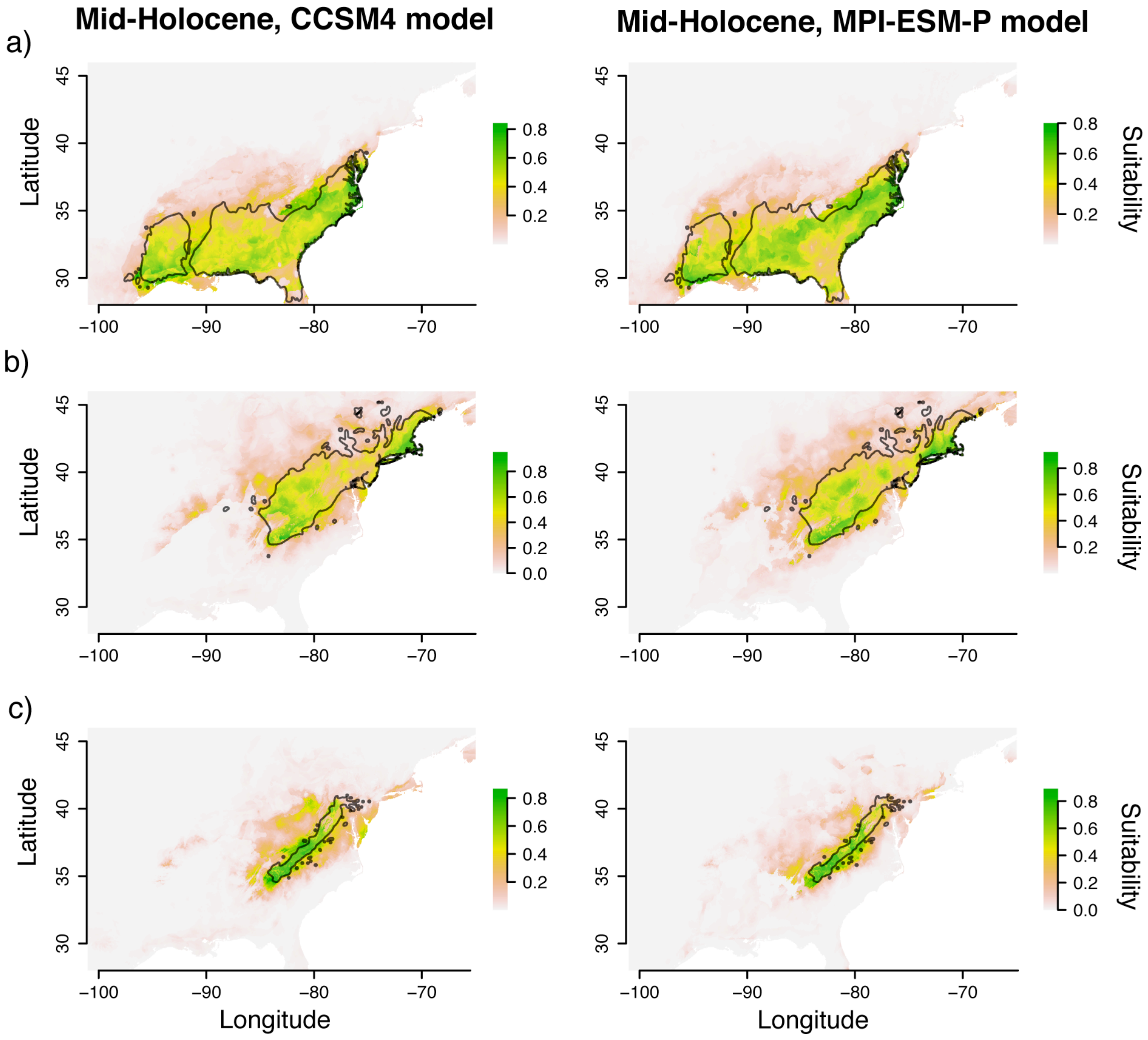
Appendix C-1

Comparing LGM hindcast projections under two different General Circulation Model **a,b)** *P. taeda* **c,d)** *P. rigida* **e,f)** *P. pungens.*



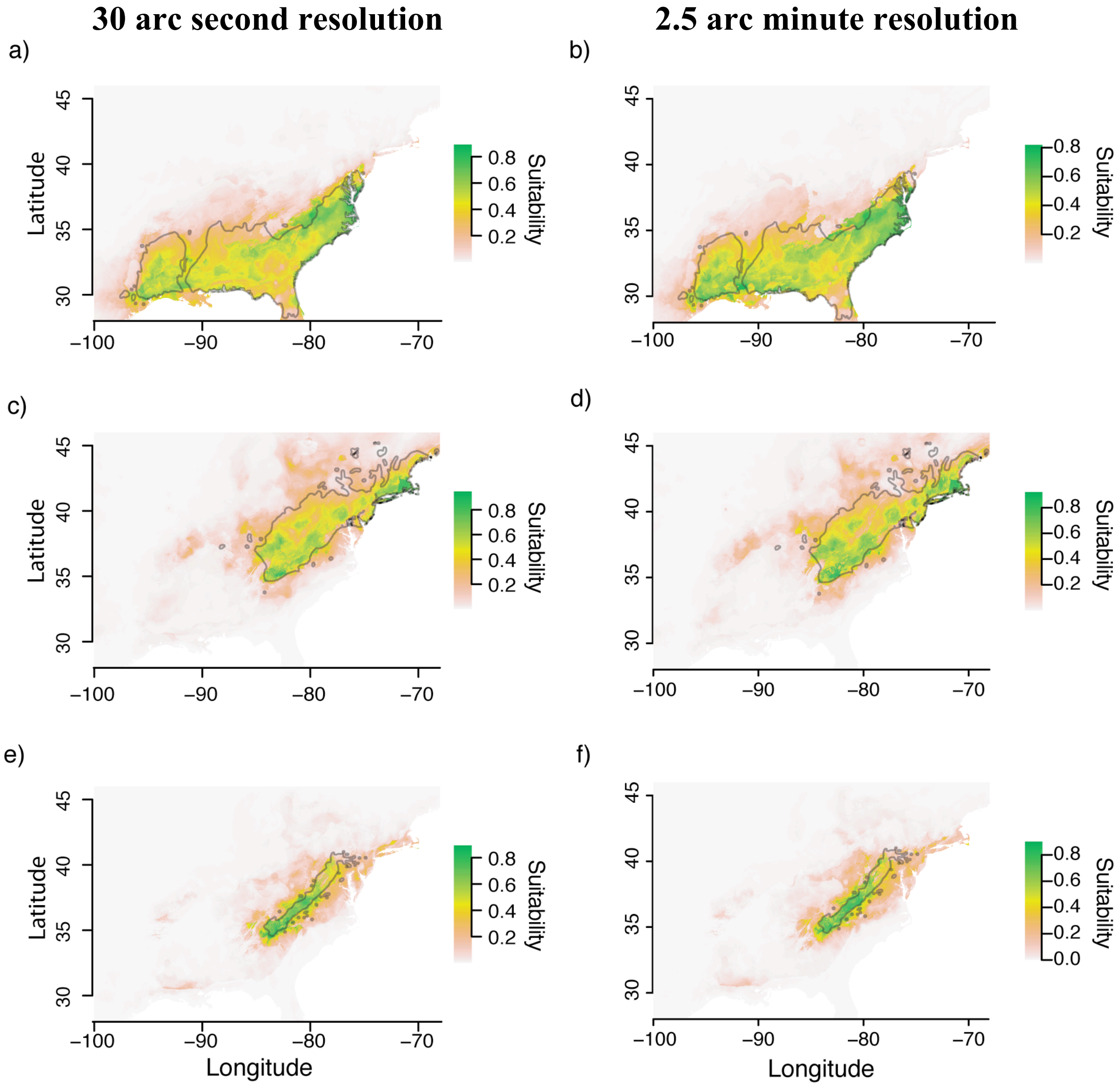
Appendix C-2

Comparing Mid-Holocene hindcast projections under two different General Circulation Model available for download on WorldClim.org; **a,b)** *P. taeda* **c,d)** *P. rigida* **e,f)** *P. pungens.*



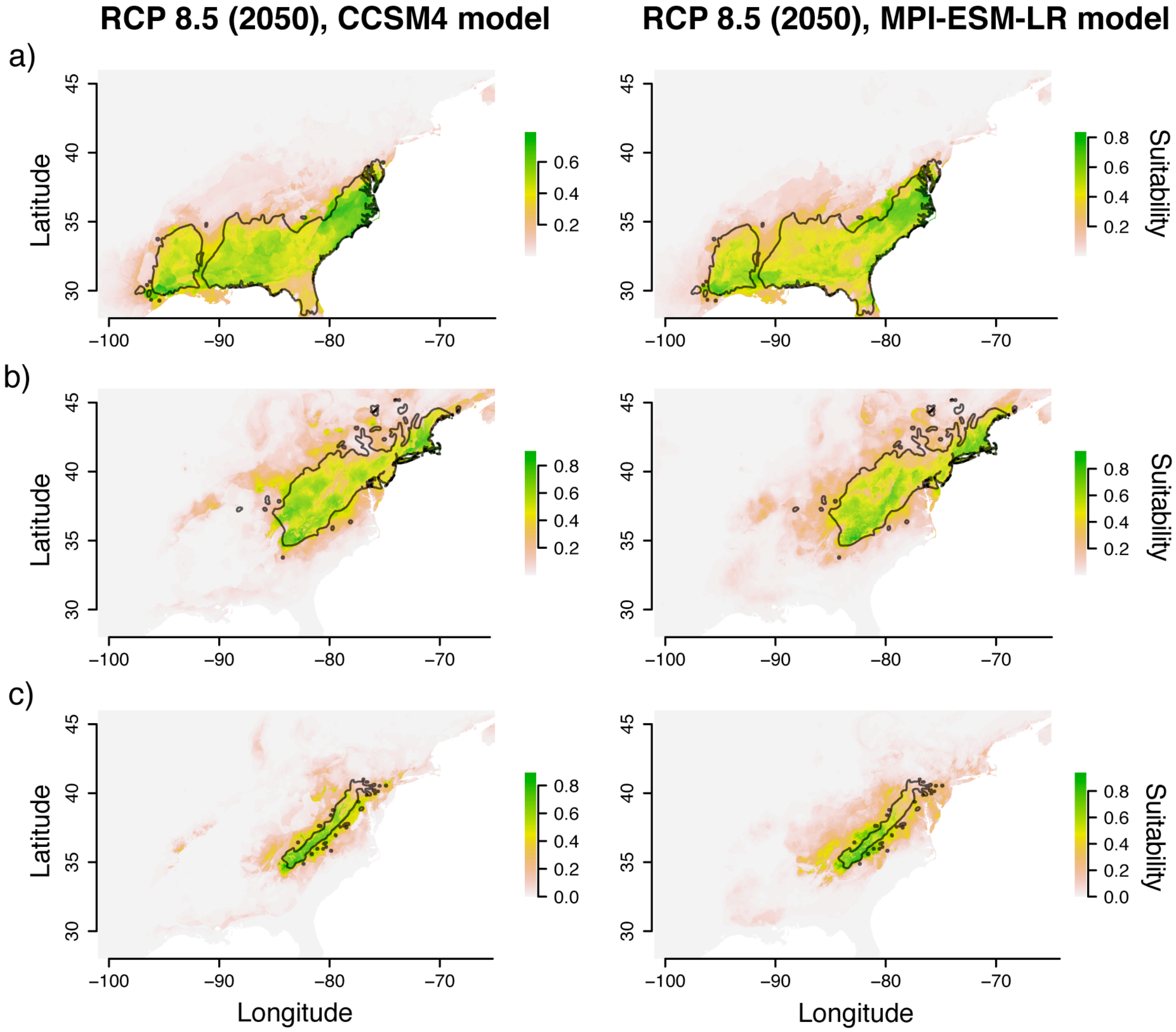
Appendix D

Comparing ENM projections under two different resolutons available for download on WorldClim.org; **a,b)** *P. taeda* **c,d)** *P. rigida* **e,f)** *P. pungens*.



Appendix E

Comparing future projections under the RCP 8.5 scenario, for the year 2050, across two General Circulation Models available for download on WorldClim.org; a) *P. taeda* b) *P. rigida* c) *P. pungens*.



Appendix F

I statistics (Warren *et al.,* 2008) from pairwise comparison across species. The upper triangular of the matrix reports estimates for *I*. Bottom, left matrix reports the corresponding p-value from the *niche.equivalency.test* function in the *phyloclim* package in R v.3.2.1. Significance testing was based on permutations (*n* = 100).

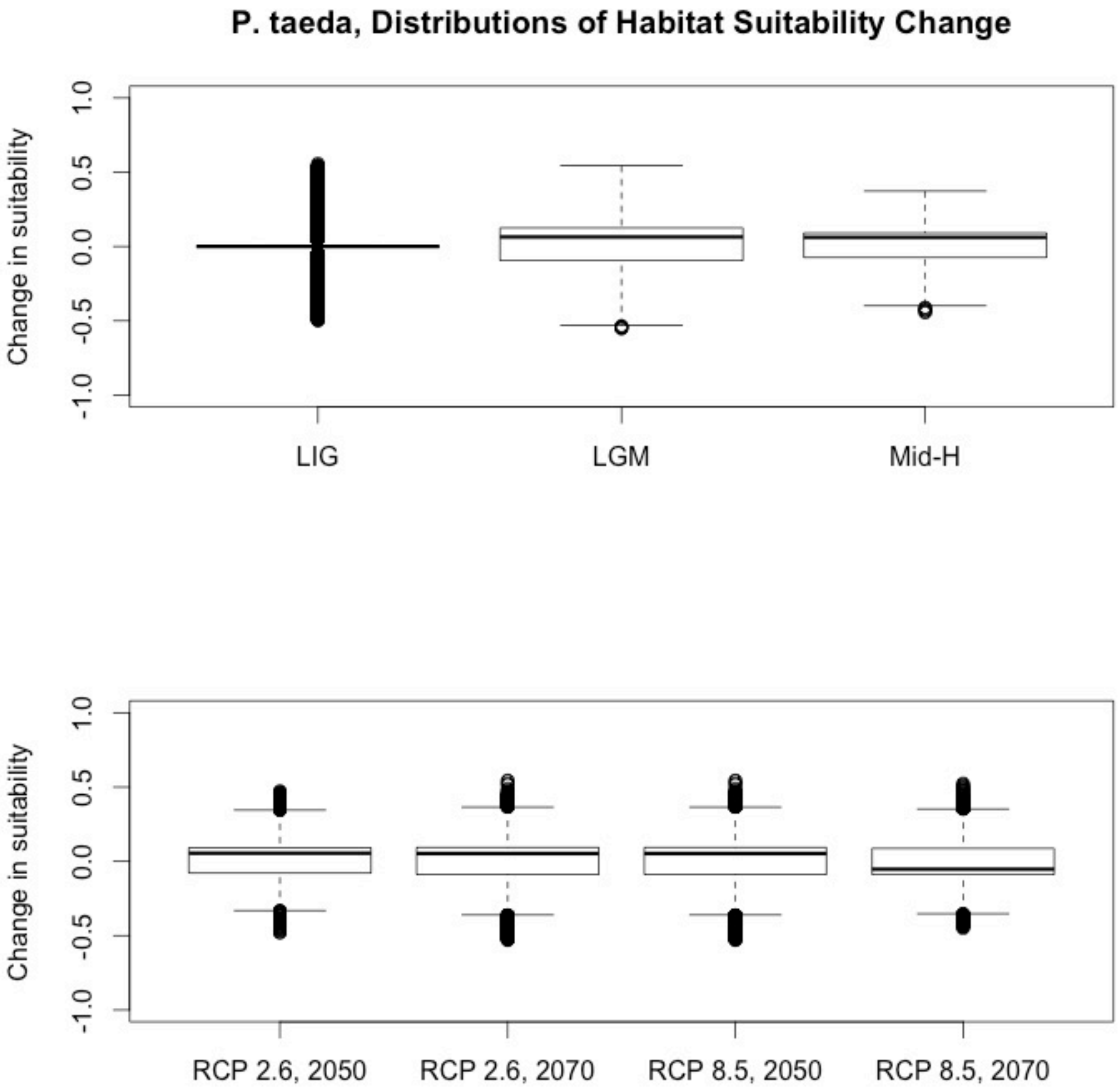
	P. pungens	*P. rigida*	*P. taeda*
P. pungens	-	0.865	0.499
P. rigida	7.39e-33		0.460
P. taeda	0	0	-

I statistics (Warren *et al*., 2008) from pairwise comparison across genetic groupings, where '*P.r.'* stands for *Pinus rigida* and *'P.t.'* stands for *Pinus taeda.* The upper triangular of the matrix reports estimates for *I*. Bottom, left matrix reports the corresponding p-value from the *niche.equivalency.test* function in the *phyloclim* package in R v.3.2.1. Significance testing was based on permutations (*n* = 100).

	P. pungens	**north *P.r.***	**mid *P.r.***	**south *P.r.***	**west *P.t.***	**east *P.t.***
P. pungens	-	0.58	0.842	0.862	0.194	0.536
north *P.r.*	4.33e-238	-	0.618	0.467	0.083	0.253
mid *P.r*	1.39e-18	8.73e-213	-	0.682	0.095	0.371
south *P.r.*	2.08e-16	4.17e-238	1.12e-116	-	0.269	0.679
west *P.t.*	0	0	0	0	-	0.571
east *P.t.*	0	0	0	9.09e-245	1.64e-271	-

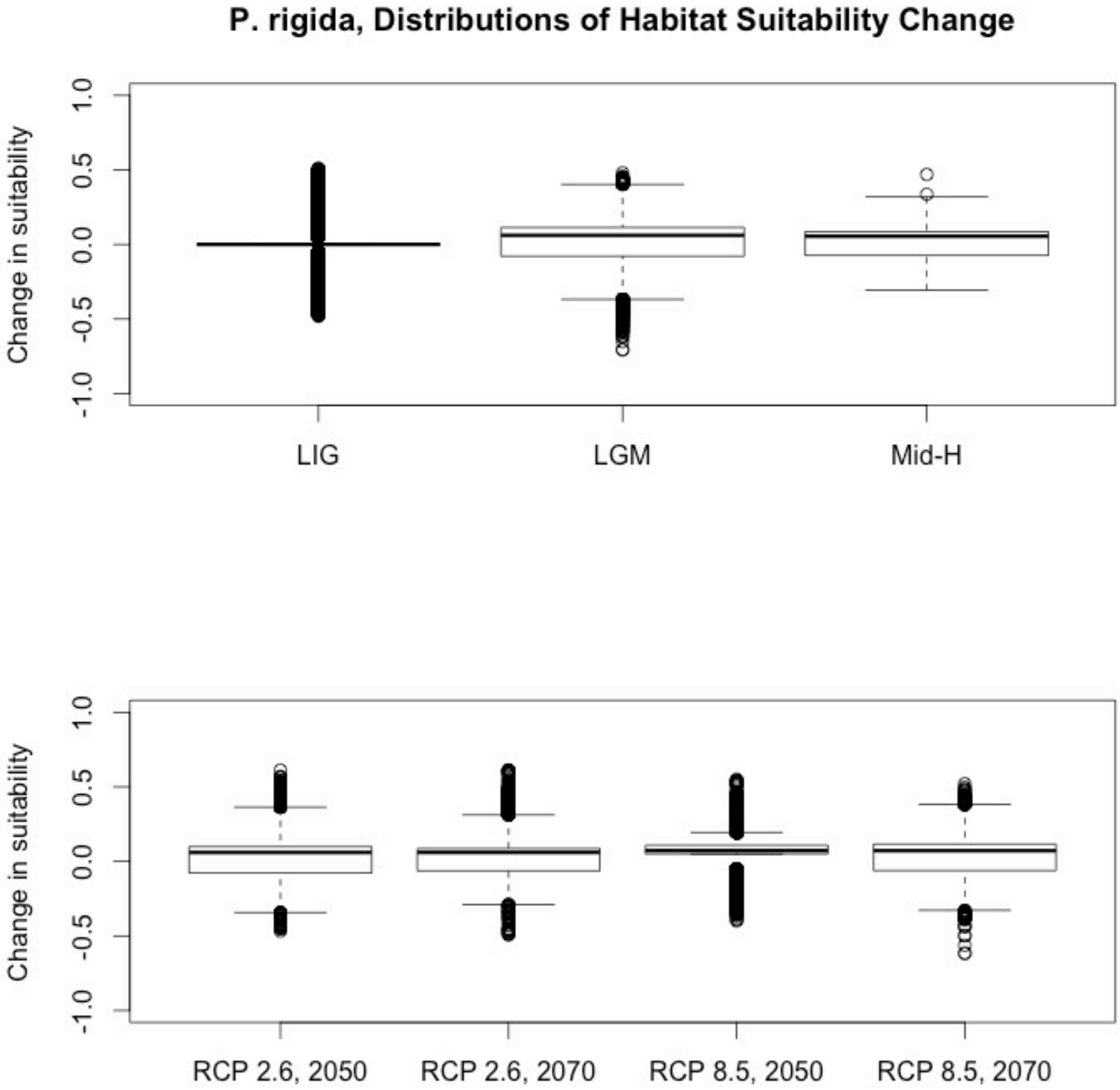
Appendix G-1

Distributions of values indicating change in suitability compared to current ENMs.



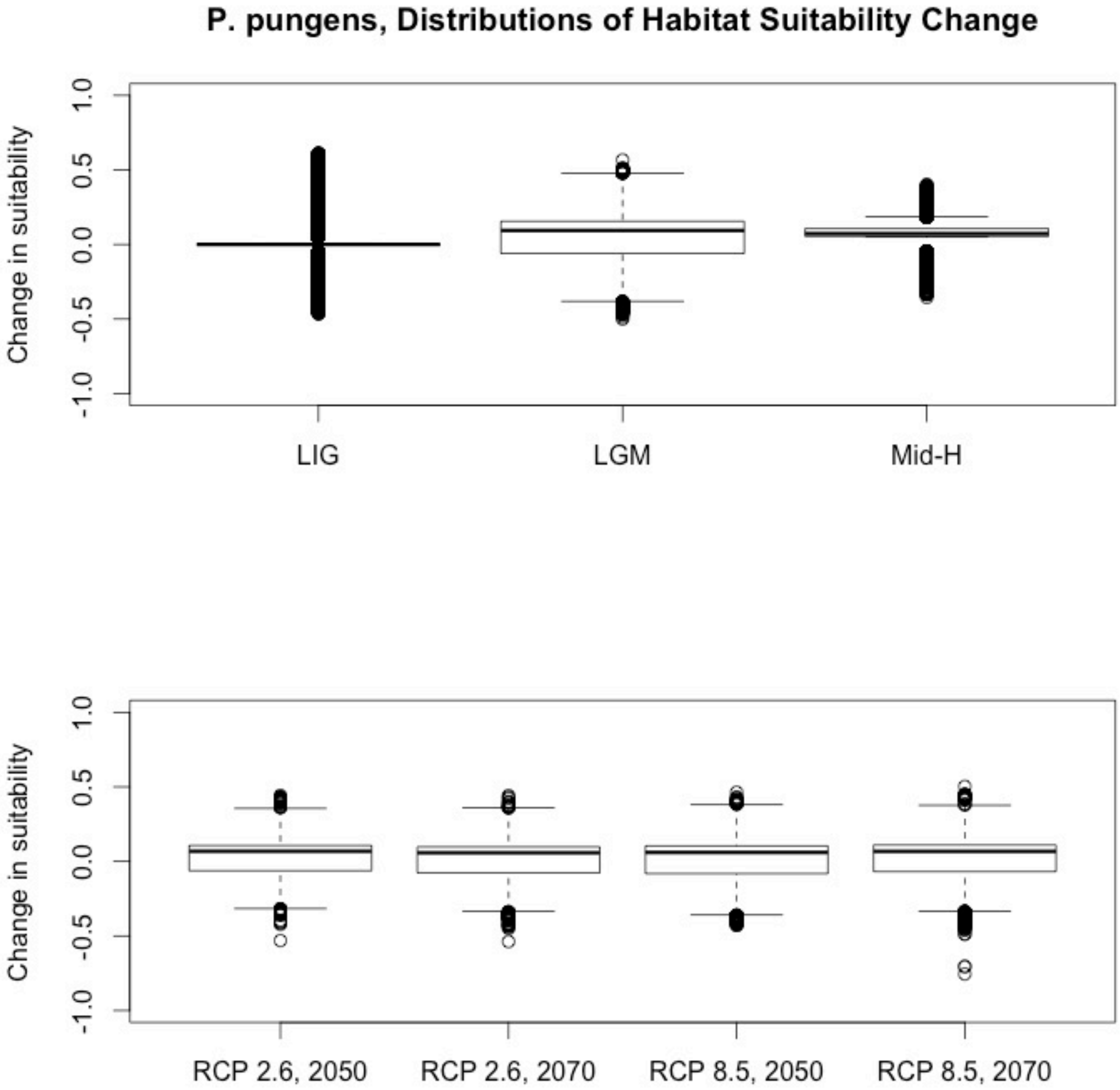
Appendix G-2

Distributions of values indicating change in suitability compared to current ENMs.



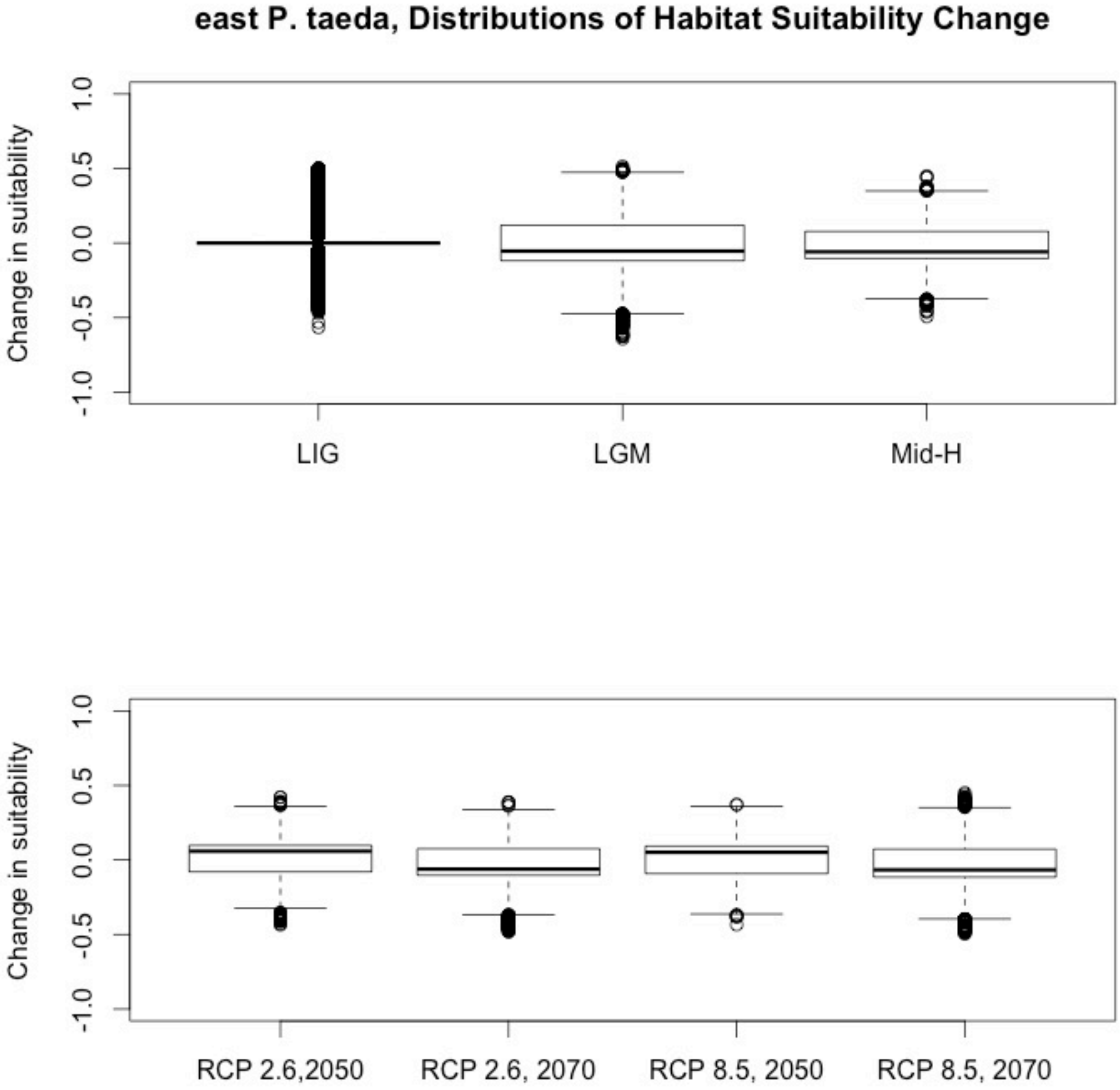
Appendix G-3

Distributions of values indicating change in suitability compared to current ENMs.



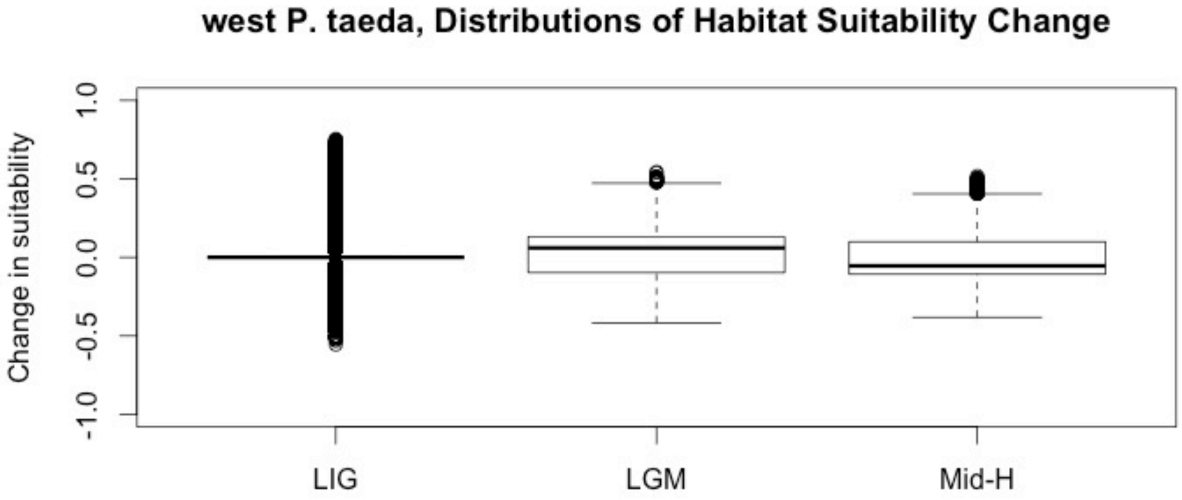
Appendix G-4

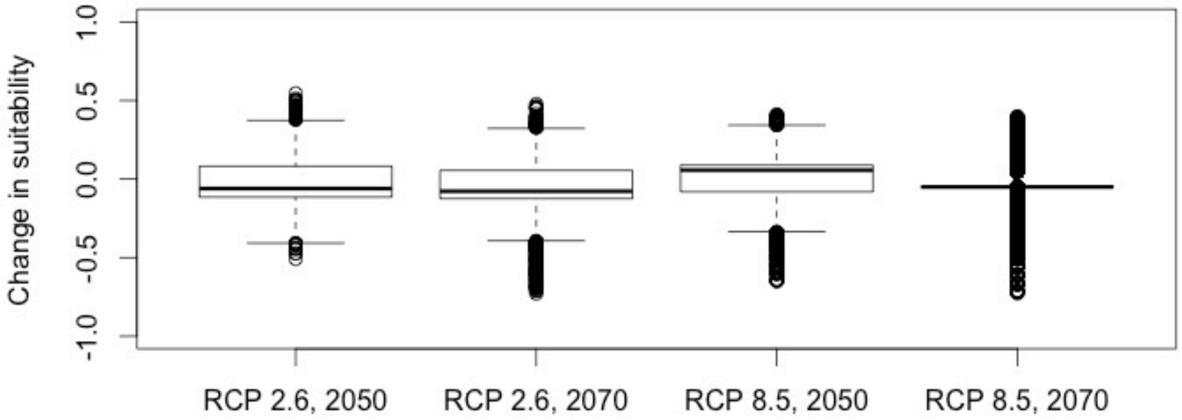
Distributions of values indicating change in suitability compared to current ENMs.



Appendix G-5

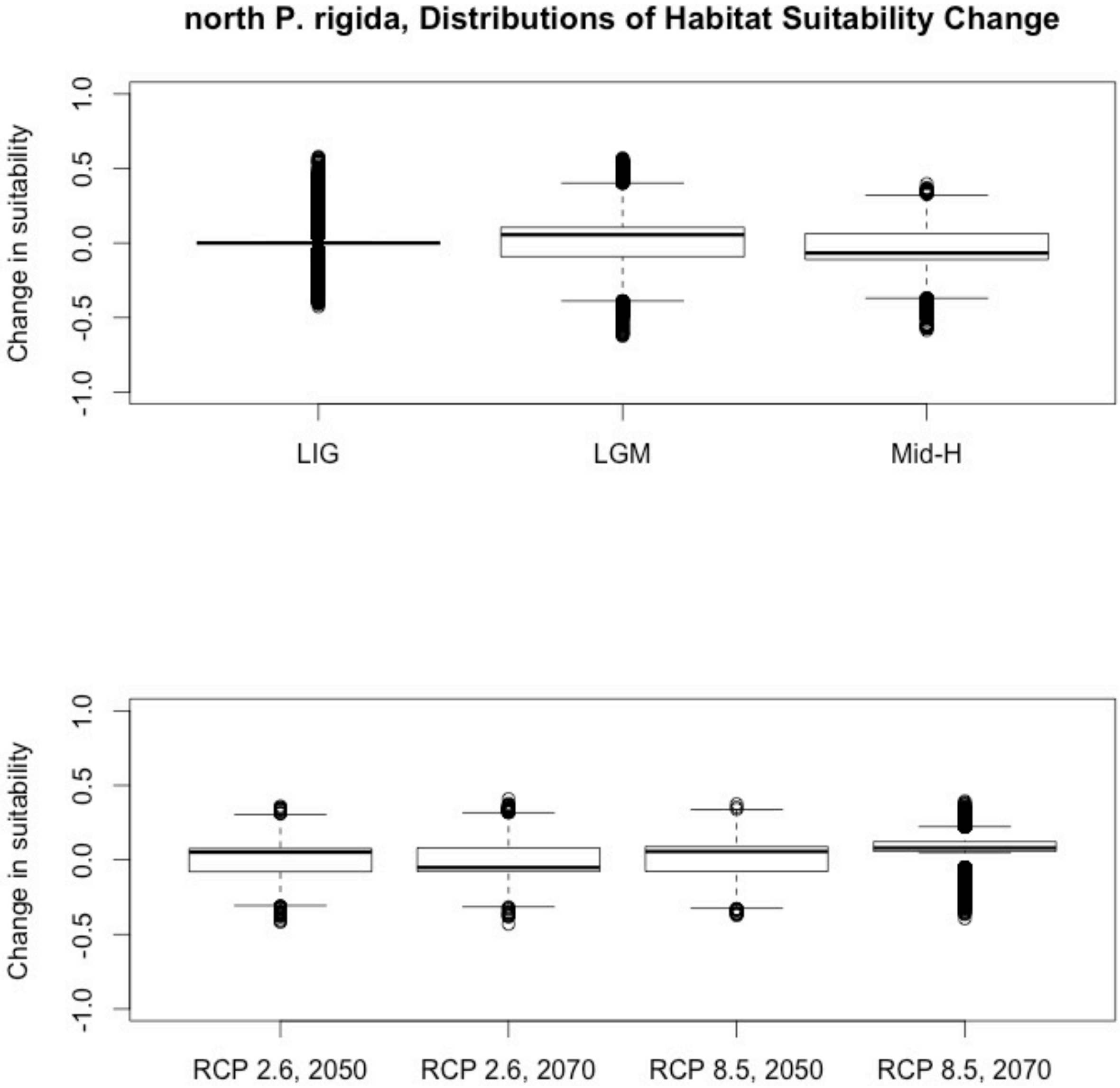
Distributions of values indicating change in suitability compared to current ENMs.





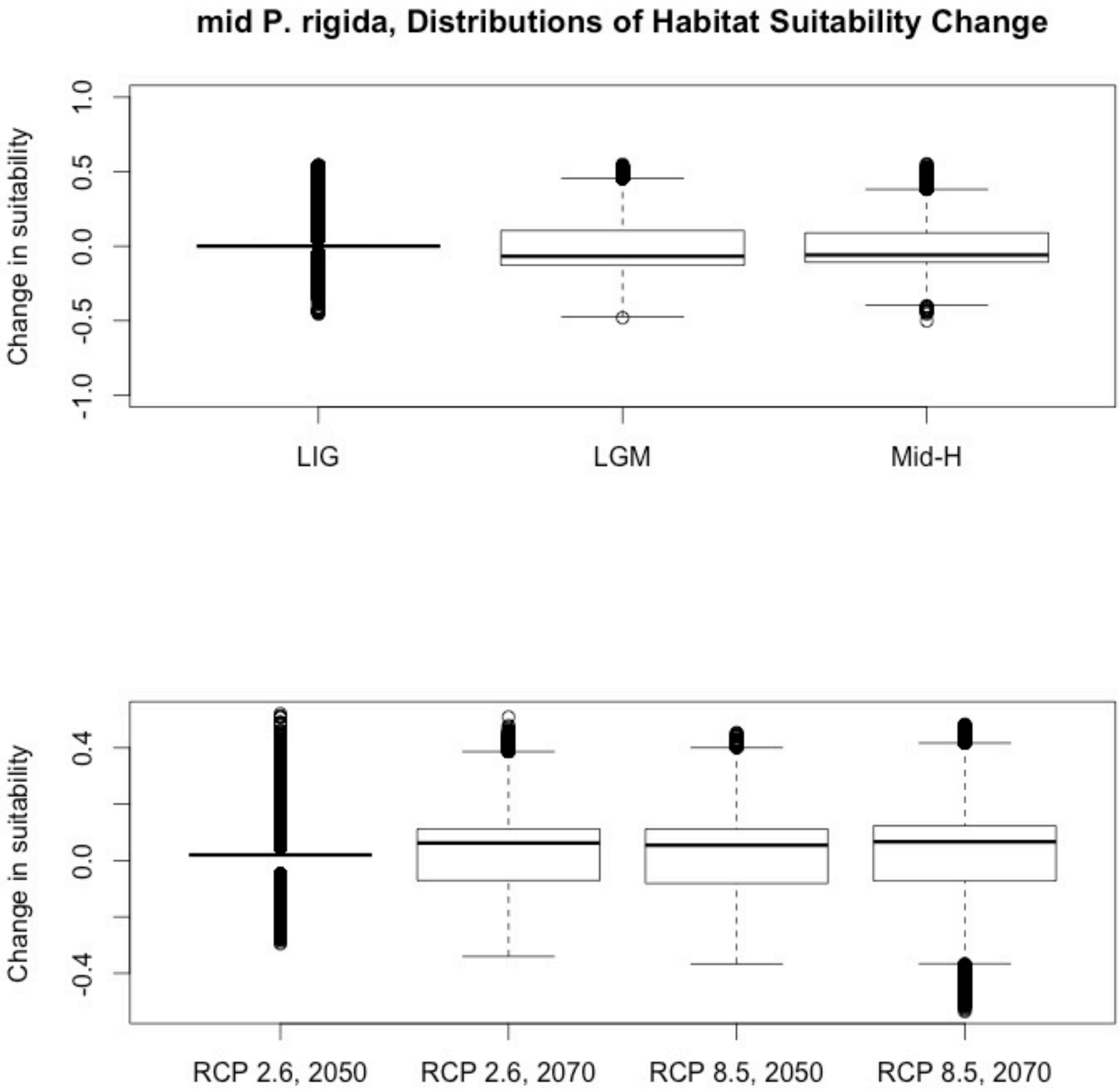
Appendix G-6

Distributions of values indicating change in suitability compared to current ENMs.



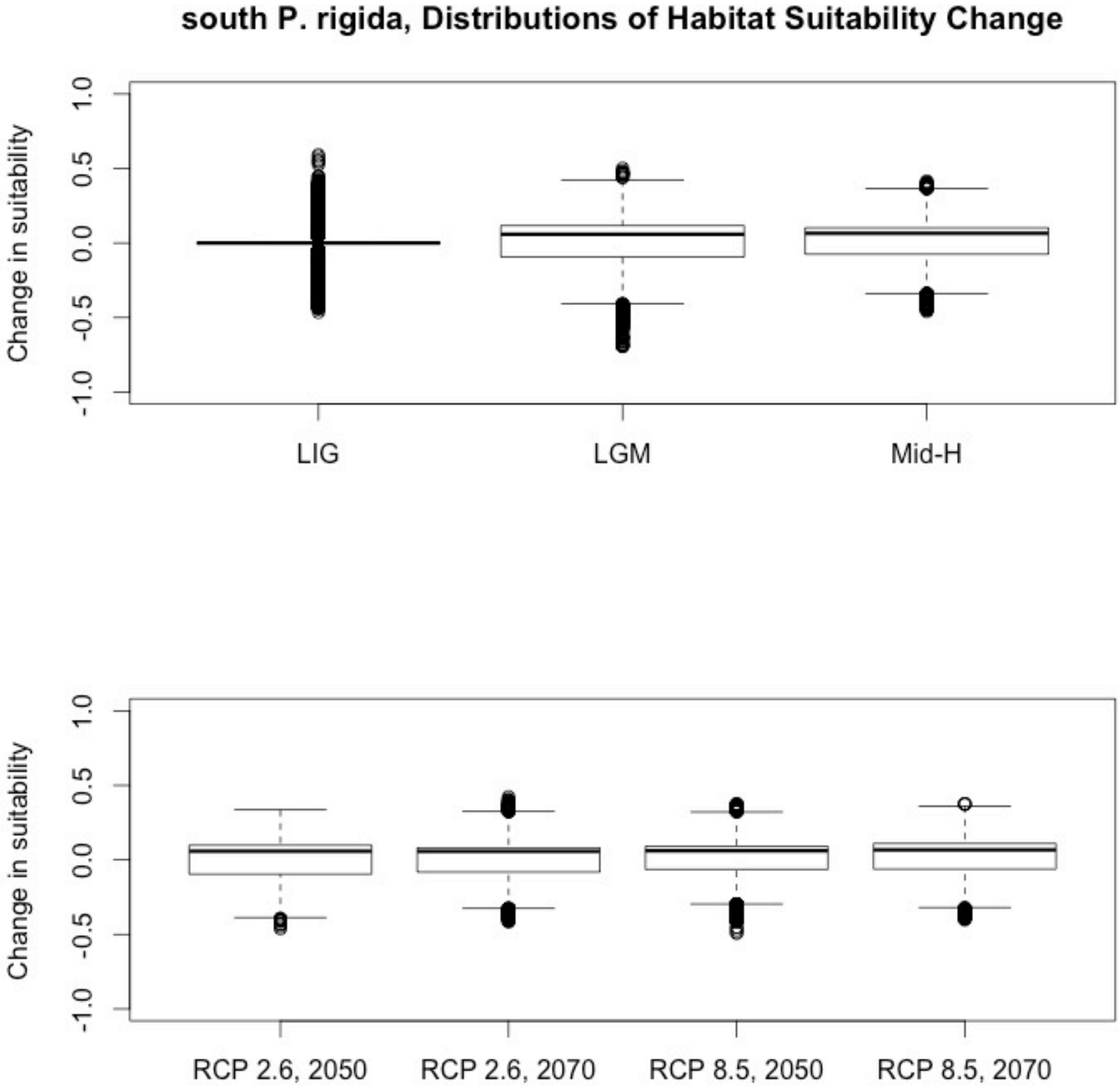
Appendix G-7

Distributions of values indicating change in suitability compared to current ENMs.



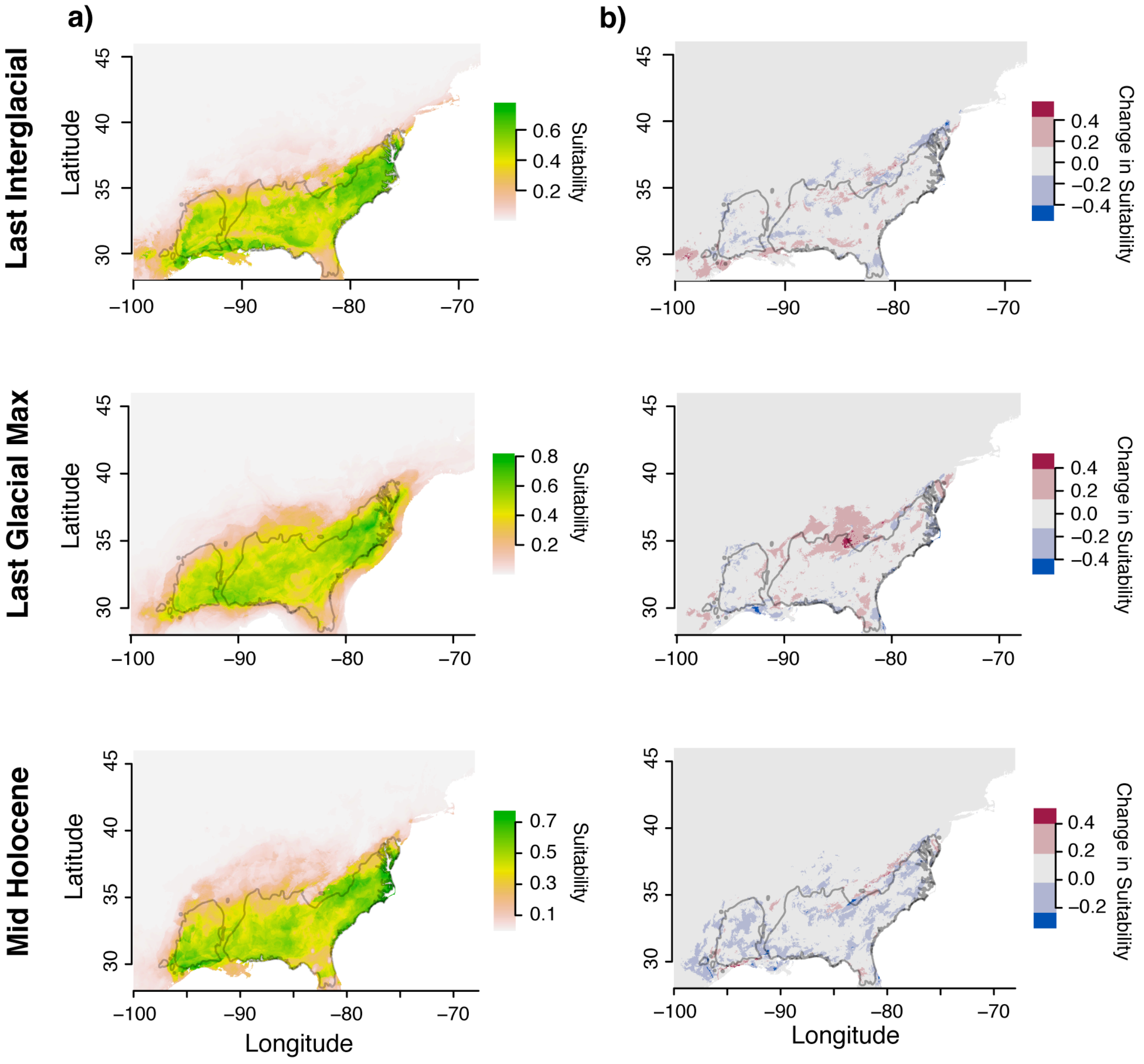
Appendix G-8

Distributions of values indicating change in suitability compared to current ENMs.



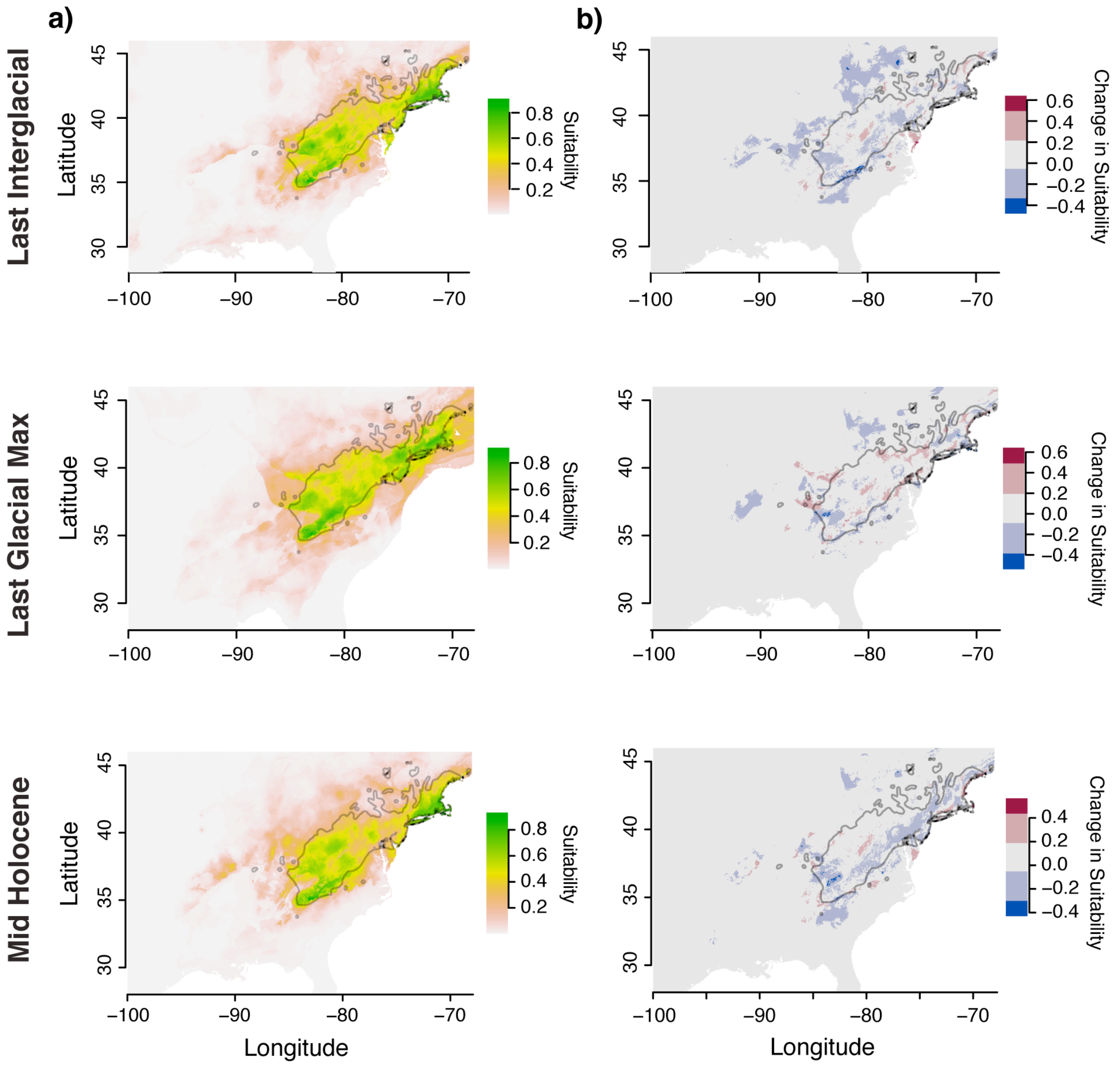
Appendix H-1

Hindcast suitability projections for *P. taeda* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



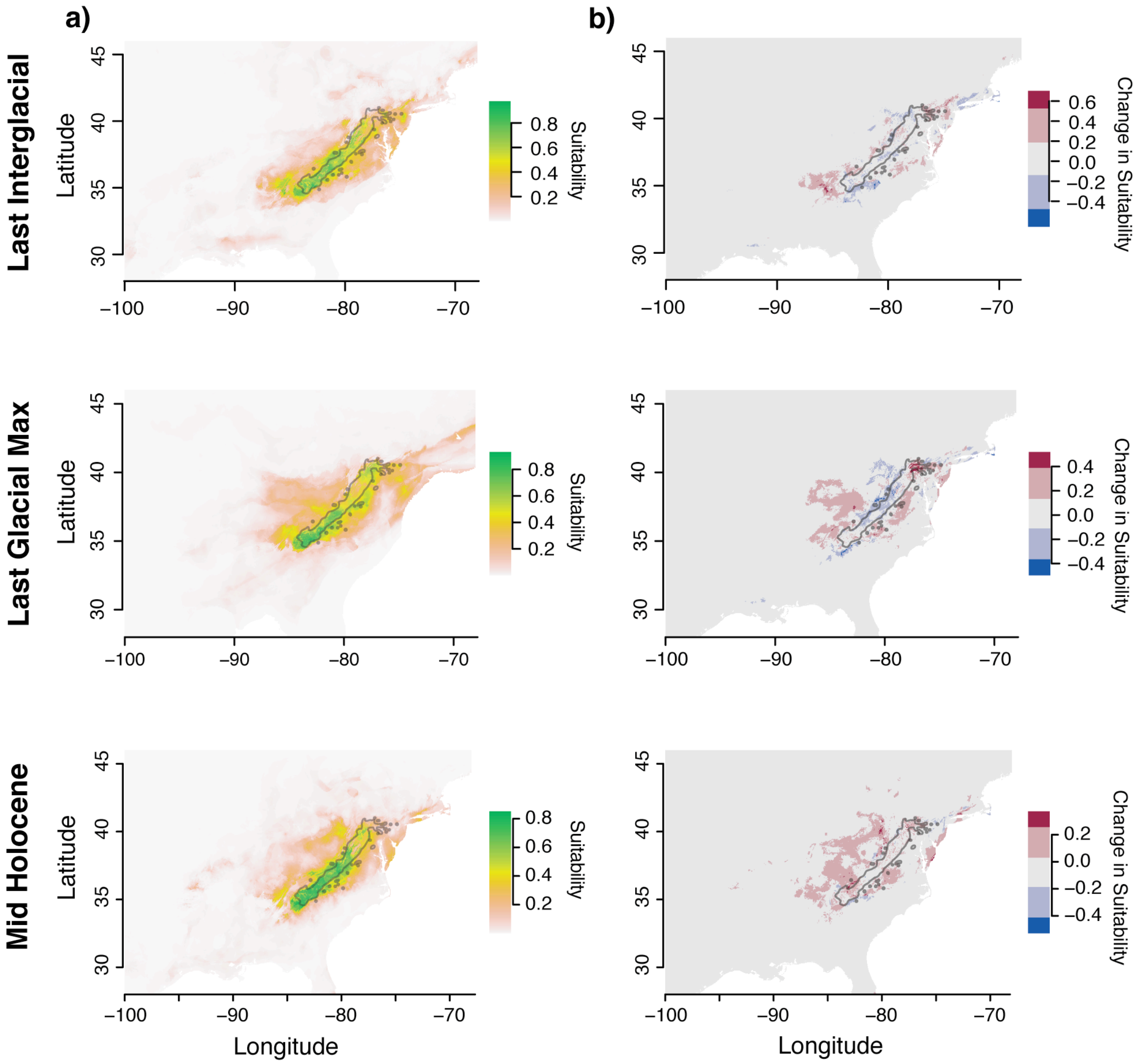
Appendix H-2

Hindcast suitability projections for *P. rigida* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



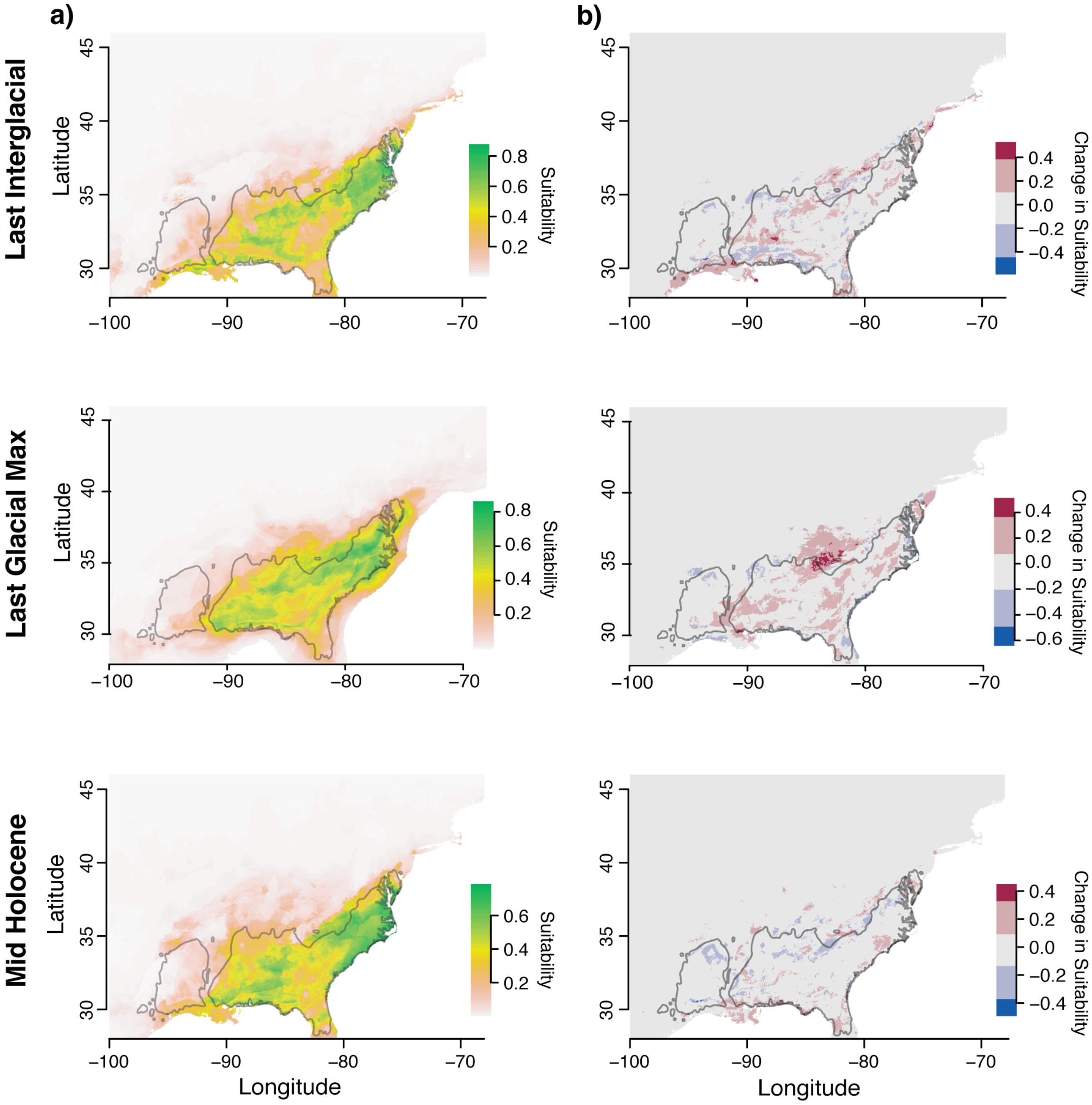
Appendix H-3

Hindcast suitability projections for *P. pungens* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



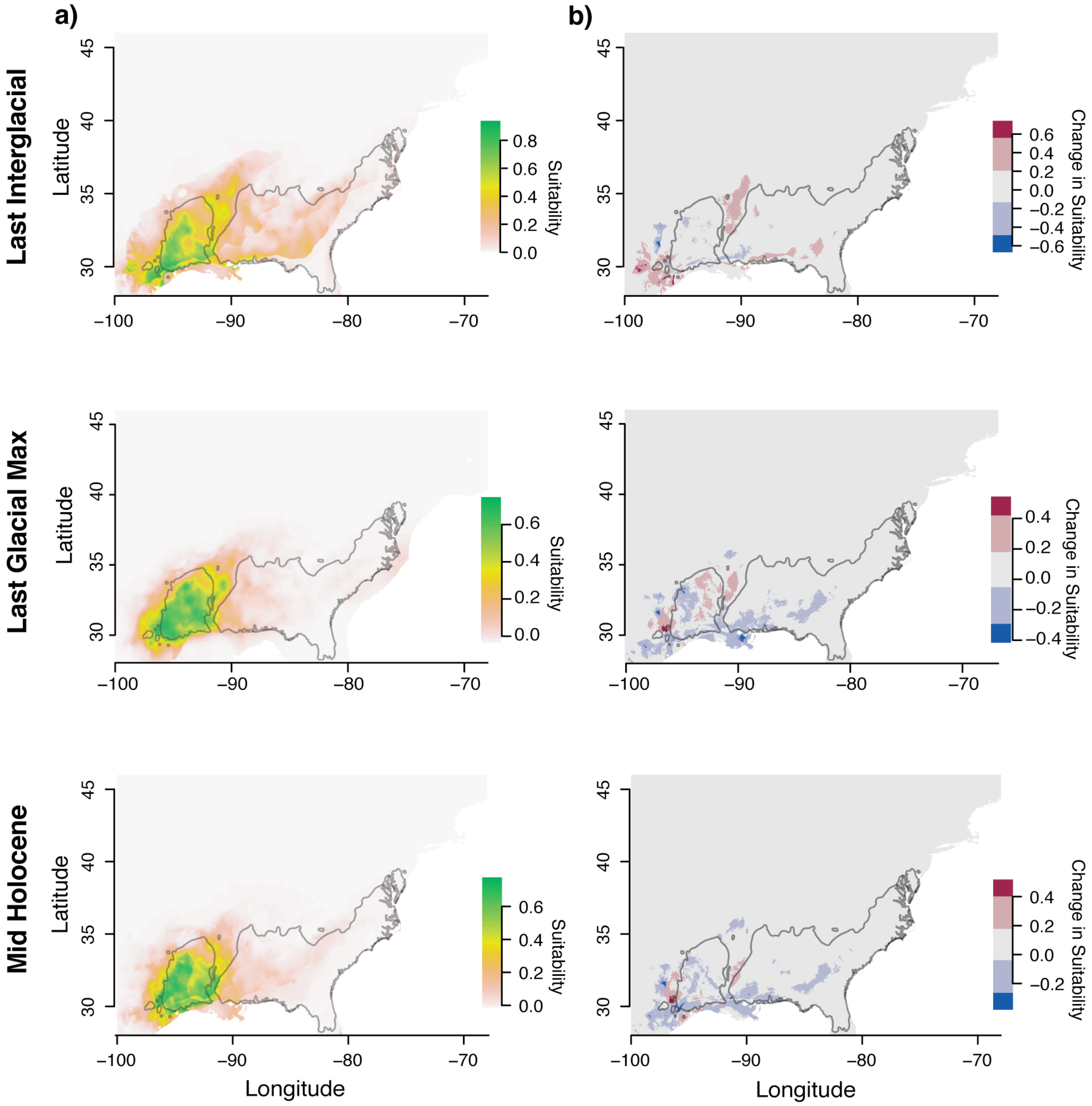
Appendix H-4

Hindcast suitability projections for east *P. taeda* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



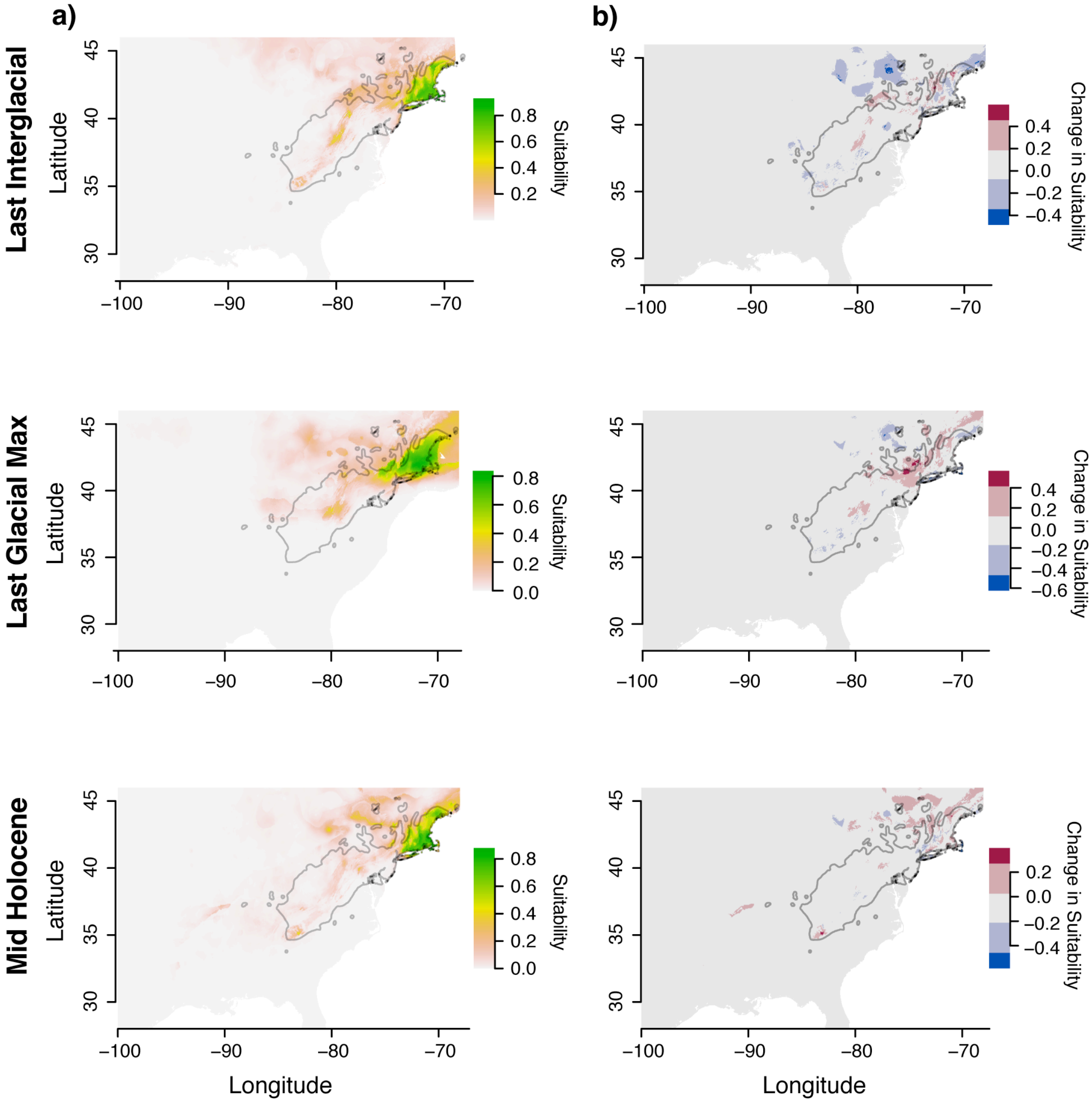
Appendix H-5

Hindcast suitability projections for west *P. taeda* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



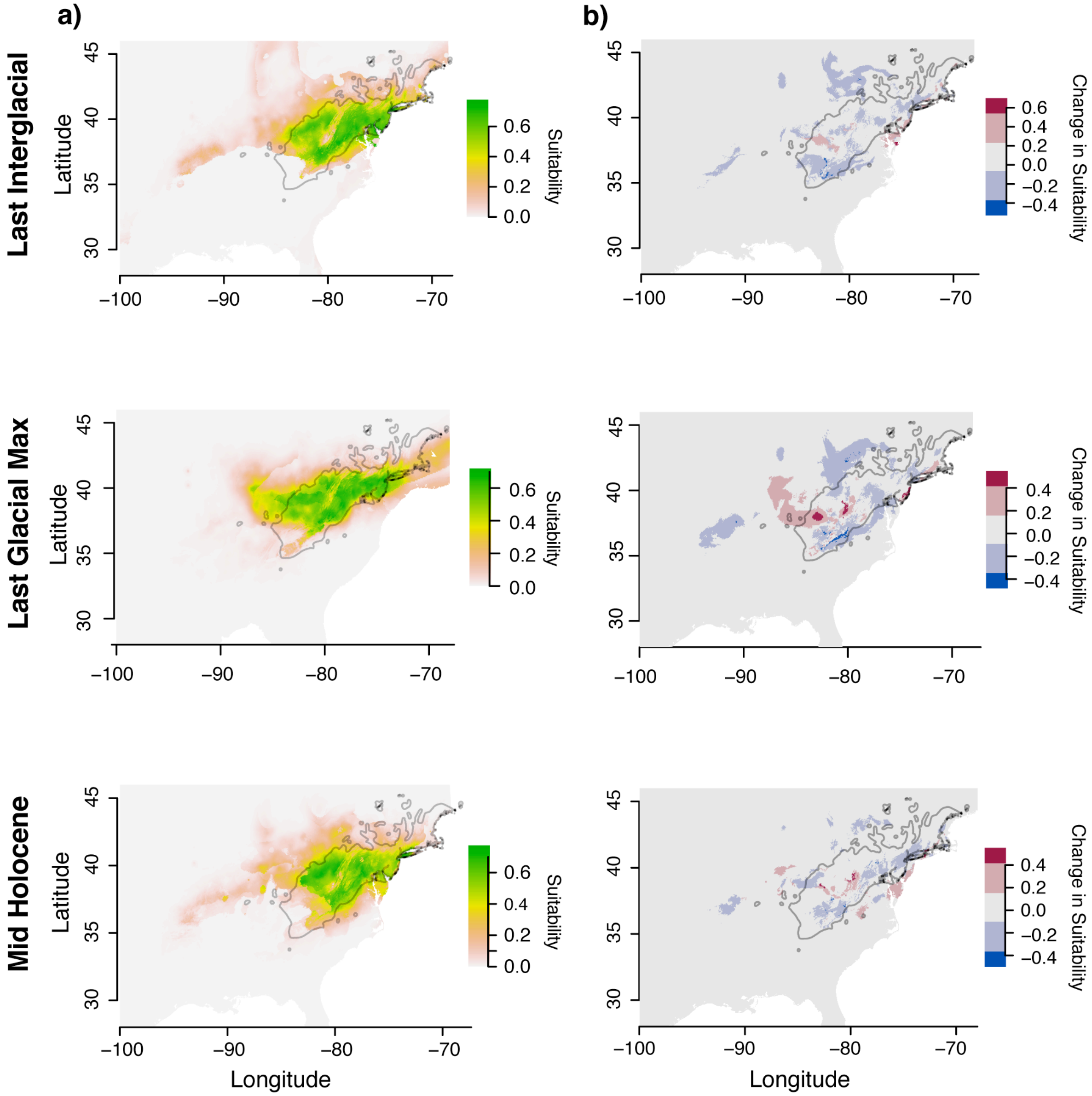
Appendix H-6

Hindcast suitability projections for north *P. rigida* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



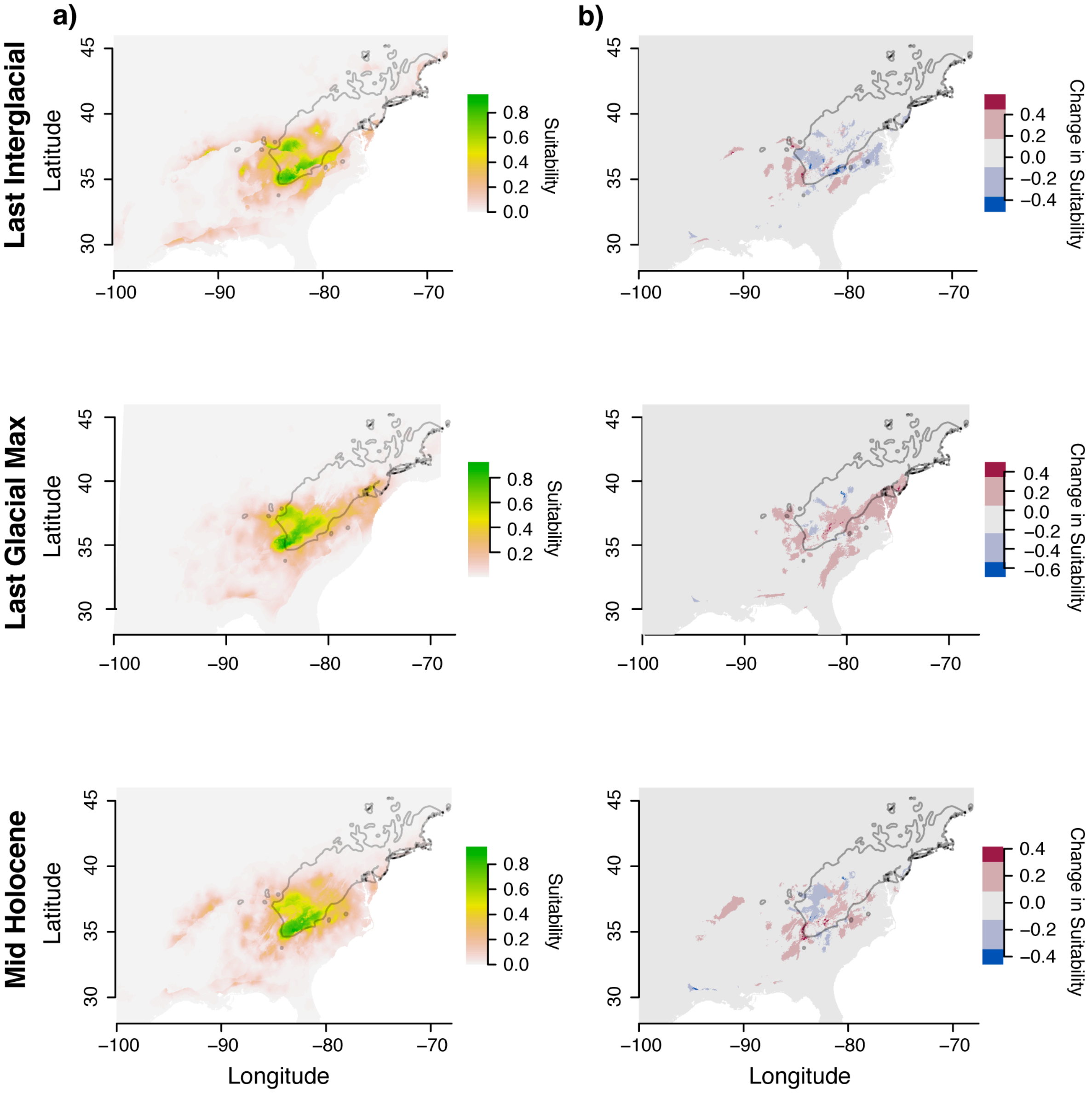
Appendix H-7

Hindcast suitability projections for mid *P. rigida* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



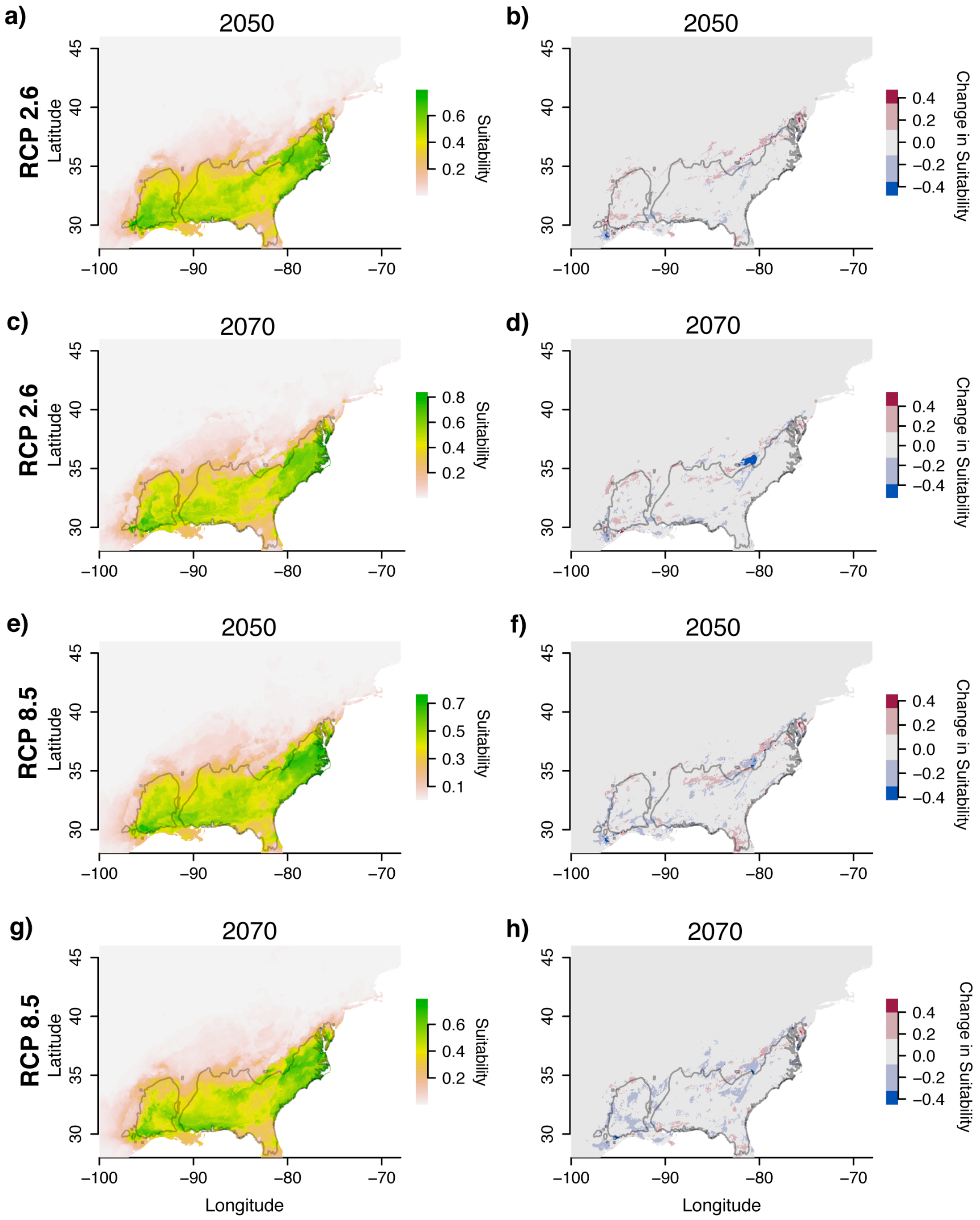
Appendix H-8

Hindcast suitability projections for south *P. rigida* across three time periods (left panel), and change in suitability map presented in the main paper (right panel).



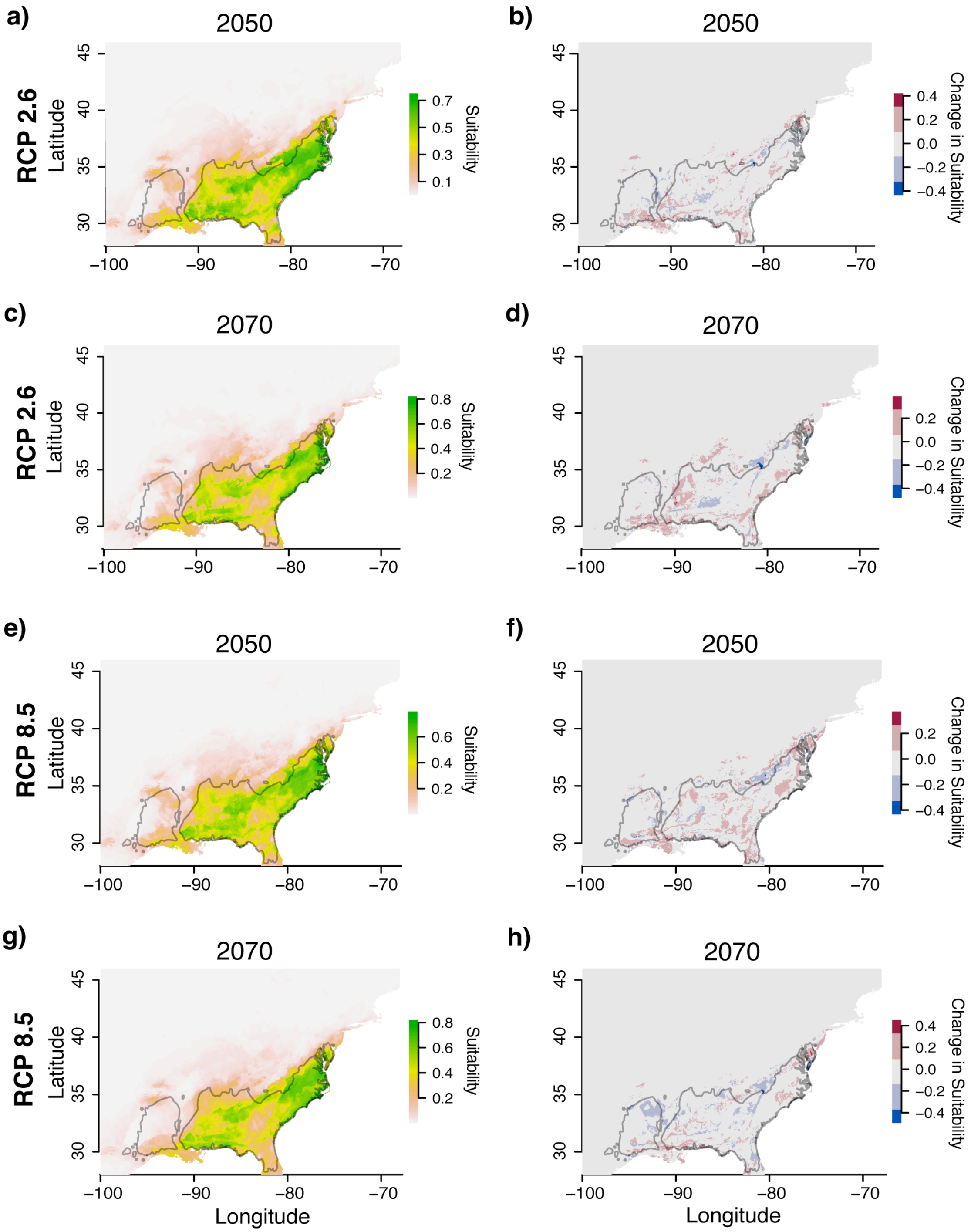
Appendix H-9

Forecast suitability projections for *P. taeda* across two time periods (left panel), under two climate scenarios, and change in suitability map presented in the main paper (right panel).



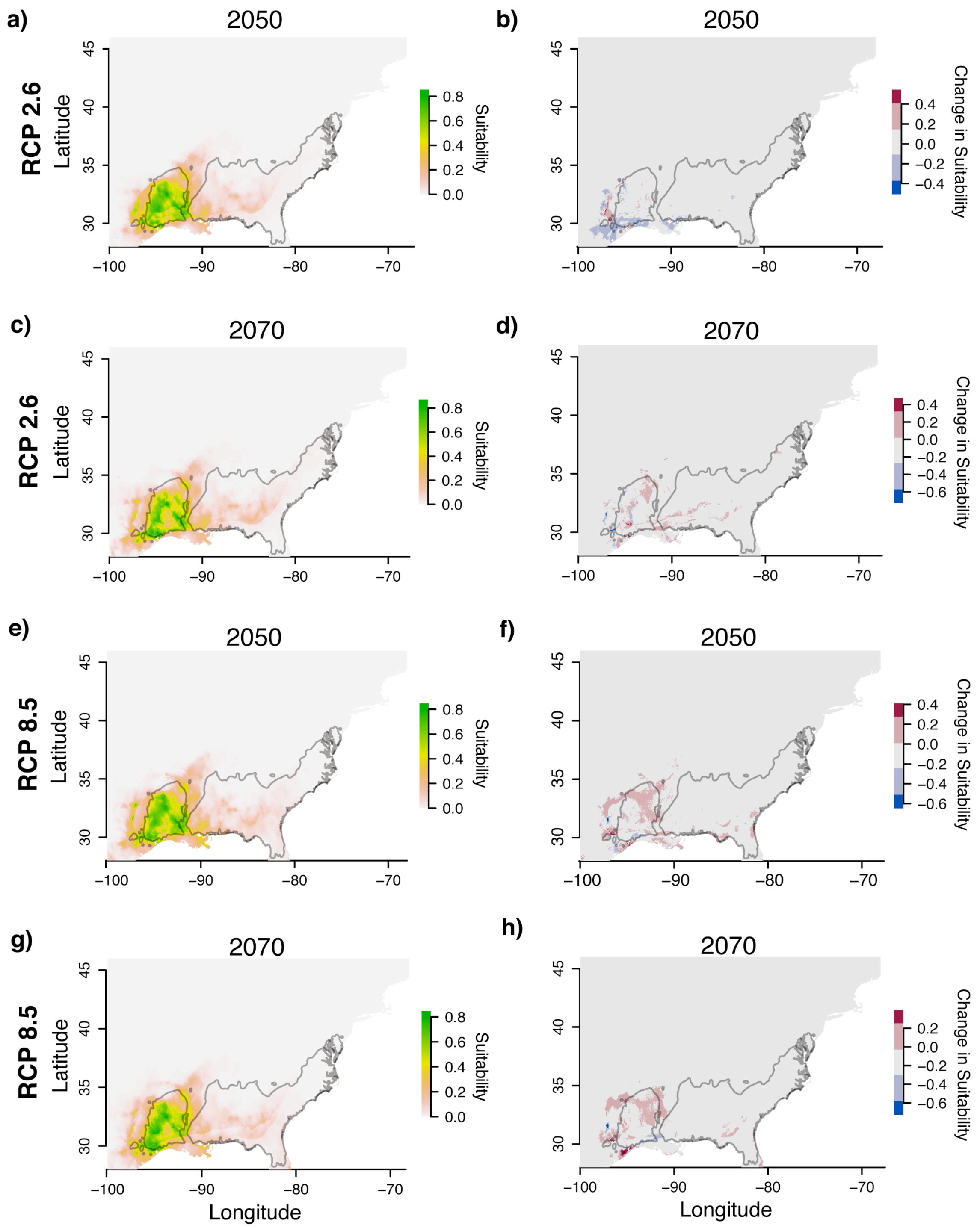
Appendix H-10

Forecast suitability projections for east *P. taeda* across two time periods (left panel), under two climate scenarios, and change in suitability map presented in the main paper (right panel).



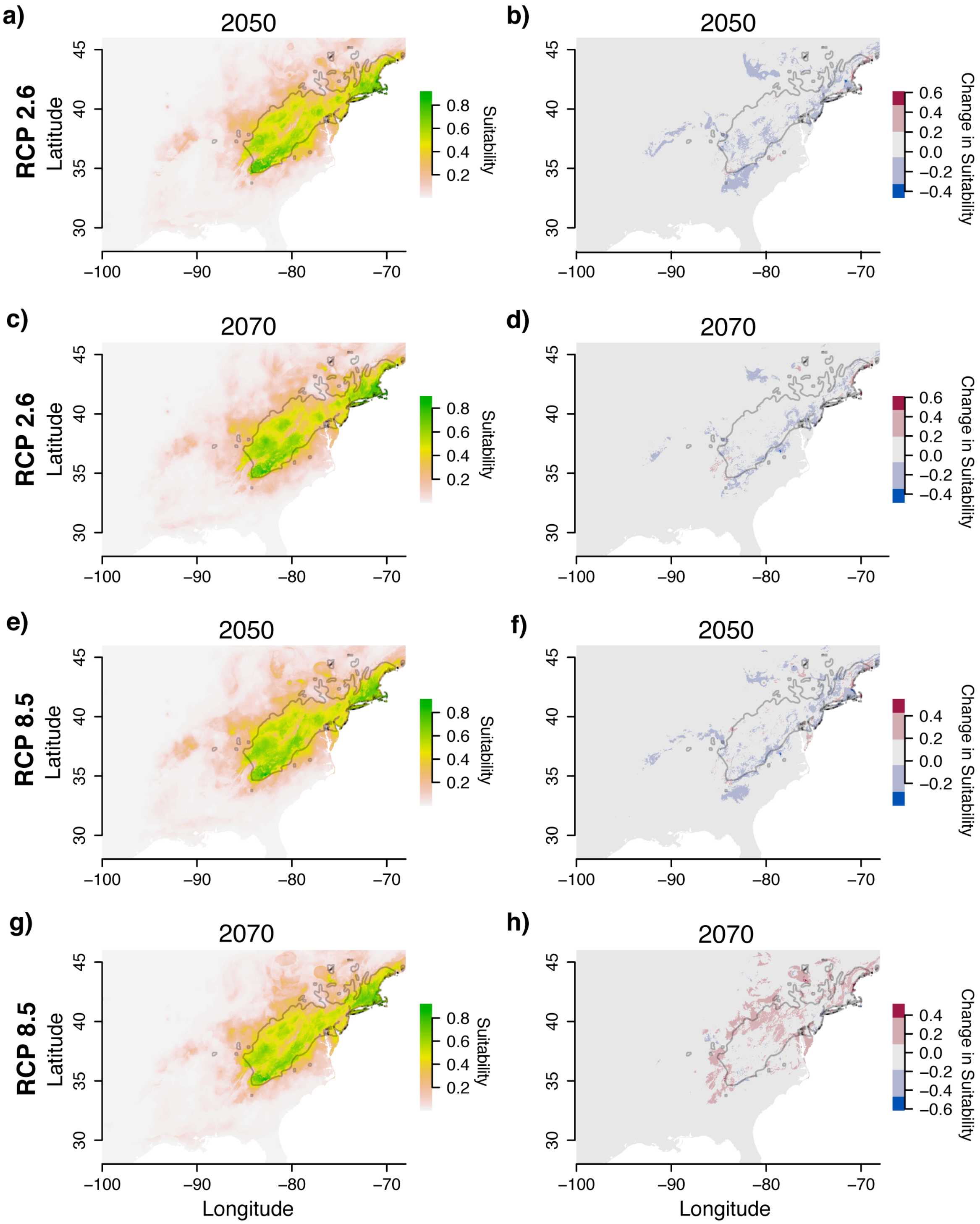
Appendix H-11

Forecast suitability projections for west *P. taeda* across two time periods (left panel), under two climate scenarios, and change in suitability map presented in the main paper (right panel).



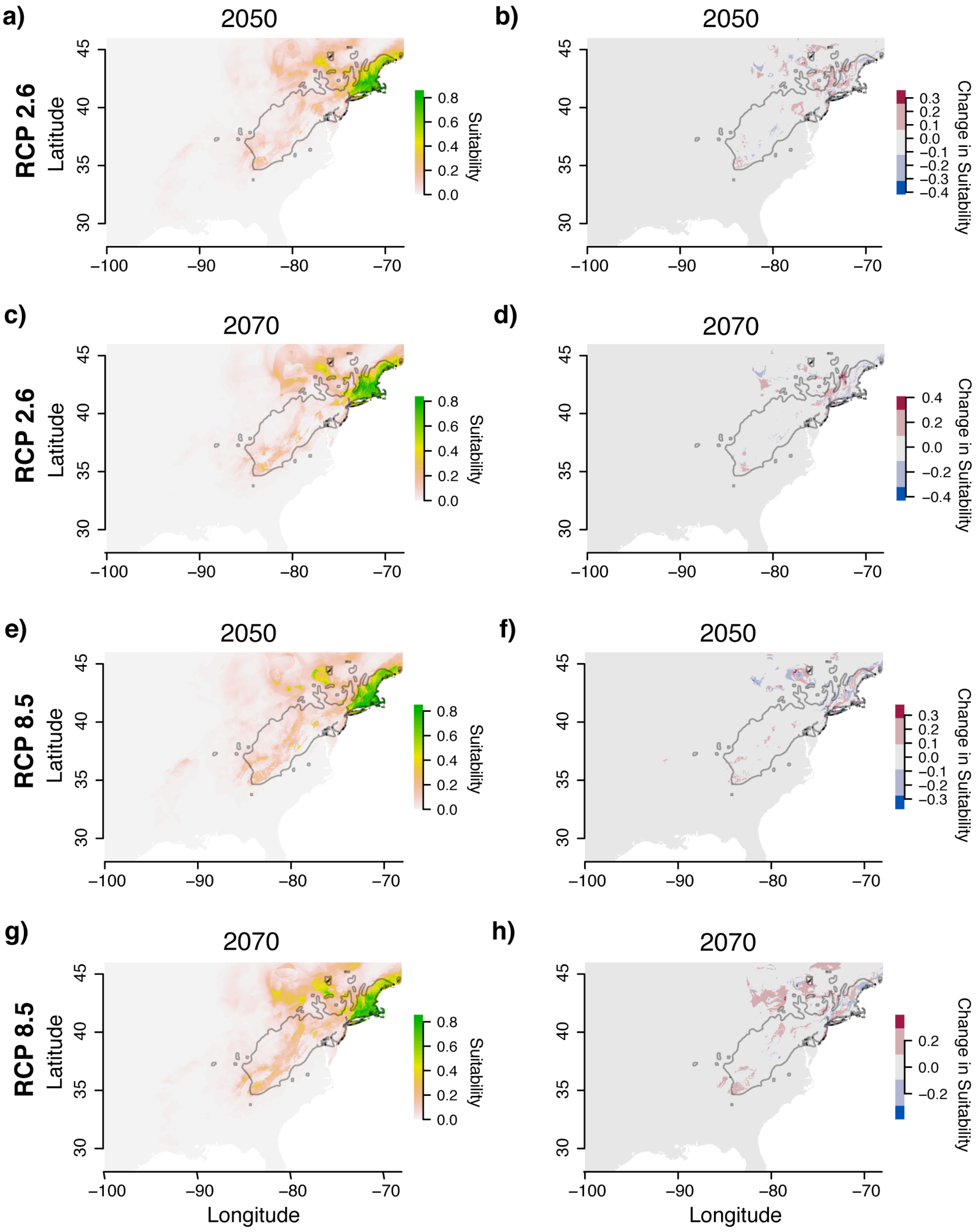
Appendix H-12

Forecast suitability projections for *P. rigida* across two time periods (left panel), under two climate scenarios, and change in suitability map presented in the main paper (right panel).



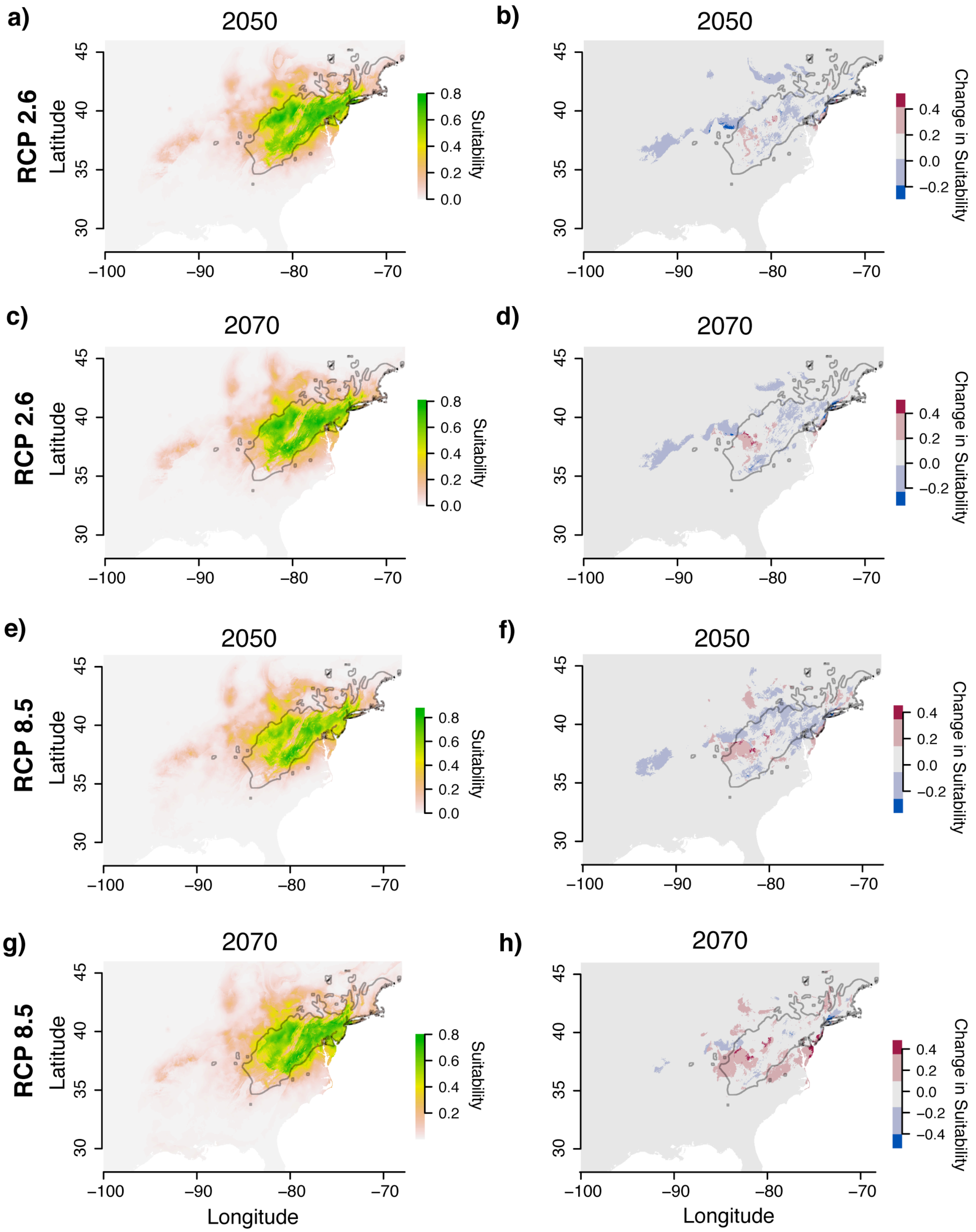
Appendix H-13

Forecast suitability projections for north *P. rigida* across two time periods (left panel), under two climate scenarios, and change in suitability map presented in the main paper (right panel).



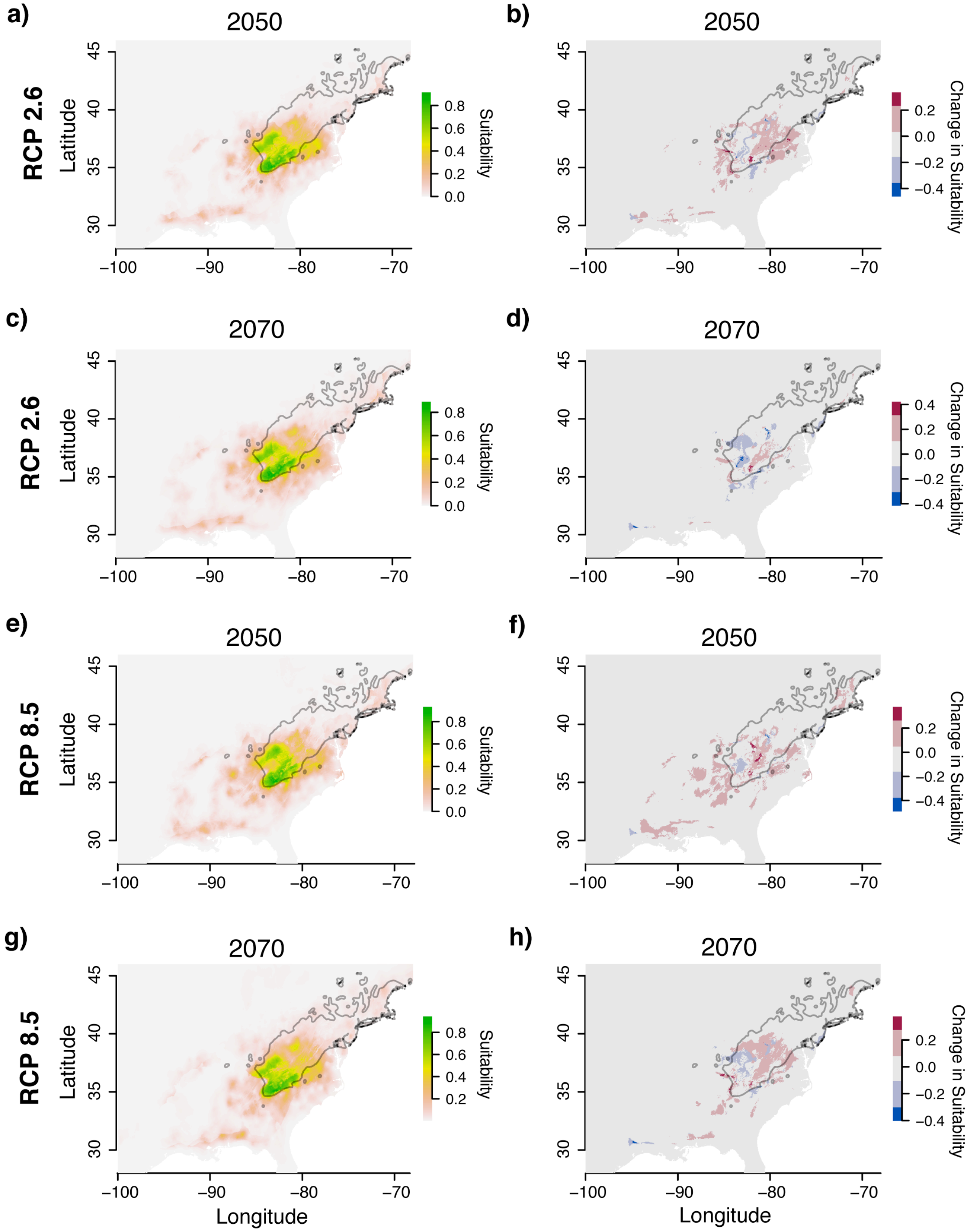
Appendix H-14

Forecast suitability projections for mid *P. rigida* across two time periods (left panel), under two climate scenarios, and change in suitability map presented in the main paper (right panel).



Appendix H-15

Forecast suitability projections for south *P. rigida* across two time periods (left panel), under two climate scenarios, and change in suitability map presented in the main paper (right panel).



VITA

Constance Ellen Bolte was born on April 2, 1982 in Alexandria, Virginia. She graduated from Monacan High School, Richmond, VA in 2000. Constance received her Bachelor of Science in Biological Sciences and Master in Teaching from Virginia Commonwealth University, Richmond, VA in 2006. She was employed by Henrico County Public Schools for two years as an Earth Science and Biology teacher from 2006-2008. Following this initial teaching experience, she was employed by Chesterfield County Public Schools for seven years as a Biology and AP Environmental Science teacher at James River High School before joining the Master of Science in Biology program at Virginia Commonwealth University, Richmond, Virginia.