History, dispersal limitation, and environment shape the current and future ranges of forest herbs of the Southern Appalachians

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TABLE OF CONTENTS

History, dispersal limitation, and environment shape the current and future ranges of forest herbs of the Southern Appalachians

Appendices

LIST OF TABLES

LIST OF FIGURES

History, dispersal limitation, and environment shape the current and future ranges of forest herbs of the Southern Appalachians

ABSTRACT

As climate changes, favorable climatic conditions for some species might cease to overlap with their current geographic ranges, due to low dispersal rates, barriers to dispersal, or lack of microhabitats, among others. Here, we focus on herbaceous paleoendemics plants in the Southern Appalachian Mountains, possibly threatened by climate change. We developed species distribution models to identify areas of predicted current suitable habitat, both inside and outside of ranges, and evaluated the extent to which these areas shift or move northwards under various future climate scenarios. We discovered predicted suitable habitat in northern areas disjunct from current ranges, suggesting dispersal limitation. We also found severe reductions in predicted suitable habitat under future climate scenarios, both in geographic extent and in percent suitability. Results from models created using more widespread species reinforced these results. Thus, it is imperative to employ conservation efforts in order to prevent species declines or extinctions.

INTRODUCTION

Species' geographic range limits are not always stable, and understanding how and why they might shift, as well as what factors limit them currently, are key questions in ecology, with implications for both invasive species and conservation biology. There is extensive evidence documenting both historical and contemporary range shifts, both contractions and expansions. Historically, many plant species' ranges have shifted dramatically in response to Pleistocene glacial cycles (Vuilleumier 1971; Lyons 2003). During the late Quaternary, climate change resulted in various responses depending on the plant species (Davis and Shaw 2001; Jackson and Overpeck 2000). Some plants, such as some temperate forest trees in the Mississippi River Valley, did not shift their range substantially (Delcourt et al. 1980; Givens and Givens 1987; Jackson and Givens 1994), while other plants shifted ranges slightly (Brubaker 1975; Betancourt 1990) or to a much greater extent (Webb 1987; Betancourt et al. 1991; Kullman 1996).

There is overwhelming evidence of contemporary range shifts, including range expansions by invasive species (Richardson and Rejmanek 2011; Sakai et. al. 2001), as well as evidence of range contractions (Pauli et. al. 2007; Moritz et. al. 2008). It is clear that species' geographic ranges are shifting northward and to higher elevations in response to contemporary climate change (Walther et. al. 2002; Parmesan 2006; Beckage et al. 2008; Kelly and Goulden 2008; Elith and Leathwick 2009). Meta-analyses have suggested that as many as 80% of taxa are currently shifting their ranges polewards or upslope (Bakkenes et. al. 2002; Root 2003). Both historically and currently, species shift ranges in response to climate change quite differently depending on their propensity to disperse and the pace at which they can track changing climatic conditions, with highly mobile species more likely to disperse farther and faster (Root 1997; Parmesan et. al. 1999; Walther et. al. 2002; De Bruyn et. al. 2009). Many species with low mobility are unable to track ideal climate conditions either due to dispersal limitation (Svenning and Skov 2004; Malcolm et. al. 2006; Midgley et. al. 2006; but see Engler et. al. 2009), a prohibitively high climate change velocity (Malcolm et. al. 2006; Sandel 2011) or the presence of barriers preventing dispersal (Finn et. al. 2006; Honnay et. al. 2002). These species are more likely to face extinction. Estimates of species extinctions by the year 2050 range from 15-37% of terrestrial species with low mobility (Thomas et. al. 2004; Zhu et. al. 2012), to 11% of all species (Maclean and Wilson 2011).

There is evidence that plant ranges may shift particularly slowly in response to climate change (Svenning and Skov 2005). It is thought that many European trees are still expanding their ranges northward in response to the warming trend after the last glacial maximum 22,000 years ago, and have not yet filled their fundamental niches (Svenning and Skov 2005). This is supported by their ability to naturalize outside their current ranges but still within the large probable fundamental niche (Svenning and Skov 2005) and suggests that their ranges have been shaped by post-glacial dispersal limitation (Svenning 2007; Van de Veken 2008). These studies seem to be an exception to the majority of niche models and transplant studies showing that niche limits coincide with range limits (Hargreaves 2013; Lee-Yaw et. al. 2016). Still, species with intrinsically slow dispersal rates are likely to have niche limits larger than their range limits (Jump and Peñuelas 2005; Stevens 2015).

Species with narrow ranges may be particularly at risk of extinction due to climate change. Narrow-ranged species tend to be concentrated into a small subset of terrestrial environments that have unusual climates, particularly in areas that are cooler and higher than surrounding areas (Ohlemüller et al. 2008). It has been argued that a number of these biodiversity hotspots (centers of endemism) have harbored refugial populations during past cycles of climate change because these environments were formerly more widespread (e.g. NE Queensland rain forest). Thus, these biodiversity hotspots may represent regions where extinction was buffered and relict species have sometimes been called "paleo-endemics" (Stebbins and Major 1965). Importantly, for hotspots occurring in relatively cool and high-elevation regions, climate change is particularly likely to result in the contraction of suitable habitat and/or greater distances among limited areas of suitable habitat, both of which pose considerable challenges for conservation.

Our work focuses on the Southern Appalachian Mountains of the United States, which is a biodiversity hotspot and center of endemism for plants and animals of eastern temperate deciduous forests (Estill and Cruzan 2001; Milanovich et. al. 2010). The concentration of species in the high-elevation regions of the Southern Appalachians is likely caused by both high rates of *in situ* diversification (Kozak et. al. 2005) and low rates of extinction during glacial cycles (Delcourt 2002; Figure 1). It has been suggested that during glacial maxima, many plant species' ranges were restricted to the southern U.S. and as glaciers retreated, species ranges retreated to higher elevations, and range expansion further north was prevented by an inability to adapt or to disperse to newly available habitat (Delcourt 2002; Root et al 2003; Thomas et al 2004; Parmesan 2006).

There is some evidence that dispersal limitation may contribute to the concentration of herbaceous endemic plants in the Southern Appalachians and influence future responses to climate change. A number of authors have noted that forest herbs, most of which are dispersed by gravity or ants, often have limited dispersal ability (Peterken 1974; Duffy 1992; Bossuyt 1999; Matlack 2005). Furthermore, a recent meta-analysis has provided support for the idea that the highest concentration of narrowly endemic forest herbs is found in the high mountainous areas south of the extent of the last glacial maximum (Bellemare and Moeller 2014). There is anecdotal evidence to suggest that some southern, narrow endemics can naturalize far north of their current range limits, but these efforts have not been formal (e.g. Case and Case 1997). A few other species with narrow ranges in the Southern Appalachian Mountains have small, disjunct northern populations (White et al 1984; Schafale and Weakley 1990; Wiser et al 1998).

We used species distribution models (SDMs) to evaluate the role of history versus current environments in limiting the ranges of endemic forest herbs, and examined the magnitude of changes in suitable territory under climate change. SDMs are commonly used to infer the controls on species' distributions, identify and prioritize areas for conservation, and predict shifts in species' ranges under changing environments. SDMs conducted in a comparative framework on sets of species with similar characteristics can provide particularly useful information on general patterns and processes influencing distributional limits. Here, we develop SDMs on a set of eight forest herb species that all have narrow distributions in the Southern Appalachian Mountains but vary in the extent to which their ranges extend north of that region. Our focal endemic species occur sparsely in nature, which poses a challenge for building SDMs; however, our comparative approach explores the sensitivity of predictions for ecologically similar species that differ in the availability of occurrence records and the north-south extent of the range. Using future climate projections, we were particularly interested in comparing the extent to which predicted future distributions shift north along the Appalachian chain and how potential dispersal barriers might influence the potential range shifts.

We developed SDMs for four species that are endemic exclusively to the Southern Appalachians (*Diphylleia cymosa, Phacelia fimbriata, Shortia galacifolia, Trillium vaseyi*) and four others that have similarly narrow ranges in the Southern Appalachians plus varying amounts of territory to the north (*Houstonia serpyllifolia, Maianthemum canadense, Prosartes lanuginosa, Trillium undulatum*). We constructed SDMs using both MaxEnt and boosted regression trees (BRT), and projected these models across eastern North America. We were particularly interested in addressing the following questions:

(1) For endemics, to what extent is apparently suitable territory present north of the species' current range, and is that potential territory contiguous with the current range or disjunct?

(2) To what extent do projections of suitable territory under future climates overlap with current ranges, and are potential dispersal barriers (environmental or physical) likely to influence northward population expansion?

(3) What is the relative magnitude of projected northward range shifts under climate change and the location of future suitable territory for narrow endemics versus intermediate and widespread forest herbs? What do these results suggest about the potential for SDM development for rare species with few occurrence records?

METHODS

Study Species

We focused on eight species of herbaceous flowering plants whose ranges overlap in the Southern Appalachian Mountains (Figure 1). Four species are endemics to western North Carolina, East Tennessee, and adjacent regions (*Phacelia fimbriata* Michx., *Diphylleia cymosa* Michx., *Shortia galacifolia* Torr. & A. Gray., and *Trillium vaseyi* Harbison); two have widespread ranges across the eastern United States (*Maianthemum canadense* Desf., *Trillium undulatum* Willd.) and two have ranges that are intermediate in size (*Prosartes lanuginosa* Michx., *Houstonia serpyllifolia* Michx.). The four widespread species have similar habitat requirements to the endemic species (Howe and Smallwood 1982; Matlack 1994), and in the southeastern United States, their ranges are restricted to the Southern Appalachian Mountains. *Phacelia fimbriata* and *Houstonia serpyllifolia* are annuals, while the remainder are herbaceous perennials.

Dispersal mechanisms vary among species. *Phacelia* seeds likely have barochory (gravity-driven) dispersal (Glass and Levy 2011); this dispersal type tends to have lower dispersal distances than other types (Van der Pijl 1982; Vittoz and Engler 2007). Species in the genus *Trillium* are myrmecochorous (Beattie and Culver 1981; Handel et al. 1981) with occasional long distance dispersal by deer and yellow-jackets (Jules 1996; Zettler and Spira 2001; Bale et al. 2003; Vellend et al. 2003). *Diphylleia* is likely dispersed by birds and/or mammals; *Maianthemum* likely has a high dispersal ability due to deer browsing (Skinner and Telfer 1974). Dispersal mechanisms for the other species are not clear.

Locality Data

We obtained presence records for all species in the field during April, May and June of 2013 and 2014, and supplemented both by herbarium records from the online database gbif (Global Biodiversity Information Facility, www.gbif.org), and correspondence with other researchers. We removed duplicate, erroneous and outlier records. Total number of presence points ranged from 20 to 1017 per species (Table 1). For each species, the spread of presence points covered the majority of the geographic range. Despite few occurrences, some simulation studies suggest that SDMs can successfully be constructed with 30 or fewer localities (Guisan et al. 2007, Pearson et. al. 2007).

For *Maiathemum canadense*, and *Trillium undulatum*, some portions of the species' range were far more heavily sampled than others; therefore, we downsampled using the R function gridSample such that there was only one presence point per raster cell.

Environmental Data

We obtained environmental data from the online database WorldClim (version 1.4, www.worldclim.org; Hijmans et al. 2005). WorldClim is a freely available set of layers of global climate data; we used a grid cell resolution of 1km by 1km (30 arc-seconds). We used the Eastern United States (30 to 60 degrees latitude; -90 to -60 degrees longitude; tile 13) as the geographic extent. For each species, we selected predictor variables from the full list of 67 predictors (36 temperature, 12 precipitation, 19 bioclim). Bioclim predictors include various interactions between temperature and precipitation predictors, such as the temperature of the wettest quarter. In order to pare down this list, we ran a principal components analysis using all 67 available predictors, then eliminated correlated predictors. This resulted in set of 5-9 predictors for each species. These were reduced further or increased, depending on the modeling method used. See Tables 2 and 3 for the predictors used to model each species.

Modeling Methods

We selected two methods (MaxEnt and boosted regression trees) as they both consistently perform well compared to other modeling methods (Elith et. al. 2006; Hijmans and Graham 2006; Phillips et. al. 2006). MaxEnt is a machine-learning, presence-only method (Phillips et al. 2004); boosted regression trees (brt) is an ensemble method that combines regression trees and boosting (Elith et. al. 2008). In this method, decision trees are generated using repeated binary splits; then many such trees are combined using boosting, which enhances overall model performance. Here, we generated brt models with R packages dismo (Hijmans et al. 2017), rgeos, and using the gbm.step function (Ridgeway 2017).

For both MaxEnt and brt, we built a total of twelve models. Eight were built using presence and pseudoabsence points only from the Southern Appalachian Mountains, specifically, inside the current geographic ranges of the endemic species (termed SA models). The SA models for the widespread species thus included only a subset of their entire ranges. We supplemented the SA models with four additional models for the widespread species that included localities from the entirety of each species' full range (full range models: FR models).

We compared the results of the full range models (FR) and Southern Appalachian models (SA) for the widespread species to assess the sensitivity of model predictions to the size of the dataset and the inclusion vs. exclusion of northern localities. If the areas of predicted suitable habitat strongly coincided (and the presence points of the widespread species occurred within that predicted suitable habitat from the SA models), this increased our confidence that a low number of presence points in the Southern Appalachians for any species (endemic or widespread) has the potential to predict the distribution of suitable habitat in the northeastern U.S.

MaxEnt Models

For MaxEnt models, we clipped environmental layers to the species' respective ranges using ArcMap software (ESRI 2016). For species with >40 occurrence points and a larger range, we delineated a box (34 to 36.5 degrees latitude; -85 to -80 degrees longitude) encompassing the entire species' range. This box includes the mountainous region where populations occurred plus adjacent lowland areas. For species with <40 occurrence points, we defined a narrower region surrounding occurrence points (an ellipse encompassing only the Appalachian Mountains, oriented SW to NE). This restricted the number of pseudoabsence points to areas closer to the actual range, which increased model performance. The number of predictors in each model was further reduced from the original list of uncorrelated variables down to 3-6, using MaxEnt's machine learning algorithm.

Pseudoabsence points were generated by MaxEnt. The number of pseudoabsence points varied among species; for some we decreased from the default of 10000 so as to accommodate the low number of presence points (Table 4). For all species except *Houstonia*, we used only linear and quadratic features; hinge and product features we turned off (Philips 2008). Other model settings were adjusted among species to increase model fit (Table 4). We increased the regularization coefficient to produce smoother response curves and prevent overfitting of the model, especially when projecting to new areas. We increased the value of τ, the default presence detectability, for the endemics, as they are immobile and showy in spring seasons, and are easily detectable during the period of time in which searches occurred (April and May). Bootstrapped models decreased model evaluation scores (AUC, TSS, and Kappa), and the models predicted highly suitable habitat in areas inconsistent with known habitat requirements within the species' current ranges. These models were discarded.

Phacelia datasets were evaluated with 5-fold cross validation. The model output and evaluation scores did not differ from models made without cross-validation. For model predictions, we used minimum training presence as the threshold value in order to minimize the omission error (false negatives); this increases the area in the model classified as "suitable habitat." We did this as areas sampled could only be visited in April and May; this small time window prevented visits to all sites with potential presence points. For a full list of parameter changes, see Table 4.

Boosted Regression Tree Models

In our second modeling method, boosted regression trees, we obtained pseudoabsence points using the rgeos and maptools packages in R. For each species, we plotted the presence points geographically. We then generated a series of circles, converted to polygons, with a specified radius centered on each presence point. We then merged them to create a larger area enveloping the presence points. Random pseudoabsence points were populated within this area. For each species, we used between 150 and 1400 pseudoabsence points, depending on the size of the species' range and the number of presence points (Table 5). We chose this method so the number of pseudoabsence points would be proportional to the number of each species' presence points.

We altered model settings to maximize model performance. We adjusted tree complexity (which allows for interactions between predictors) and learning rate (the amount of error reduction applied in each run) for each species in order to maximize both the number of trees and model accuracy. Tree complexity ranged from 1 to 5, and the learning rate ranged from 0.01 to 0.001 (Table 5).

The selection of environmental variables to be retained in brt models differed from the method used in MaxEnt models. We used the gbm.simplify command first to reduce the full set of 67 predictors. This command uses k-fold cross-validation to selectively remove low-contributing environmental predictors from the model. After this process, highly correlated predictors (determined using the PCA) were removed manually. We retained slightly correlated predictors in the model and used a second round of gbm.simplify to eliminate low-contributing predictors. Final models contained between 5-16 predictors.

Model Evaluation

We used AUC, TSS, and Kappa for model evaluation. AUC, the area under the (receiver operating characteristic) curve, is an indication of model fit. If the relationship between sensitivity versus the commission error (1-specificity) lies above the diagonal of 0.5, it is considered to make predictions that are better than random chance (Phillips and Dudík 2008). TSS, true skill statistic, is the sensitivity (true positive rate) + the specificity (true negative rate) – 1. Values range from -1 to +1, with 0 or negative numbers indicating model performance no better than chance. We chose maximum true positive rate + true negative rate as the threshold value. Similar to TSS, Kappa assesses concordance (agreement) between the model predictions and the presence/absence data, taking into account the possibility of the agreement occurring due to chance. A value of 1 indicates a perfectly accurate model; values less than or equal to zero indicate model performance no better than random chance. TSS is viewed as a more reliable statistic, as Kappa relies on prevalence values, which introduces statistical artifacts not tied to biological realities (Allouche et al. 2006; McHugh 2012).

Projections under climate change

We chose two global climate models (GCMs) and two emission scenarios. We selected GCMs HadGEM2-ES and NorESMI-M from the five recommended by McSweeny and Jones (2015) and Warszawski et. al. (2013). These represent opposite extremes in temperature and precipitation variability in the Eastern United States. The HadGEM2-ES model has high temperature variability and low precipitation variability, while NorESMI-M is the reverse. The NorESMI-M model is more conservative in temperature but has a high variability in precipitation. As the HadGEM2-ES model makes more extreme predictions as far as the severity of climate change compared to NorESMI-M, we chose to focus on the more moderate NorESMI-M models. The resulting models were then projected into years 2050 and 2070. Emission scenarios take into account human carbon emissions; we chose to examine both the best-case (emissions peak around 2020 due to stringent emissions regulations: rcp2.6) and worst-case scenarios (no change in emissions: rcp8.5).

RESULTS

Endemic species: current ranges and SDM model predictions

MaxEnt and brt models predicted similar geographic areas of high suitability, but they differed in the level of that suitability. Brt models were more conservative in predicting smaller areas of highly suitable habitat; MaxEnt models predicted more areas with high suitability. Model evaluation showed high AUC scores for all endemic species (MaxEnt: 0.94-0.97; brt: 0.81-0.99), indicating good model fit, as well as high TSS (MaxEnt: 0.84-0.94; brt: 0.89-0.97) indicating accurate model predictions. MaxEnt kappa scores (indicators of the reliability of model predictions) were low while brt kappa scores were high (MaxEnt: 0.05-0.07; brt: 0.81-0.94).

Predicted suitable habitat in all models overlapped with the current ranges of the endemic species (Figures 2-3, panels A, E, I, M). Presence points occurred in areas of predicted high suitability, with few presences in areas outside of the predicted suitable habitats. Suitable territory for *Phacelia* and *Diphylleia* spanned most of the Appalachian ranges along the border of North Carolina (NC) and Tennessee (TN), while suitable territory for *T. vaseyi* and *Shortia* was concentrated in the southern half of that region.

Phacelia and *Diphylleia* models predicted highly suitable habitat in northern areas outside their current ranges (Figures 2-3, panels C and O), as far as 1140 km north of the range margins. For *Phacelia*, both models (MaxEnt and brt) predicted suitable habitat in West Virginia (WV), Pennsylvania (PA), and portions of New York (NY) and New England. For *Diphylleia*, both models predicted areas in WV to be highly suitable; however, only the MaxEnt model predicted suitable habitat in parts of NY. Importantly, both models predicted a gap in predicted suitable habitat in Virginia (VA), spanning west-to-east across the Appalachians. This gap in suitability (approx. 140km wide) along the Appalachians results in a discontinuous distribution of suitable habitat that could hinder a between the two areas. *Shortia* was predicted to have a small (brt models) to large (MaxEnt models) amount of continuous suitable habitat slightly further northeast of its current range (Figures 2-3, panel K). Both *T. vaseyi* models predicted no suitable habitat outside the current range (Figures 2-3, panel G).

Endemic species: future projections under climate change

All future climate projections showed moderate to significant reductions in suitable habitat within the endemics' current ranges, and in most cases also showed losses of suitable habitat to the north of their current ranges (Figures 2-3). For simplicity, we describe the results of future projections for one climate change scenario (NorESM1-M, rcp8.5, 2070) and then briefly describe how other scenarios differ. In MaxEnt models, only *Diphylleia* and *Shortia* retained within-range highly suitable habitat (Figure 2, panels J and N). Habitat suitability for *Phacelia* and *T. vaseyi* declined to below 50% (Figure 2, panels B and F). To the north of the species' ranges, only *Phacelia* and *Diphylleia* retained areas of suitable habitat with climate change; portions of PA and NY remained suitable for both species, and portions of WV remained suitable for *Phacelia* (Figure 2, panels D and P). *Phacelia* also gained suitable habitat in Maine and southeastern Ontario and Quebec. Brt models differed slightly in that all species retained some suitable habitat within their current ranges (Figure 3). In addition, brt predictions for *Diphylleia* seemed anomalous in that suitable habitat shifted coastward and to lower elevations, unlike all other species (Figure 3, panels N and P).

Projections using the GCM HadGEM2-ES predicted more severe reductions in suitable habitat within and outside of the ranges of the endemics (near complete loss), as compared to NorESM1-M models. For *Diphylleia* and *T. vaseyi*, HadGEM2-ES models predicted no suitable territory. For *Phacelia*, there was suitable habitat predicted in NY and further north. Surprisingly, *Shortia* models predicted a gain in suitable habitat within its current range.

As expected, projections for 2050 had smaller reductions than 2070 in predicted suitable territory within and outside of species' current ranges. In addition, models using carbon emission scenario rcp26 instead of rcp85 resulted in less severe losses of suitable habitat within and outside of current ranges.

Nonendemic species: current ranges and SDM model predictions

The Southern Appalachian (SA) models for the widespread species showed high AUC scores (MaxEnt: 0.95-0.98; brt: 0.97-0.99) as well as high TSS scores (MaxEnt: 0.80-0.87; brt: 0.90-0.97). Kappa scores were low for MaxEnt and moderate to high for brt (MaxEnt: 0.02-0.13; brt: 0.49-0.94). Full Range (FR) models showed high AUC scores for all nonendemic species (MaxEnt: 0.83-0.99; brt: 0.79-0.96) as well as moderately high TSS scores (MaxEnt: 0.54-0.92; brt: 0.48-0.81). Kappa scores were low for MaxEnt and moderate for brt (MaxEnt: 0.17-0.26; brt: 0.46-0.69).

FR model predictions overlapped strongly with the species' current ranges (Figures 4-5, panels C, G, K, O). For *Maianthemum*, *T. undulatum* and *Prosartes*, SDM predictions captured the restriction of both species to the high elevation sections of the Appalachians in the Southeast and the much broader east-west distribution north of PA. Predictions from MaxEnt models for *Houstonia* also closely corresponded to its current range (Figure 4, panel G); however, the brt model predicted a large expanse of suitable habitat north of the current range in PA and NY (Figure 5, panel G).

In comparison to the FR models, the nonendemic SA models for *Maianthemum* (both MaxEnt and brt) and *T. undulatum* (MaxEnt) performed *better* than the FR models in predicting their current ranges (Figures 6-7, panels C, G, K, O). By contrast, for *Prosartes* the SA MaxEnt model failed to predict all occurrences north of VA (Figure 6, panel C); whereas, the FR model predicted abundant suitable habitat that is continuous along the Appalachians as far north as NY (Figure 4, panel C). These results suggest that SA endemic models have the potential to predict suitable habitat north of current ranges for at least some species.

Nonendemic species: future projections

Nonendemic species' ranges responded variably to future climate scenarios (NorESM1-M, rcp8.5, 2070). For all species, losses of suitable habitat were greater from SA compared to FR models (Figures 4-7). For example, SA models predicted that

Maianthemum lost virtually all suitable habitat in North America (Figures 6-7, panel P); whereas, FR models predicted a shift to northern NY and New England (Figures 4-5, panel P). For most species, the FR models predicted significant reductions in suitable habitat within current ranges and often losses outside of ranges as well; however, those losses were not nearly as severe as in the SA models. For example, SA models predicted *T. undulatum*'s range to recede primarily to parts of Ontario and Quebec (Figures 6-7, panel L) whereas FR models are less severe in predicting recession to northern NY, New England, and parts of Canada (Figures 4-5, panel L).

Projections using the GCM HadGEM2-ES predicted more severe reductions in suitable habitat within and outside of the ranges of the nonendemics, as compared to NorESM1-M models. *Prosartes* retained habitat only in New Hampshire. *Houstonia* retained substantial suitable habitat in the Southern Appalachian Mountains and in New Hampshire (NH) and Vermont (VT). *T. undulatum* retained habitat in NH and VT. *Maianthemum* retained substantial suitable habitat in New England.

Finally, models using carbon emission scenario rcp26 instead of rcp85 resulted in model predictions more closely resembling present day predictions than any of the other models.

Environmental predictors and limiting factors

Common environmental predictors emerged among models for different species. These give insight into the specific environmental conditions that define each species' range. Unsurprisingly, temperature and precipitation during the growing season were nearly ubiquitous among models. Some variation of these predictors was found in 92% of the models. The other 8% of models included predictors during the winter. Mean temperature of the wettest quarter and mean precipitation of the warmest quarter were present in at least half of the models. Other important predictors were temperature annual range and precipitation seasonality. Based on response curves to these predictors, most species prefer narrow temperature annual ranges and low precipitation seasonality. All prefer high precipitation (regardless of time of year), and cool temperatures year-round. This correlates well with the cool, moist, cove habitats in which they are typically found. Some nonendemics prefer warmer temperatures in the wettest quarter and higher precipitation seasonality than the endemics (*Houstonia*, *Maianthemum*). Key predictors for each species also appear to reflect life history variation. *Shortia and Phacelia* are evergreen and/or overwinter as seedlings, respectively; both species SDMs include environmental predictors for fall and winter months and *Shortia* persists only in areas with very narrow temperature and precipitation variability. In contrast, the remaining species, which retain no aboveground tissue, do not have any predictors during fall and winter months.

As almost all species show an area of predicted unsuitable habitat in VA, resulting in a discontinuous distribution along the Appalachians, the predictor that most influences the model in that area is of some interest. For all of the endemics, precipitation was a key limiting factor in this region (as well as geographic regions to the north). For the nonendemics, the SA models also predicted precipitation to be a key limiting factor for all species except for *Prosartes*, where (high/low) temperature is the strongest limiting factor. The FR models, by contrast, predicted temperature to be the key limiting factor for all species except for *Houstonia* (where precipitation in May is the strongest limiting factor).

DISCUSSION

In response to climate change, the ranges of some plant species are shifting upslope or northwards, as favorable climatic conditions are moving in similar directions. Most species are limited by dispersal or an inability to adapt to novel climatic conditions. Species with restricted ranges and low dispersal capacity may more likely face extinction either because they fail to migrate quickly enough or adapt *in situ*. Particularly susceptible are “paleoendemics” because they often are restricted to cool, high-elevation areas surrounded by unsuitable habitat (Ohlemüller et al. 2008). In this study, we focused on four plant species endemic to the Southern Appalachian Mountains (SAM), a hotspot of biodiversity for temperate deciduous forests (Bellemare and Moeller 2014), and four moderately to very widespread species with ranges overlapping those of the endemics in the SAM. Our aim was to identify areas of predicted high habitat suitability both inside and outside of current ranges, and to evaluate the extent to which these areas shift or move northwards under various future climate scenarios. For three endemics, SDMs revealed areas of high suitability up to 1140 km north of their current ranges. Interestingly, in all cases, there was a gap in suitable territory separating the current range from highly suitable areas north of the range; this gap consistently occurred in southwest Virginia (VA). The same “VA gap” also appeared in most of the nonendemic SDM predictions. Under climate change, we found severe reductions of predicted suitable habitat for most species in their current ranges regardless of the climate change scenario modeled. These results suggest that conservation efforts should consider both the strong decline in habitat suitability within current ranges and the disjunct nature of suitable habitat to the north of current ranges.

History and current distributions

For *Phacelia* and *Diphylleia,* predicted suitable habitat appeared in northern areas disjunct from their current ranges. Predicted areas were large and of high suitability, especially for *Phacelia* and *Diphylleia.* The largest areas of predicted suitable habitat occurred in the Allegheny Mountains of West Virginia (WV). This location receives similar amounts of both annual precipitation and precipitation in the driest month as the Southern Appalachian Mountains. For most SA nonendemic models, the Allegheny Mountains were predicted to be suitable as well (with 60-100% suitability), indicating agreement among model predictions for a wide variety of Southern Appalachian forest herbs. The Allegheny Mountains of WV host many endemic plant species and constitute the northern section of a biodiversity hotspot for temperate forest herbs (Bellemare and Moeller 2014). Similarly, there is evidence that the region served as refugium for animals such as a subspecies of flying squirrel, *Glaucomys sabrinus fuscus*, a relict of Pleistocene glaciation which has a sister subspecies restricted to the Southern Appalachians (Odom et. al. 2001; Wells-Gosling and Heaney 1984), and the salamander *Plethodon nettingi* (Dillard, Russel and Ford 2008). These broader patterns of endemism are consistent with our SDM predictions that this region of WV contains a substantial amount of habitat similar to that in the Southern Appalachian Mountains, and that it is suitable for many of our study species.

Notably, all eight SA models (both endemic and nonendemic) predicted highly unsuitable habitat in southwest VA, spanning across the east-west extent of the Appalachians. Without this distinct gap, suitable territory would be continuous along the Appalachians for most species. Therefore, this gap could have been a dispersal barrier preventing northern migration of the endemics following the LGM. It may also prevent northern range expansion in response to contemporary climate change given that this gap is about 140km in width. The broad north-to-south distribution of the non-endemics despite this gap in suitability could be due to at least two non-exclusive hypotheses. First, nonendemics may differ from endemics in their dispersal capacity, which may have enabled long-distance dispersal across the gap. Based on our current knowledge, there is no obvious relationship between dispersal mode and range size (endemics vs non-endemics) in our pool of species (e.g. *Trillium*). Second, the non-endemics may have persisted through the LGM in northern microrefugia rather than retreating only to the Southern Appalachians. Herbaceous taxa such as *Monotropa hypopitys* and *Smilax* spp. appear to have persisted through glaciation in the “driftless area” of Minnesota, Iowa and Wisconsin (Beatty and Provan 2011; Li et. al. 2013). For example, Li et. al. (2013) found that haplotypes of eastern U.S. *Smilax* spp. segregate into two groups, one in the “driftless area” (centered in Wisconsin) and one on the eastern seaboard, with populations concentrated in the Southern Appalachian Mountains. The endemic species’ ranges, by contrast, may have contracted more severely during advances in glaciation such that they persisted only south of the VA gap.

Robust tests of species distribution model predictions often involve field transplant experiments in areas predicted to be suitable versus unsuitable. Some transplant studies show agreement between model predictions and performances of transplant populations (e.g. Douglas fir transplants in Europe; Isaac-Renton et. al. 2014). Conversely, some transplant experiments reveal discordance between predicted habitat suitability and vital rates of transplanted populations (e.g. Swab et. al. 2014; Pattison and Mack 2008). For forest herbs of the North American temperate deciduous forest (TDF), transplant experiments would be especially useful in the unsuitable region of southwest VA and the suitable, but unoccupied northern areas, especially the Allegheny Mountains of WV. We have conducted transplant experiments for *Phacelia* and *Diphylleia* that include sites in areas predicted to be suitable (within and beyond the range) as well as areas predicted to be unsuitable (e.g. southwest VA). Preliminary results from a 10-year transplant experiment show that *Diphylleia* can both survive and reproduce in predicted suitable unoccupied areas up to 850km outside the range (e.g. central NY) but exhibit low survivorship in the VA gap (Bellemare and Moeller, unpublished data). Results from *Phacelia* transplant experiments were similar in that germination and survival rates were only slightly lower in suitable but unoccupied areas outside the range as compared to within the range. By contrast, in southwest VA, germination and survival were quite low but those few survivors had high fecundity (Erlandson and Moeller, unpublished data). These experimental results lend some support to the predictions of our SDMs.

Factors Limiting Ranges

There is support in the literature for dispersal limitation and for maladaptation to areas outside the range in preventing range expansion. Dispersal limitation impedes range expansion in many European trees, as evidenced by their ability to naturalize outside their current ranges (Svenning and Skov 2005). Limited adaptation may also prevent range expansion, which may be caused by insufficient genetic variation or maladaptive gene flow (Kirkpatrick and Barton 1997; Barton 2000). Transplant experiments within and beyond geographic ranges have examined whether population fitness outside of range limits is sufficiently high to enable long-term persistence. In many cases, there is evidence for strong declines in fitness that coincide with range limits (Angert and Schemske 2005; Geber and Eckhart 2005; Hargreaves 2013). There is also evidence in some systems that niche limits predicted by SDMs coincide with population fitness of transplants across the range edge, or the patterns of population growth (Eckhart et al. 2011; Lee-Yaw et. al. 2016).

In most cases, researchers have focused on how abiotic factors contribute to limited adaptation at range margins. However, it has been suggested that biotic factors may strongly influence the location of range limits (HilleRisLambers et al. 2013; Louthan et al. 2015) and there is some recent evidence for this. For example, in California vernal pool plant species, local population boundaries were influenced by competition with neighboring plants (Emery et. al. 2009). In *Clarkia xantiana ssp. xantiana* populations, there is evidence that populations might persist beyond the range boundary if damage from herbivores was eliminated (Benning et al., in review). Because SDMs are typically based only on abiotic factors, as we have done here, it is unclear whether their predictions would be affected by biotic interactions. Thus, experimental studies are needed to evaluate not only whether organisms can persist in abiotic environments predicted to be suitable outside their ranges but also how lifetime fitness is affected by species interactions.

Correlations between life history and model output

For each species, final model predictors emerged that corresponded well to their specific habitat requirements, substantiating the ability of correlative SDMs to select relevant predictors. Models for both *Phacelia* and *Shortia* include predictors in the fall and winter months. *Phacelia* seeds germinate in October and overwinter as basal rosettes; model output showed temperature in the coldest month and precipitation in October as important contributing predictors. *Shortia* is an evergreen herbaceous perennial and persists underneath snow cover. Its top contributing predictors included high temperatures in the winter months, as well as low precipitation seasonality. In contrast, the other two endemics produce aboveground organs only during the spring and summer (*Diphylleia*, *T. vaseyi*). Those species have SDM predictors for only those seasons. These correlations add support to the models' abilities to parse out significant predictors.

Climate change and implications for conservation

Currently occupied within-range habitat of the endemic species' was either predicted to become almost completely unsuitable by the year 2070 (MaxEnt), with the exception of *Diphylleia*, or was predicted to shift (brt). Suitable habitat north of WV and Pennsylvania (PA) was retained only by *Phacelia* and *Diphylleia*. Only *Phacelia* retained predicted suitable habitat in the more northern areas (NY, etc). For nonendemics, predicted suitable habitat in the Southern Appalachian Mountains shrank or disappeared, depending on the species, and the remaining predicted suitable habitat was located in WV and/or northeast, including PA and NY through to Maine, New Brunswick and southern Quebec. In this case the MaxEnt models were more optimistic than the brt models. Either both *Maianthemum* and *T. undulatum* retained some southern predicted suitable habitat (MaxEnt), or no species did (brt). In northern areas *Maianthemum* and *T. undulatum* retained most of their predicted suitable habitat (MaxEnt) or only *T. undulatum* did (brt).

Dispersal to northern areas is likely to be difficult for endemic species. Temperatures are predicted to increase 0.3-0.7°C per decade (Walther et. al. 2002), 0.19-0.34°C per decade, or 0.1°C per decade depending on the level of carbon emissions and topography (LoPresti et. al. 2015; Loarie 2009). Diffenbaugh and Field (2013) predict range shifts of several kilometers per year needed to track warming climate. Endemic plants would need to be able to disperse at least 2.7km per decade in order to reach predicted suitable habitat in eastern WV by 2070, if dispersal was diffuse. Long distance dispersal events are possible but do not likely occur frequently. While *Shortia* and *T. vaseyi* would be the most vulnerable to extinction, as they had no predicted suitable habitat in northern areas, it is important to note that for *Diphylleia*, suitable habitat in WV disappeared. This area may be a crucial stepping-stone if they would ever be able to reach habitat further north.

There is evidence that some species can persist in areas predicted to be unsuitable under SDMs; this suggests that model predictions of completely unsuitable habitat may not result in species extinctions. For example, Bocsi et. al. (2016) found that as many and 86% of US native species transplanted outside their ranges persisted in sites with wider climatic conditions. This suggests that potential suitable habitat is underpredicted by SDMs, and that persistence in sites within current ranges is possible. Incorporating physiology, phenotypic plasticity, and adaptation into SDMs can reduce the amount of predicted range loss (Bush et. al. 2016; Lyons 2017). Therefore, in light of possible shortcomings of traditional SDM predictions, targeted in-situ conservation of some existing populations may be warranted. In those cases, short-term efforts may focus on mitigating demographic and environmental stochasticity (Schemske et. al. 1994).

Although our models performed well, they may have deficiencies in terms of predicting the distributions of suitable habitat under climate change that are mitigated in other modeling methods. Indeed, some other studies have shown that losses of habitat under climate change are considerably less severe when using mechanistic compared to correlative models (e.g. Lyons 2017). Mechanistic models incorporate species' biology and physiology (e.g. energy mass and photosynthetic capability). This information may improve model performance (Lyons 2017; Mathewson et. al. 2017; Singer et. al. 2016); some authors find similar predictions using both mechanistic and correlative models (Shabani et. al. 2016; Kearney 2010). Process based models incorporate population vital rates, such as development, growth and reproduction (Eckhart et al. 2011). Both mechanistic and process based models offer a different approach and may offer different insights into the distribution of predicted future suitable habitat.

Given the severity of reductions in suitable habitat within the range and the disjunct nature of suitable habitat outside the range, assisted migration may be an important strategy for long-term conservation. McLachlan et. al. (2007) coin the term "constrained assisted migration," which allows for cautious implementation of methods coupled with extensive planning, monitoring, and flexible management plans. There are, of course, concerns about its cost effectiveness, implementation success, and decisions about how to prioritize species (Hoegh-Guldberg et. al. 2008; McLachlan et. al. 2007); however, in cases where suitable habitat is quickly disappearing and an organism's ability to track rapid climate change is minimal, it might be the only option. Plant re-introductions to native habitat vary in success rate. Many factors affect success rate, such as knowledge of species biology and genetic diversity (Godefroid 2011), and environmental similarity between source and transplant locations (Houde et. al. 2015). Success may depend upon knowledge of species' natural history, introducing appropriate genetic diversity, and selecting transplant locations that are environmentally similar to those in the native range.

Natural range shifts appear to have often involved adaptation to novel aspects of the environment (Davis and Shaw 2001). By the same token, assisted relocation efforts are likely to require consideration of genetic variation in ecologically-important traits and adaptive capacity. Given appropriate genetic variation, adaptation to novel environments can be rapid. There is considerable evidence from invasive plant species that adaptation has occurred in relatively few generations (Prentis et al. 2008). For example, Colautti and Barrett (2013) found that *Lythrum salicaria* adapted to invaded sites within 50-100 years of arrival. However, few studies exist evaluating the ability of transplanted native populations to adapt and persist over time in novel areas outside of their geographic distribution (but see Angert et al. 2008). Most reciprocal transplants for native plants occur at the range edge; these populations may be key for adapting to novel climate conditions (Rehm et. al. 2015). In any case, insights from studies on both invasive and native range limits can inform in-situ conservation efforts and assisted migration. These are strategies worth considering in order to mitigate effects of climate change on these endemic species.

Table 1. Number of presence points for each species. Presences obtained from gbif, herbarium records, and personal field observations.

Species	Number of presence points
Phacelia fimbriata	60
Trillium vaseyi	40
Shortia galacifolia	20
Diphylleia cymosa	38
Prosartes lanuginosa	139
Houstonia serpyllifolia	66
Trillium undulatum	236
Maianthemum canadense	1017

Table 2. MaxEnt models: Top six predictors that contributed to the models for all species. The total number of contributing predictors in a model are listed if there are fewer than six in the model. SA models include presence points found only in the Southern Appalachians; FR models include all the presence points in the full range of the nonendemic species.

Model	Species	Predictors
SA	*Phacelia fimbriata*	bio6, bio9, bio7, bio18, bio8, bio16
	Trillium vaseyi	bio19, tmin5, prec3, bio16, prec5, prec6
	Shortia galacifolia	bio14, bio15, tmin7
	Diphylleia cymosa	bio18, bio9, bio8, bio19
	Prosartes lanuginosa	bio4, bio11, bio7, bio8, bio17
	Houstonia serpyllifolia	tmin7, prec5, bio17, bio8, bio9
	Trillium undulatum	bio1, bio18, bio15, bio6, bio12
	Maianthemum canadense	bio1, bio15, bio9, bio3, bio11
FR	*Prosartes lanuginosa*	bio7, bio11, bio4, bio8, bio17
	Houstonia serpyllifolia	prec5, bio17, bio5, bio9, bio8
	Trillium undulatum	bio1, bio15, bio12, bio18, bio6
	Maianthemum canadense	bio11, bio1, bio15, bio9, bio3

Table 3. Brt models: Top six predictors that contributed to the models for all species. The total number of contributing predictors in a model are listed if there are fewer than six in the model. SA models include presence points found only in the Southern Appalachians; FR models include all the presence points in the full range of the nonendemic species.

Model	Species	Predictors
SA	*Phacelia fimbriata*	tmin5, bio9, prec4, bio10, bio8, prec10
	Trillium vaseyi	bio8, prec6, prec5, bio3, bio18, tmin5
	Shortia galacifoli	bio14, tmax1, bio8, prec1, bio15
	Diphylleia cymosa	tmin7, bio18, bio7
	Prosartes lanuginosa	bio5, bio8, bio12, bio17
	Houstonia serpyllifolia	bio1, bio18, bio6, bio7
	Trillium undulatum	bio5, bio9, bio7, bio1
	Maianthemum canadense	tmax9, bio2, bio7, tmin3, bio10, bio9
FR	*Prosartes lanuginosa*	bio8, bio12, bio7, bio17, bio5, bio6
	Houstonia serpyllifolia	bio1, bio18, bio5, bio7
	Trillium undulatum	bio1, bio5, bio18, prec5, bio7, bio9
	Maianthemum canadense	bio7, bio11, bio8, bio14, bio9, bio15

Table 4. MaxEnt model settings. SA models include presence points found only in the Southern Appalachians; FR models include all the presence points in the full range of the nonendemic species.

Model	Species	pseudoabsence points	beta multiplier	default prevalence
SA	*Phacelia fimbriata*	9000	1.3	0.6
	Trillium vaseyi	8000	1	0.6
	Shortia galacifolia	8000	1.5	0.5
	Diphylleia cymosa	6000	2	0.7
	Prosartes lanuginosa	10000	3	0.5
	Houstonia serpyllifolia	10000	1	0.5
	Trillium undulatum	10000	1	0.5
	Maianthemum canadense	10000	1	0.5
FR	*Prosartes lanuginosa*	10000	3	0.5
	Houstonia serpyllifolia	10000	1	0.5
	Trillium undulatum	10000	1	0.5
	Maianthemum canadense	10000	1	0.5

Table 5. Brt model settings. SA models include presence points found only in the Southern Appalachians; FR models include all the presence points in the full range of the nonendemic species.

Model	Species	absence points	number of trees (output)	tree complexity	learning rate	bag fraction
SA	*Phacelia fimbriata*	148	5400	1	0.006	0.7
	Trillium vaseyi	179	4650	1	0.002	0.7
	Shortia galacifolia	149	6600	2	0.001	0.5
	Diphylleia cymosa	248	5150	2	0.001	0.7
	Prosartes lanuginosa	449	7400	2	0.003	0.5
	Houstonia serpyllifolia	1492	5300	2	0.001	0.7
	Trillium undulatum	496	5000	2	0.003	0.7
	Maianthemum canadense	150	5300	5	0.001	0.6
FR	*Prosartes lanuginosa*	399	9350	2	0.0025	0.4
	Houstonia serpyllifolia	523	9700	1	0.001	0.7
	Trillium undulatum	400	1900	3	0.001	0.6
	Maianthemum canadense	1419	1400	3	0.002	0.6

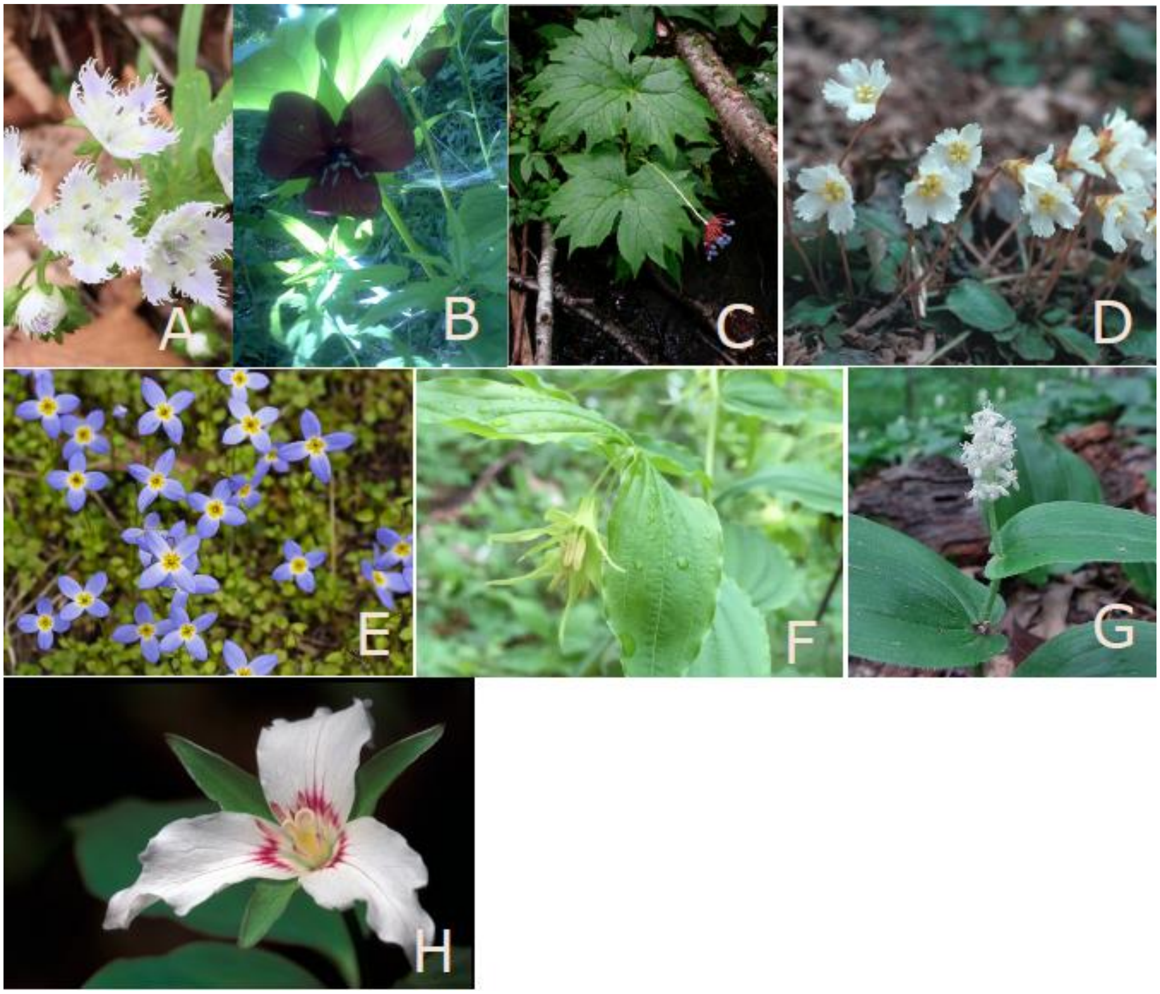

Figure 1. Images of the eight herbaceous wildflowers used in the study. A-D are endemic to the Southern Appalachian Mountains while E-H have more widespread distributions. (A) *Phacelia fimbriata*; (B) *Trillium vaseyi*; (C) *Diphylleia cymosa*; (D) *Shortia galacifolia*; (E) *Houstonia serpyllifolia*, (F) *Prosartes lanuginosa*, (G) *Maianthemum canadense*; (H) *Trillium undulatum*.

Credits: *Shortia galacifolia*. By Jean Buermeyer. Copyright © New England Wild Flower Society
Bluets (*Houstonia serpyllifolia*) copyright © William Britten
Trillium undulatum copyright © Larry Lynch

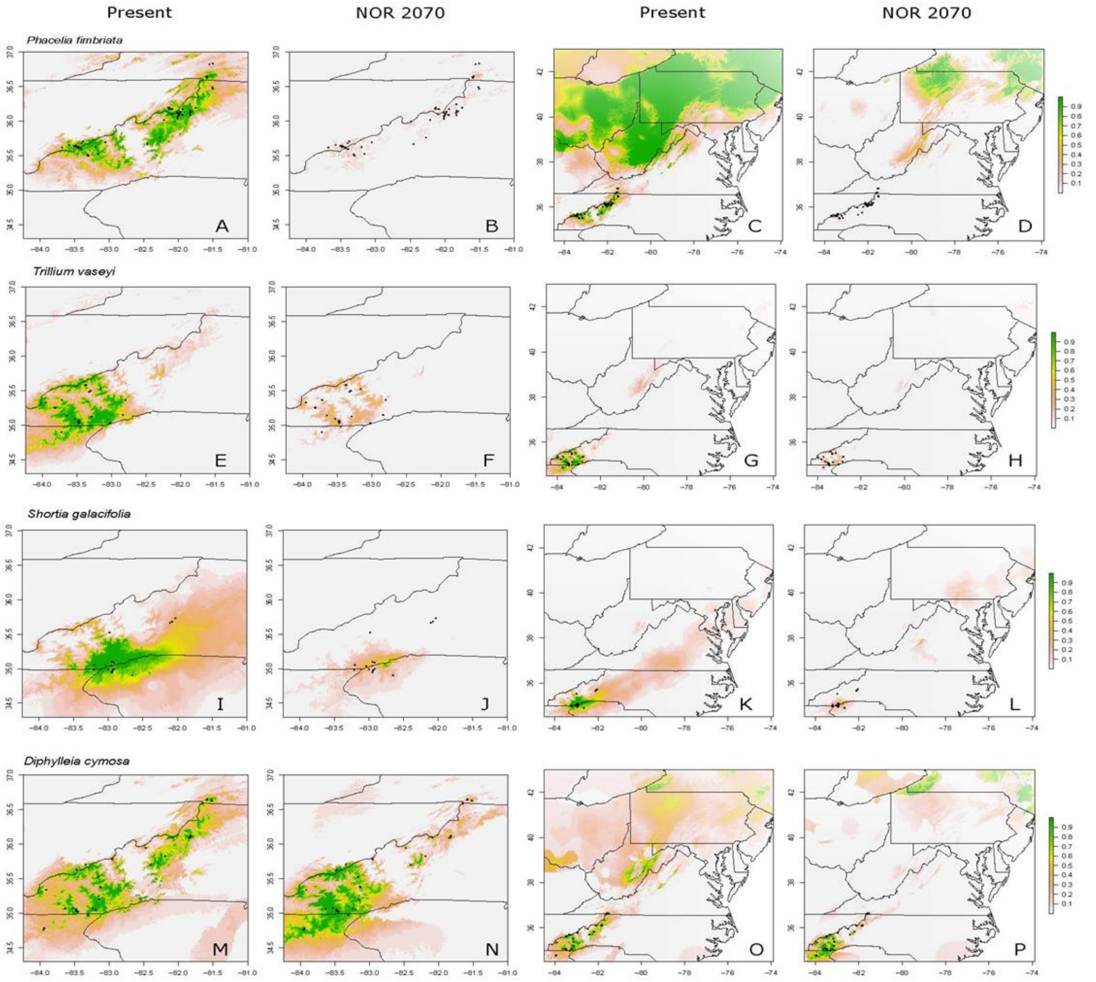

Figure 2. Predicted suitable habitat of endemic species using the MaxEnt modeling method. Both present and future climate scenarios are shown. Rows indicate species, columns indicate climate data used. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the GCM model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5.

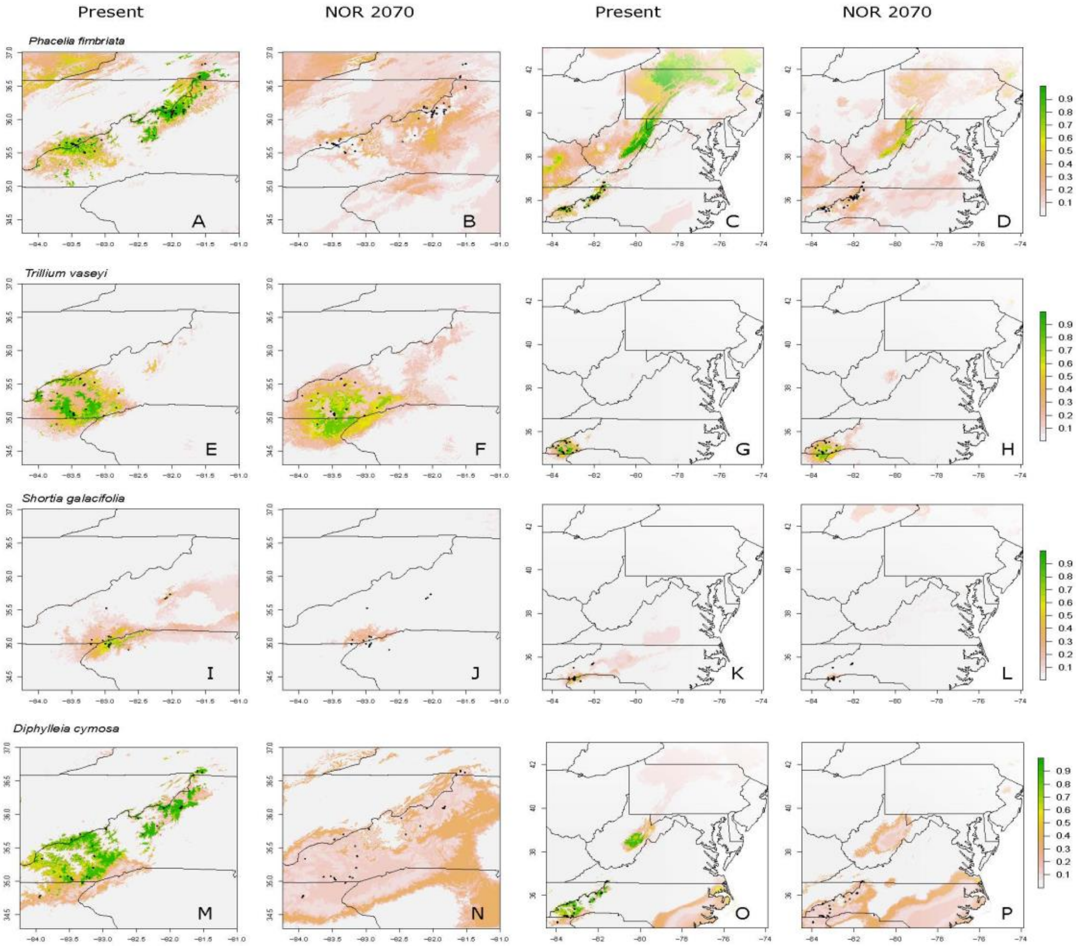

Figure 3. Predicted suitable habitat of endemic species using the brt modeling method. Both present and future climate scenarios are shown. Rows indicate species, columns indicate climate data used. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the GCM model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5.

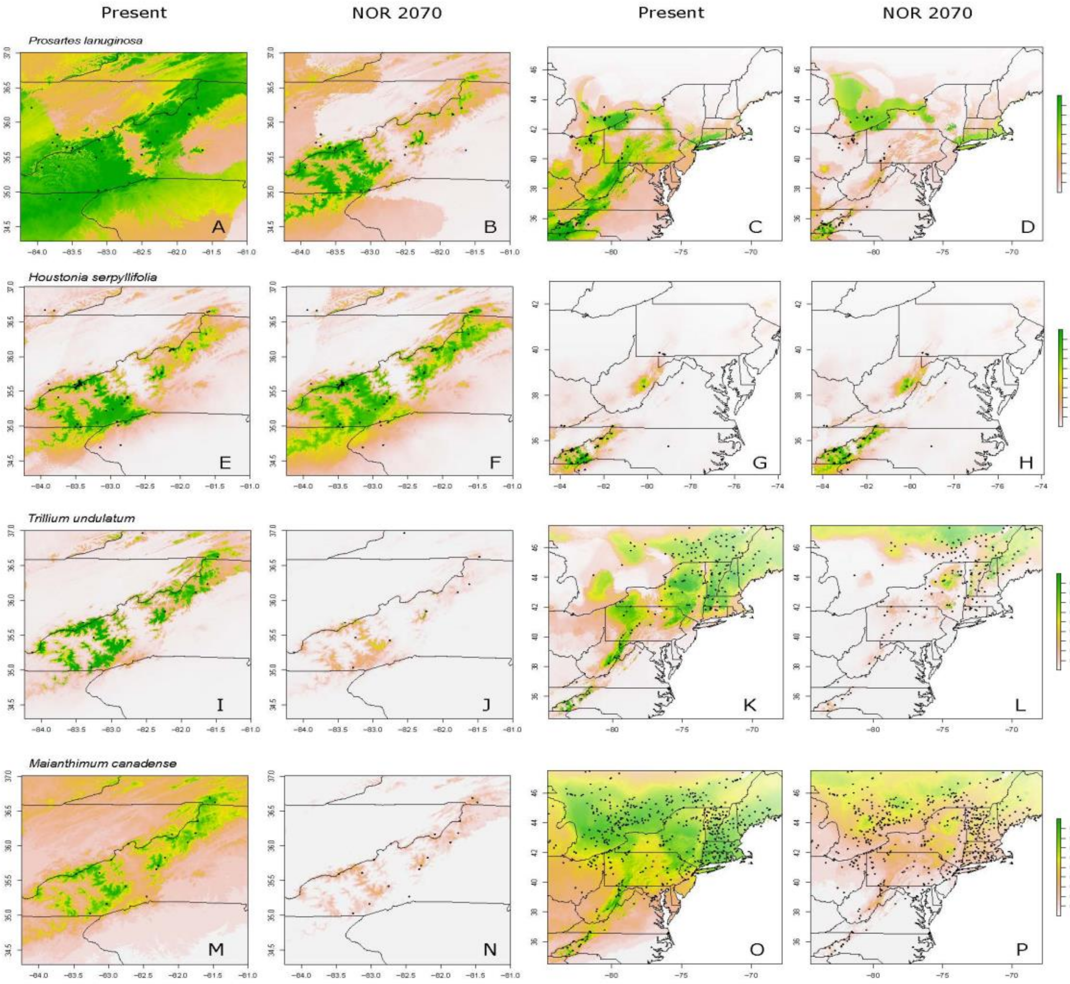

Figure 4. Predicted suitable habitat of FR models for nonendemic species using the MaxEnt modeling method. FR (full range) models were constructed using presence points found within the entire range of the species. Rows indicate species, columns indicate climate data used. Both present and future climate scenarios are shown. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the GCM model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5.

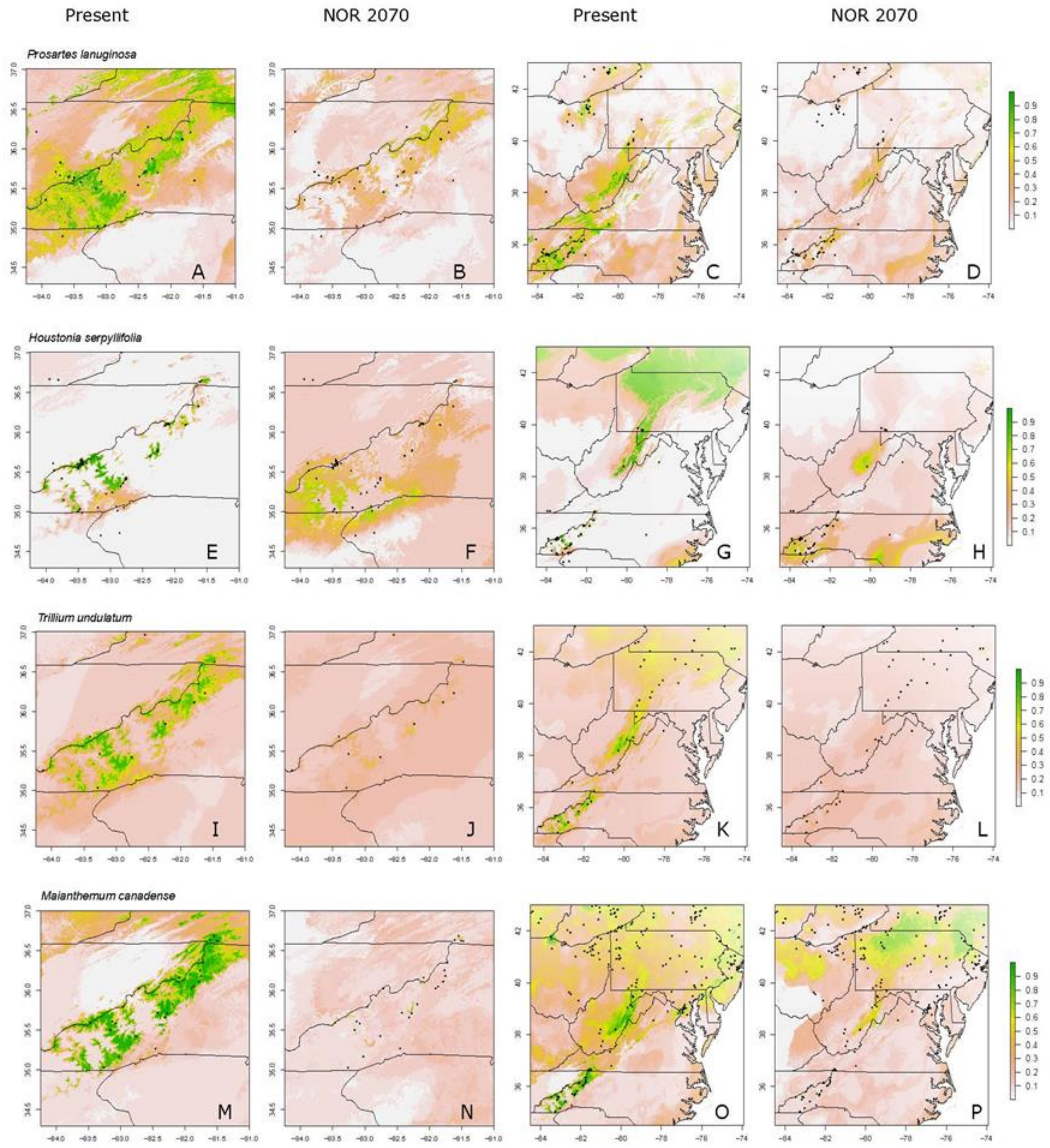

Figure 5. Predicted suitable habitat of FR models for nonendemic species using the brt modeling method. FR (full range) models were constructed using presence points found within the entire range of the species. Rows indicate species, columns indicate climate data used. Both present and future climate scenarios are shown. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the GCM model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5.

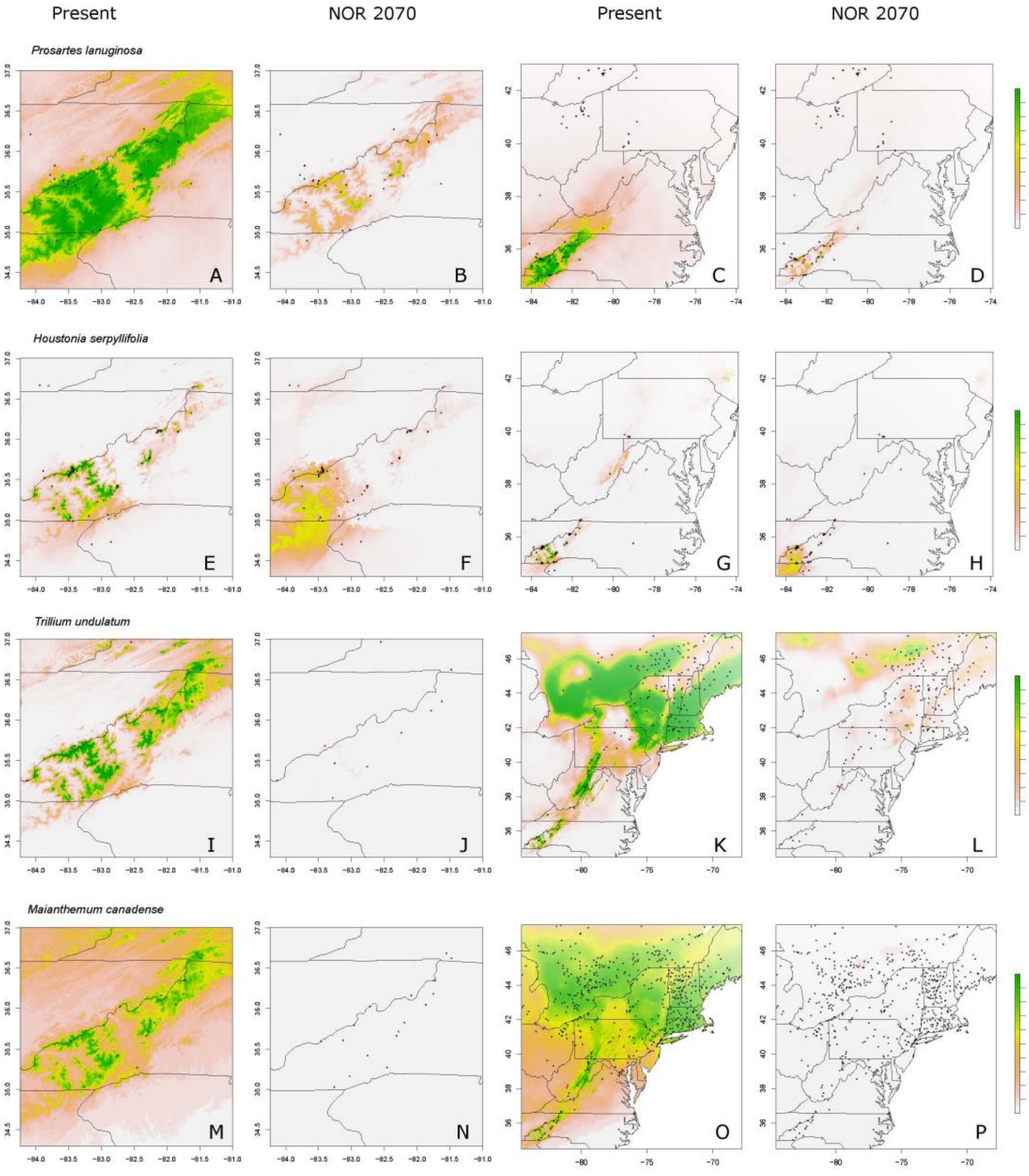

Figure 6. Nonendemic species SA models with MaxEnt modeling method

Figure 6. Predicted suitable habitat of SA models for nonendemic species using the MaxEnt modeling method. SA (Southern Appalachian) models were constructed using presence points found only within the Southern Appalachian Mountains. Rows indicate species, columns indicate climate data used. Both present and future climate scenarios are shown. Present and future climate data are taken from WorldClim version 1.4. "NOR" indicates the GCM model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5.

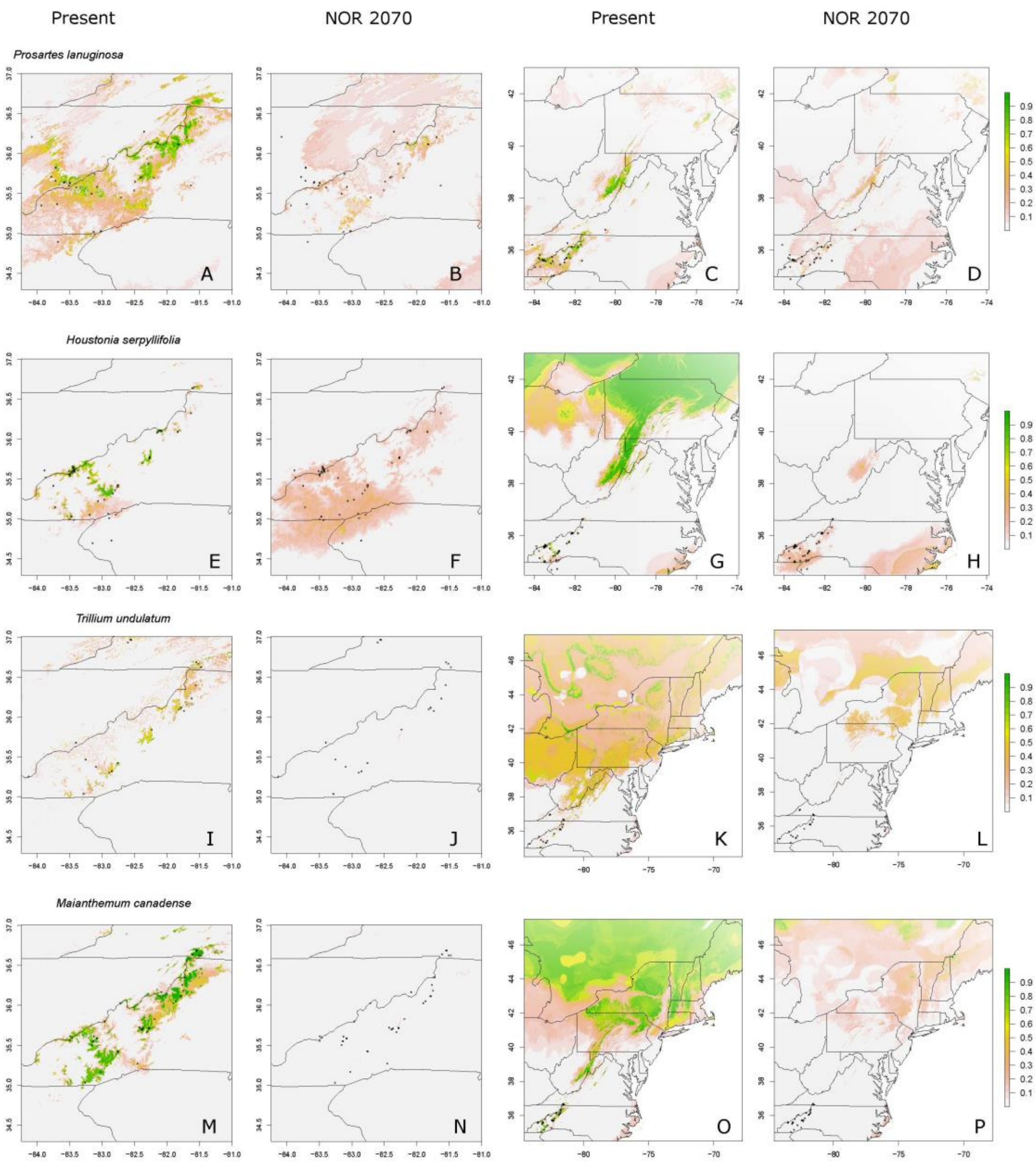

Figure 7. Predicted suitable habitat of SA models for nonendemic species using the brt modeling method. SA (Southern Appalachian) models were constructed using presence points found only within the Southern Appalachian Mountains. Rows indicate species, columns indicate climate data used. Both present and future climate scenarios are shown. Present and future climate data are taken from WorldClim version 1.4. “NOR” indicates the GCM model NorESMI-M. Models are projected into the year 2070 using the climate emission scenario rcp8.5.

BIBLIOGRAPHY

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.

Anderson, R. C., J. S. Fralish, and J. M. Baskin. 1999. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press.

Angert, A. L. 2006. Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. Lewisii*). Ecology 87:2014–2025.

Angert, A. L., H. D. B. Jr, and D. W. Schemske. 2008. Using experimental evolution to investigate geographic range limits in monkeyflowers. Evolution 62:2660–2675.

Angert, A. L., and D. W. Schemske. 2005. The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. Evolution 59:1671–1684.

Barton, N. H. 2000. Genetic hitchhiking. Philosophical Transactions of the Royal Society of London B: Biological Sciences 355:1553–1562.

Beatty, G. E., and J. Provan. 2011. Phylogeographic analysis of North American populations of the parasitic herbaceous plant *Monotropa hypopitys* L. reveals a complex history of range expansion from multiple late glacial refugia. Journal of Biogeography 38:1585–1599.

Bellemare, J., and D. A. Moeller. 2014. 21 Climate Change and Forest Herbs of Temperate Deciduous Forests.

Benning, J., V. M. Eckhart, M. A. Geber, and D. A. Moeller. 2018. Biotic interactions limit the geographic range of an annual plant: herbivory and phenology mediate fitness beyond a range margin. bioRxiv:300590.

Bentancourt J. L. 1990. Late Quaternary biogeography of the Colorado Plateau. Pp. 259–292 in Bentancourt et al. 1990.

Bentancourt, J. L., W. S. Schuster, J. B. Mitton, and R. S. Anderson. 1991. Fossil and genetic history of a pinyon pine (*Pinus edulis*) isolate. Ecology 72:1685–1697.

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Bocsi, T., J. M. Allen, J. Bellemare, J. Kartesz, M. Nishino, and B. A. Bradley. 2016. Plants' native distributions do not reflect climatic tolerance. Diversity and Distributions 22:615–624.

Bossuyt, B., M. Hermy, and J. Deckers. 1999. Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. Journal of Ecology 87:629–638.

Bridle, J. R., and T. H. Vines. 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends in Ecology & Evolution 22:140–147.

Brubaker, L. B. 1975. Postglacial forest patterns associated with till and outwash in northcentral upper Michigan. Quaternary Research 5:499–527.

Bruyn, M. de, B. L. Hall, L. F. Chauke, C. Baroni, P. L. Koch, and A. R. Hoelzel. 2009. Rapid response of a marine mammal species to Holocene climate and habitat change. PLOS Genetics 5:e1000554.

Bush, A., K. Mokany, R. Catullo, A. Hoffmann, V. Kellermann, C. Sgrò, S. McEvey, and S. Ferrier. 2016. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. Ecology Letters 19:1468–1478.

Case F., and R. Case. 1997. Trilliums. Ed. Timberland Press.

Colautti, R. I., and S. C. H. Barrett. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. Science 342:364–366.

Crespi, E. J., L. J. Rissler, and R. A. Browne. 2003. Testing Pleistocene refugia theory: phylogeographical analysis of *Desmognathus wrighti*, a high-elevation salamander in the southern Appalachians. Molecular Ecology 12:969–984.

Crowder, A. A., and G. J. Taylor. 1984. Characteristics of sites occupied by wild lily-of-the-valley, *Maianthemum canadense*, on Hill Island, Ontario. Canadian field-naturalist.

Damschen, E. I., S. Harrison, and J. B. Grace. 2010. Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). Ecology 91:3609–3619.

"Database Search" North Carolina Natural Heritage Program, North Carolina Department of Environment and Natural Resources (accessed August 18, 2016).

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673–679.

Davis, M. B., R. G. Shaw, and J. R. Etterson. 2005. Evolutionary responses to changing climate. Ecology 86:1704–1714.

De Bruyn, M., B. L. Hall, L. F. Chauke, C. Baroni, P.L. Koch, and A.R. Hoelzel. 2009. Rapid response of a marine mammal species to Holocene climate and habitat change. PLoS Genetics, 5 p.e1000554.

Delcourt H. 2002. Forests in peril: tracking deciduous trees from ice-age refuges into the greenhouse world. Ed. McDonald and Woodward.

Diffenbaugh, N. S., and C. B. Field. 2013. Changes in ecologically critical terrestrial climate conditions. Science 341:486–492.

Dillard, L. O., K. R. Russell, and W. M. Ford. 2008. Site-level habitat models for the endemic, threatened Cheat Mountain salamander *Plethodon nettingi*: the importance of geophysical and biotic attributes for predicting occurrence. Biodiversity and Conservation 17:1475–1492.

Dirnböck, T., F. Essl, and W. Rabitsch. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biology 17:990–996.

Dlugosch, K. M., S. R. Anderson, J. Braasch, F. A. Cang, and H. D. Gillette. 2015. The devil is in the details: genetic variation in introduced populations and its contributions to invasion. Molecular Ecology 24:2095–2111.

Don D. 1839. *Prosartes lanuginosa* (Michaux). Proc. Linn. Soc. London. 1: 48. Flora of North America database 26: 142-143.

Duffy, D. C., and A. J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? Conservation Biology 6:196–201.

Eckhart, V. M., M. A. Geber, W. F. Morris, E. S. Fabio, P. Tiffin, and D. A. Moeller. 2011. The Geography of Demography: Long-Term Demographic Studies and Species Distribution Models Reveal a Species Border Limited by Adaptation. The American Naturalist 178:S26–S43.

Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology 81:1667–1674.

Ellstrand, N. C., and D. R. Elam. 1993. Population genetic consequences of small population size: Implications for plant conservation. Annual Review of Ecology and Systematics 24:217–242.

Emery, N. C., M. L. Stanton, and K. J. Rice. 2009. Factors driving distribution limits in an annual plant community. New Phytologist 181:734–747.

Engler, R., C. F. Randin, P. Vittoz, T. Czáka, M. Beniston, N. E. Zimmermann, and A. Guisan. 2009. Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? Ecography 32:34–45.

Eriksson, O. 1992. Evolution of Seed Dispersal and Recruitment in Clonal Plants. Oikos 63:439–448.

Estill, J. C., and M. B. Cruzan. 2001. Phytogeography of Rare Plant Species Endemic to the Southeastern United States. Castanea 66:3–23.

Finn, D. S., D. M. Theobald, W. C. Black, and N. L. Poff. 2006. Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. Molecular Ecology 15:3553–3566.

Fordham, D. A., T. M. L. Wigley, and B. W. Brook. 2011. Multi-model climate projections for biodiversity risk assessments. Ecological Applications 21:3317–3331.

Franklin, J., F. W. Davis, M. Ikegami, A. D. Syphard, L. E. Flint, A. L. Flint, and L. Hannah. 2013. Modeling plant species distributions under future climates: how fine scale do climate projections need to be? Global Change Biology 19:473–483.

Geber, M. A., and V. M. Eckhart. 2005. EXPERIMENTAL STUDIES OF ADAPTATION IN *Clarkia xantiana*:II. FITNESS VARIATION ACROSS A SUBSPECIES BORDER. Evolution 59:521–531.

Glass, P. M., and F. Levy. 2011. Correspondence of morphology, phytogeny and reproductive barriers in *Phacelia* subgenus *cosmanthus* (Hydrophyllaceae). The Journal of the Torrey Botanical Society 138:341–352.

Godefroid, S., C. Piazza, G. Rossi, S. Buord, A.-D. Stevens, R. Aguraiuja, C. Cowell, C. W. Weekley, G. Vogg, J. M. Iriondo, I. Johnson, B. Dixon, D. Gordon, S. Magnanon, B. Valentin, K. Bjureke, R. Koopman, M. Vicens, M. Virevaire, and T. Vanderborght. 2011. How successful are plant species reintroductions? Biological Conservation 144:672–682.

Godt, M. J. W., B. R. Johnson, and J. L. Hamrick. 1996. Genetic diversity and population size in four rare southern Appalachian plant species. Conservation Biology 10:796–805.

Hargreaves, A. L., and C. G. Eckert. 2014. Evolution of dispersal and mating systems along geographic gradients: implications for shifting ranges. Functional Ecology 28:5–21.

Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. The American Naturalist 183:157–173.

Hill, S. R. 1992. Calciphiles and calcareous habitats of South Carolina. Castanea 57:25–33.

HilleRisLambers, J., M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald. 2013. How will biotic interactions influence climate change–induced range shifts? Annals of the New York Academy of Sciences 1297:112–125.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted Colonization and Rapid Climate Change. Science 321:345–346.

Honnay, O., K. Verheyen, J. Butaye, H. Jacquemyn, B. Bossuyt, and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters 5:525–530.

Houde, A. L. S., S. R. Garner, and B. D. Neff. 2015. Restoring species through reintroductions: strategies for source population selection. Restoration Ecology 23:746–753.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228.

Isaac-Renton, M. G., D. R. Roberts, A. Hamann, and H. Spiecker. 2014. Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change. Global Change Biology 20:2607–2617.

Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 26:194–220.

Jacquemyn, H., J. Butaye, and M. Hermy. 2001. Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. Journal of Biogeography 28:801–812.

Jenkins, Charles F. 1991. "Asa Gray and His Quest for *Shortia galacifolia*." Arnoldia 51(4), pp.5-11.

Jump, A. S., and J. Peñuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8:1010–1020.

Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3:203–213.

Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a Sspecies' range. The American Naturalist 150:1–23.

Kozak, K. H., A. Larson, R. M. Bonett, and L. J. Harmon. 2005. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). Evolution 59:2000–2016.

Krause, C. M., N. S. Cobb, and D. D. Pennington. 2015. Range shifts under future scenarios of climate change: dispersal ability matters for Colorado Plateau endemic plants. Natural Areas Journal 35:428–438.

Kullman, L. 1996. Norway spruce present in the Scandes Mountains, Sweden at 8000 BP: new light on Holocene tree spread. Global Ecology and Biogeography Letters 5:94–101.

Lee-Yaw, J. A., H. M. Kharouba, M. Bontrager, C. Mahony, A. M. Csergő, A. M. E. Noreen, Q. Li, R. Schuster, and A. L. Angert. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. Ecology Letters 19:710–722.

Li, P., M. Li, Y. Shi, Y. Zhao, Y. Wan, C. Fu, and K. M. Cameron. 2013. Phylogeography of North American herbaceous *Smilax* (Smilacaceae): Combined AFLP and cpDNA data support a northern refugium in the Driftless Area. American Journal of Botany 100:801–814.

Loarie, S. R., B. E. Carter, K. Hayhoe, S. McMahon, R. Moe, C. A. Knight, and D. D. Ackerly. 2008. Climate change and the future of California's endemic flora. PLOS ONE 3:e2502.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. Nature 462:1052–1055.

LoPresti, A., A. Charland, D. Woodard, J. Randerson, N. S. Diffenbaugh, and S. J. Davis. 2015. Rate and velocity of climate change caused by cumulative carbon emissions. Environmental Research Letters 10:095001.

Louthan, A. M., D. F. Doak, and A. L. Angert. 2015. Where and when do species interactions set range limits? Trends in Ecology & Evolution 30:780–792.

Lynch, M. 1993. Evolution and extinction in response to environ mental change. Biotic Interactions and Global Change:234–250.

Lynch M., and R. Lande. 1993. Evolution and extinction in response to environmental change. In P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, eds. Biotic Interactions and Global Change, pp. 234–250. Sinauer, Sunderland, MA.

Lyons, S. K. 2003. A quantitative assessment of the range shifts of Pleistocene mammals. Journal of Mammalogy 84:385–402.

Lyons, M. 2017. Moving up: Using climate, physiology, and gene flow to characterize current and future geographic range limits in montane salamanders.

Maclean, I. M. D., and R. J. Wilson. 2011. Recent ecological responses to climate change support predictions of high extinction risk. Proceedings of the National Academy of Sciences 108:12337–12342.

Malcolm, J. R., C. Liu, R. P. Neilson, L. Hansen, and L. Hannah. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conservation Biology 20:538–548.

Mathewson, P. D., L. Moyer-Horner, E. A. Beever, N. J. Briscoe, M. Kearney, J. M. Yahn, and W. P. Porter. 2017. Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. Global Change Biology 23:1048–1064.

Matlack, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75:1491–1502.

Matlack, G. R. 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. Journal of Ecology 93:50–59.

McHugh, M. L. 2012. Interrater reliability: the kappa statistic. Biochemia medica : Biochemia medica 22:276–282.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21:297–302.

Midgley, G. F., G. O. Hughes, W. Thuiller, and A. G. Rebelo. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. Diversity and Distributions 12:555–562.

Milanovich, J. R., W. E. Peterman, N. P. Nibbelink, and J. C. Maerz. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. PLOS ONE 5:e12189.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261–264.

Murdock, N. A. 1994. Rare and endangered plants and animals of southern Appalachian wetlands. Pages 189–209 wetlands of the interior southeastern United States. Springer, Dordrecht.

Newsletter of the Western Carolina Botanical Club. 2015. *Shortia*. https://wcbotanicalclub.files.wordpress.com/2015/10/shortia_2015_xxxvi_04_spring.pdf.

Odom, R. H., W. M. Ford, J. W. Edwards, C. W. Stihler, and J. M. Menzel. 2001. Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia. Biological Conservation 99:245–252.

Ohlemüller, R., B. J. Anderson, M. B. Araújo, S. H. M. Butchart, O. Kudrna, R. S. Ridgely, and C. D. Thomas. 2008. The coincidence of climatic and species rarity: high risk to small-range species from climate change. Biology Letters 4:568–572.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583.

Pattison, R. R., and R. N. Mack. 2008. Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: evaluating CLIMEX predictions with field trials. Global Change Biology 14:813–826.

Pauli, H., M. Gottfried, K. Reiter, C. Klettner, and G. Grabherr. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA* master site Schrankogel, Tyrol, Austria. Global Change Biology 13:147–156.

Peterken, G. F. 1974. A method for assessing woodland flora for conservation using indicator species. Biological Conservation 6:239–245.

Prentis, P. J., J. R. U. Wilson, E. E. Dormontt, D. M. Richardson, and A. J. Lowe. 2008. Adaptive evolution in invasive species. Trends in Plant Science 13:288–294.

"Protected Plant Species List." North Carolina Plant Conservation Program, NC Department of Agriculture and Consumer Services. (accessed August 18, 2016).

Rehm, E. M., P. Olivas, J. Stroud, and K. J. Feeley. 2015. Losing your edge: climate change and the conservation value of range-edge populations. Ecology and Evolution 5:4315–4326.

Richardson, D. M., and M. Rejmánek. 2011. Trees and shrubs as invasive alien species – a global review. Diversity and Distributions 17:788–809.

Root, T. L.in Elements of Change 1996(eds Hassol, S. J. & Katzenberger, J.) 203–206 (Aspen Global Change Institute, Aspen, Colorado, (1997).

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332.

Sandel, B., L. Arge, B. Dalsgaard, R. G. Davies, K. J. Gaston, W. J. Sutherland, and J.-C. Svenning. 2011. The influence of late Quaternary climate-change velocity on species endemism. Science:1210173.

Schafale M. P., and A. S. Weakley. 1990. Classification of the Natural Communities of North Carolina. Third Approximation. North Carolina Natural Heritage Program, State of North Carolina Department of Environment, Health, and Natural Resources, Raleigh, North Carolina, USA.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606.

Schlaepfer, D. R., M. Glättli, M. Fischer, and M. van Kleunen. 2010. A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. New Phytologist 185:1087–1099.

Segurado, P., and M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. Journal of Biogeography 31:1555–1568.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Shabani, F., L. Kumar, and M. Ahmadi. 2016. A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area. Ecology and Evolution 6:5973–5986.

Shaw, R. G., and J. R. Etterson. 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. New Phytologist 195:752–765.

Sheppard, C. S., B. R. Burns, and M. C. Stanley. 2014. Predicting plant invasions under climate change: are species distribution models validated by field trials? Global Change Biology 20:2800–2814.

Shortia galacifolia. By Jean Buermeyer. Copyright © New England Wild Flower Society

Singer, A., K. Johst, T. Banitz, M. S. Fowler, J. Groeneveld, A. G. Gutiérrez, F. Hartig, R. M. Krug, M. Liess, G. Matlack, K. M. Meyer, G. Pe'er, V. Radchuk, A.-J. Voinopol-Sassu, and J. M. J. Travis. 2016. Community dynamics under environmental change: How can next generation mechanistic models improve projections of species distributions? Ecological Modelling 326:63–74.

Skinner, W. R., and E. S. Telfer. 1974. Spring, summer, and fall foods of deer in New Brunswick. The Journal of Wildlife Management 38:210–214.

Song, B., J. Stöcklin, Z. Zhang, Y. Yang, and H. Sun. 2013. Seed and microsite limitation in *Rheum nobile*, a rare and endemic plant from the subnival zone of Sino-Himalaya. Plant Ecology & Diversity 6:503–509.

Stevens, S. M., and N. C. Emery. 2015. Dispersal limitation and population differentiation in performance beyond a northern range limit in an asexually reproducing fern. Diversity and Distributions 21:1242–1253.

Storfer, A. 1996. Quantitative genetics: a promising approach for the assessment of genetic variation in endangered species. Trends in Ecology & Evolution, 11(8), pp.343-348.

Svenning, J.-C., and F. Skov. 2004. Limited filling of the potential range in European tree species. Ecology Letters 7:565–573.

Svenning, J.-C., and F. Skov. 2005. The relative roles of environment and history as controls of tree species composition and richness in Europe. Journal of Biogeography 32:1019–1033.

Svenning, J.-C., and F. Skov. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10:453–460.

Swab, R. M., H. M. Regan, D. Matthies, U. Becker, and H. H. Bruun. 2015. The role of demography, intra-species variation, and species distribution models in species' projections under climate change. Ecography 38:221–230.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427:145–148.

Thuiller, W., G. F. Midgley, G. O. Hughes, B. Bomhard, G. Drew, M. C. Rutherford, and F. I. Woodward. 2006. Endemic species and ecosystem sensitivity to climate change in Namibia. Global Change Biology 12:759–776.

Thuiller, W., D. M. Richardson, P. Pyšek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11:2234–2250.

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Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238.

Ulrey, C., P. F. Quintana-Ascencio, G. Kauffman, A. B. Smith, and E. S. Menges. 2016. Life at the top: Long-term demography, microclimatic refugia, and responses to climate change for a high-elevation southern Appalachian endemic plant. Biological Conservation 200:80–92.

Van der Pijl, L. 1982. Principles of dispersal in higher plants. Berlin: Springer-Verlag 10, pg. 978-3.

Vellend, M., J. A. Myers, S. Gardescu, and P. L. Marks. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. Ecology 84:1067–1072.

Viera, A. J., and J. M. Garrett. 2005. Understanding interobserver agreement: the kappa statistic. Family Medicine 37:360-363.

Vitt, P., K. Havens, and O. Hoegh-Guldberg. 2009. Assisted migration: part of an integrated conservation strategy. Trends in Ecology & Evolution 24:473–474.

Vittoz, P., and R. Engler. 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. Botanica Helvetica 117:109–124.

Vivian, V. E. 1967. *Shortia galacifolia*: its life history and microclimatic requirements. Bulletin of the Torrey Botanical Club 94:369–387.

Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173:771–780.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Webb, S. L. 1987. Beech range extension and vegetation history: pollen stratigraphy of two Wisconsin lakes. Ecology 68:1993–2005.

Wells-Gosling, N., and L. R. Heaney. 1984. *Glaucomys sabrinus*. Mammalian species, (229), pp.1-8.

White, P. S., and R. I. Miller. 1988. Topographic models of vascular plant richness in the southern Appalachian high peaks. Journal of Ecology 76:192–199.

White, P. S., R. I. Miller, and G. S. Ramseur. 1984. The species-area relationship of the southern Appalachian high peaks: vascular plant richness and rare plant distributions. Castanea 49:47–61.

Willdenow, Ges. Naturf. 1801. *Trillium undulatum*. Freunde Berlin Neue Schriften. 3: 422. Flora of North America database 26: 92, 99, 105.

Williams, J. N., C. Seo, J. Thorne, J. K. Nelson, S. Erwin, J. M. O’Brien, and M. W. Schwartz. 2009. Using species distribution models to predict new occurrences for rare plants. Diversity and Distributions 15:565–576.

Winsor, J. 1983. Persistence by habitat dominance in the annual *Impatiens capensis* (Balsaminaceae). Journal of Ecology 71:451–466.

Wiser, S. K., R. K. Peet, and P. S. White. 1998. Prediction of rare-plant occurrence: a southern Appalachian example. Ecological Applications 8:909–920.

Wiser S. K., and P. S. White. 1999. High-elevation outcrops and barrens of the southern Appalachian Mountains. Savannas, barrens, and rock outcrop plant communities of North America 119-132.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology 18:1042–1052.

APPENDICES

Appendix S1

Detailed species information

Phacelia fimbriata (Hydrophyllaceae) is a small, herbaceous annual plant. It is found in hardwood forests and rich cove forests with high moisture availability (Schafale and Weakley 1990). Its range is likely restricted to the high elevations of North Carolina, Tennessee, and Virginia. Within its range, it has a patchy distribution and grows in high within-patch densities, sometimes with *Impatiens capensis* and *Urtica dioica* (personal observation; Winsor 1983). *Phacelia* seeds likely have barochory (gravity-driven) dispersal (Glass and Levy 2011); this dispersal type tends to have lower dispersal distances than other types (Van der Pijl 1982; Vittoz and Engler 2007).

Trillium vaseyi (Melanthiaceae) is a long-lived, herbaceous perennial plant found in scattered, infrequent locations in the southern Appalachian Mountains, including Georgia, Tennessee, and North Carolina (Harbison 1901; NatureServe; Carmen 2001; Case and Case 1997; Webster and Jenkins 2008). These infrequent locations include rich cove forests (Harbison 1901). Species in the genus *Trillium* are myrmecochorous (Beattie and Culver 1981; Handel et al. 1981) with occasional long distance dispersal by deer and yellow-jackets (Jules 1996; Zettler and Spira 2001; Bale et al. 2003; Vellend et al. 2003).

Shortia galacifolia (Diapensiaceae) is a low-growing, small herbaceous plant. It grows along riverbanks, rocky outcrops, or gorges in dense monocultures (Vivian 1967; North Carolina Department of Environment and Natural Resources). It is endemic to the tri-state borders of North Carolina, Tennessee, and Georgia (Jenkins 1991). It is very rare (Jenkins 1991); endangered in North Carolina (North Carolina Plant Conservation

Program; USFWS), and is considered to be a glacial relict. Its dispersal strategy is unknown.

Diphylleia cymosa (Berberidaceae) is an herbaceous perennial plant. It grows in areas with high soil calcium content (Hill 1992) and rich cove forests. It is endemic to the southern Appalachian Mountains, specifically North Carolina, Tennessee, Georgia, and Virginia. It is likely dispersed by birds and mammals.

Houstonia serpyllifolia (Rubiaceae) is an herbaceous annual plant with a range extending from the southern Appalachian Mountains to Pennsylvania. It is a facultative wetland plant, preferring wet rocky outcrops (Wiser and White 1999), rich cove forests near streams (Encyclopedia of Life, accessed 8/17/16, http://www.eol.org/pages/1111550/details), and disturbed areas (Newsletter of the Western Carolina Botanical Club. 2015. Shortia.). Its dispersal strategy is unknown. Its southern range overlaps greatly with the other four endemic species.

Prosartes lanuginosa (Liliaceae) is an herbaceous plant growing in the Southern Appalachian Mountains; its range extends north to New York and includes isolated populations in Alabama and Ontario (Don 1839). It prefers rich, moist deciduous forests. Its red berries suggest animal dispersal.

Trillium undulatum (Melanthiaceae) is a long-lived herbaceous perennial found from the Southern Appalachians into Ontario and Quebec, and as far west as Michigan. It is found in high elevation areas with deep shade, and in highly acidic soils, especially around pines and other coniferous trees (Willdenow, Ges. Naturf. 1801). Its dispersal strategy is similar to that of *T. vaseyi*.

Maianthemum canadense (Asparagaceae) is a perennial herbaceous lily with a widespread range. It occurs from the Southern Appalachian Mountains north to Ontario and Quebec, and west to Montana (USDA plant profile). Its preferred habitat incudes mixed boreal forests (Crowder and Taylor 1984) with moist to mesic soils. It likely has a high dispersal ability, with persistence upon arrival to a novel area augmented by its clonal growth. It readily spreads clonally, and produces few seeds (Eriksson 1992).