ISSN 1946-7664. MCFNS 2013
Vol. 5, Issue 2, pp. 151–169
Mathematical and Computational
Forestry & Natural-Resource Sciences

AVAILABLE ONLINE AT HTTP://MCFNS.COM

Submitted: Apr. 30, 2013
Accepted: Jul. 19, 2013
Published: Sep. 30, 2013
Last Correction: Sep. 3, 2013

QUANTITATIVE METRICS FOR ASSESSING PREDICTED CLIMATE CHANGE PRESSURE ON NORTH AMERICAN TREE SPECIES

Kevin M Potter[1], William W Hargrove[2]

[1] *Department of Forestry and Environmental Resources, North Carolina State University, Research Triangle Park, NC, USA*
[2] *USDA Forest Service, Southern Research Station, Asheville, NC, USA*

Abstract. Changing climate may pose a threat to forest tree species, forcing three potential population-level responses: toleration/adaptation, movement to suitable environmental conditions, or local extirpation. Assessments that prioritize and classify tree species for management and conservation activities in the face of climate change will need to incorporate estimates of the risk posed by climate change to each species. To assist in such assessments, we developed a set of four quantitative metrics of potential climate change pressure on forest tree species: (1) percent change in suitable area, (2) range stability over time, (3) range shift pressure, and (4) current realized niche occupancy. All four metrics are derived from climate change environmental suitability maps generated using the Multivariate Spatio-Temporal Clustering (MSTC) technique, which combines aspects of traditional geographical information systems and statistical clustering techniques. As part of the Forecasts of Climate-Associated Shifts in Tree Species (ForeCASTS) project, we calculated the predicted climate change pressure statistics for North American tree species using occurrence data from the USDA Forest Service Forest Inventory and Analysis (FIA) program. Of 172 modeled tree species, all but two were projected to decline in suitable area in the future under the Hadley B1 Global Circulation Model/scenario combination. Eastern species under Hadley B1 were predicted to experience a greater decline in suitable area and less range stability than western species, although predicted range shift did not differ between the regions. Eastern species were more likely than western species, on average, to be habitat generalists. Along with the consideration of important species life-history traits and of threats other than climate change, the metrics described here should be valuable for efforts to determine which species to target for monitoring efforts and conservation actions.

Keywords: climate change; range shift pressure; risk assessment; multivariate clustering; human-assisted migration; niche occupancy; forest health monitoring; conservation.

1 INTRODUCTION

The forests of the United States are expected to experience extensive ecological, social and economic effects as a result of climate change (Malmsheimer et al., 2008). Specifically, forest ecosystem functions and attributes are likely to be altered as a result of climatic changes (Stenseth et al., 2002) that are forecast to include an increase in mean surface temperatures of 2 °C to 4.5 °C, longer growing seasons, and changes in temporal and spatial precipitation patterns (International Panel on Climate Change, 2007). Climate change is likely to pose a severe threat to the viability of forest tree species themselves, which will be forced either to adapt to new conditions or to shift their ranges to more favorable environments. Evidence suggests that tree species are currently exhibiting changes in distribution and phenology in response to climate change (Parmesan and Yohe, 2003; Root et al., 2003; Woodall et al., 2009; Zhu et al., 2012). As species move poleward or upslope in the face of climate change, some species will likely disappear or be restricted to isolated refugia, while others may expand greatly (Iverson and McKenzie, 2013). Biologists have expressed concerns that species may be extirpated as their access to suitable habitat decreases (Thomas et al., 2004). The growth and survival of forest tree species will depend on the maintenance of suitable habitats and on the availability of genotypes for colonization of those habitats (Rehfeldt, 1999). Managers and decision-makers will need tools to assess the potential impacts of climate change on the broad diversity of forest tree species across North America and elsewhere.

As environmental changes push the habitat of plant species out of their climatic tolerance limits, species may respond by adapting to the new conditions, by shifting via migration to suitable environmental conditions, or by becoming locally extirpated (Davis et al., 2005). Adaptation via natural selection may be unlikely for forest tree species in many cases, given their long generation times (Rehfeldt et al., 1999; St. Clair and Howe, 2007), although some tree species may be able to evolve quickly in the face of new environmental conditions (Petit et al., 2004). Much innovative work has predicted the future distribution of habitat suitability for forest tree species under climate change (Iverson et al., 2004a, 2004b, 2008; Matthews et al., 2011; Rehfeldt et al., 2006; Schwartz et al., 2006), although the results of such efforts typically do not account for whether tree species can span, without human assistance, the distances expected between locations with suitable conditions currently and those with suitable conditions in the future. Indeed, many tree species successfully migrated long distances following the most recent cold period of the Pleistocene, but there is concern that these same species may not be able to match the much more rapid climate shifts expected in the near future (Davis and Shaw, 2001).

Areas within the distributions of forest tree species are likely to experience different degrees of climate change pressure. For example, the paleorecord suggests that populations at the trailing edge of a species' shifting distribution were often extirpated, resulting in a latitudinal displacement of range rather than a simple expansion into newly favorable region (Davis and Shaw, 2001). Already, a disproportionate number of population extinctions have been documented along southern and low-elevation range edges in response to recent climate warming, resulting in contraction of species' ranges at these warm boundaries (Parmesan, 2006). At the same time, these trailing edge populations appear to have played a key role for the maintenance of biodiversity through the Quaternary, and Hampe and Petit (2005) argue that rear-edge populations are disproportionately important for the long-term conservation of genetic diversity, phylogenetic history and evolutionary potential of species.

Assessments that prioritize and classify tree species for management and conservation activities in the face of climate change (e.g., Aubry et al., 2011; Devine et al., 2012; Matthews et al., 2011) need to incorporate estimates of the risk climate change poses to each species. To assist in such assessments, we developed a set of four quantitative metrics of predicted climate change pressure on forest tree species: (1) percent change in suitable area, (2) range stability over time, (3) range shift pressure, and (4) current realized niche occupancy. All four metrics are derived from climate change environmental suitability maps generated using the Multivariate Spatio-Temporal Clustering (MSTC) technique (Hargrove and Hoffman, 2005). Combining aspects of traditional geographical information systems (GIS) and statistical clustering techniques, MSTC can be used to statistically predict environmental niche envelopes to forecast a species' potential geographic range under altered environmental conditions such as those expected under climate change (Hargrove and Hoffman 2003). Global in scope, it incorporates 16 spatial climate, soils, and geomorphology variables, and generates maps at a resolution of 4 km^2. The advantages of the MSTC technique include its capacity to easily generate climate change environmental suitability maps for a large number of species, its relatively high-resolution results applicable at the population level, and its ability to predict suitable habitat globally (for species potentially moving from Mexico to the United States, for example, or from the United States to Canada).

As a part of the Forecasts of Climate-Associated Shifts in Tree Species (ForeCASTS) project (Potter et al., 2010), we calculated the climate change pressure metrics for 172 North American tree species using occurrence data from the USDA Forest Service Forest Inventory and Analysis (FIA) program as training occurrence locations. FIA data are an unparalleled source of tree location information in the United States because the FIA program maintains a national network of approximately 125,000 fixed-area forested plots from which tree inventory data are collected in a consistent manner and on a regular basis (Woudenberg et al., 2010). Because of the large number of plots and because each plot represents a little more than 2,400 ha of forest (Bechtold and Patterson, 2005), the FIA data reliably represent the general extent of common tree species.

2 MATERIALS AND METHODS

2.1 Tree occurrence data We generated metrics of projected climate change pressure for 172 North American forest tree species (Appendix A, Tab. 4). Because we used inventory data collected by the USDA Forest Service as training occurrence locations for our tree species climate projections, and because we wanted to provide range-wide estimates of climate change pressure on species, we included only species for which more than 75 percent of the estimated range area occurs within the borders of the conterminous 48 United States, based on E.L. Little's range maps (Little, 1971; United States Geological Survey, 1999).

To select climate change training data for each of our study species, we used coarsely georeferenced species occurrence data available from the USDA Forest Service Forest Inventory and Analysis (FIA) program (Woudenberg et al., 2010), available at http://www.fia.fs.fed.us/tools-data/. The FIA program is the primary source of information about the extent, condition, status, and trends of forest resources across all ownerships in the United States (Smith, 2002). FIA applies a nationally consistent sampling protocol using a quasi-systematic design to conduct a multi-phase inventory of all forested land ownerships; the national sample intensity is approximately one plot per 2,428 ha of land (Bechtold and Patterson, 2005). It maintains a system of approximately 125,000 fixed-area (each approximately 0.067 hectares) inventory plots on accessible forested land across the 48 conterminous United States and southeastern Alaska; field crews collect data on more than 300 variables, including forest type, tree species, tree size and tree condition (Smith, 2002; Woudenberg et al., 2010). The plots consist of four, 7.2-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Woudenberg et al., 2010). All trees with a diameter at breast height (dbh) of at least 12.7 cm are inventoried on forested subplots. The FIA system is designed so that field crews revisit plots in the eastern United States every five years, with 20 percent of all plots remeasured every year on a 5-year rotating basis. In the western United States, 10 percent of plots are remeasured every year on a 10-year rotating basis. Initial annual inventory plots were established between 1999 and 2005. All inventory data are publicly available. By law, the exact coordinates of FIA plots are slightly altered to protect the privacy of forest landowners, with most of the adjusted coordinates located within 0.8 km (0.5 miles) and all within 1.61 km (1 mile) of the actual plot coordinates. Additionally, some private plot coordinates may be “swapped” with those of another private plot within the same county with similar attributes, such as forest type, stand-size class, latitude and longitude (Woudenberg et al., 2010). Obscuring the original plot coordinates should have little effect on the results of this study given the resolution of the analysis and measures undertaken to avoid overtraining the data.

In some cases, we combined multiple FIA species codes into a single species group when doing so was taxonomically justified (e.g., combining all hawthorn species, which are difficult to differentiate even by experts, into a single “*Crataegus* spp.” category). We excluded species which occurred on fewer than 10 FIA plots, to ensure adequate sampling. We wanted to include only plots where a given tree species has been able to attain reproductive maturity, so an FIA plot was used as a training occurrence location for a large tree species if it contained at least one tree greater than 25.4 cm dbh or 9.14 m in height (class 1), and for a smaller tree species if it contained a tree at least 12.7 cm dbh or 6.1 m in height (class 2). For the smallest tree species, including those that often occur in a shrubby form, such as *Prunus americana* and *Quercus gambelii*, plots were included if they contained an individual at least 6.35 cm dbh or 3.048 m in height (class 3). The same was true for American chestnut (*Castanea dentata*), a species that has been decimated by an exotic fungal disease caused by *Cryphonectria parisitica* (Loo, 2009; Russell, 1987), and which continues to exist in upland hardwood forests of the eastern United States in the form of sprouts from blight-killed trees (Stephenson et al., 1991). Each of the 172 species was classified as western or eastern, with eastern species subdivided into northern, southern and general species, as in Woodall et al. (2009).

2.2 Predictions of future habitat suitability

MSTC is a technique that employs non-hierarchical clustering to classify GIS raster cells with similar environmental conditions into categories (Hargrove and Hoffman, 2005). It uses the normalized values of each environmental condition for every raster cell as a set of coordinates that together specify a position for that cell in a data space having a separate dimension for each of the environmental characteristics. Normalization gives environmental parameters measured in different units equal spacing by establishing a mean of zero and unit standard deviation (Hargrove and Hoffman, 2005). Two cells from anywhere on the map with similar combinations of environmental characteristics will be located near each other in this data space. Their proximity and relative positions in data space will quantitatively reflect their environmental similarities, allowing these cells to be classified into groups or “ecoregions” with other cells possessing similar environmental conditions; each ecoregion contains roughly an equal amount of multivariate environmental heterogeneity (Hargrove and Hoffman, 2005; Hoffman et al., 2005). The MSTC process generates output maps which group and display each pixel as part of an “ecoregion” with other pixels possessing similar environmental conditions. It is possible to choose whether the map contains many small ecoregions, each containing little environmental heterogeneity, or only a few ecoregions, each containing a relatively large amount of environmental heterogeneity. The results presented here were generated using a fine division of 4 km^2 (1.25 arcmin) pixels globally into 30,000 ecoregions, each with a relatively small amount of environmental heterogeneity. This is the finest resolution at which global data are available; the MSTC method has been applied at a finer resolution when appropriate input data were available (e.g., Hargrove and Hoffman, 2003, 2005).

Global in scope, this MSTC analysis incorporates 16 spatial bioclimatic, topographic, and edaphic environmental variables (Tab. 1) and generates maps using georeferenced occurrence information as training data for a given species (Potter and Hargrove, 2012). These variables were used because they play an important role in determining the geographic distribution of plants across large areas (Lugo et al., 1999; Neilson, 1995; Prentice et al., 1992). Climatic data were custom downscaled from Hijmans et al. (2005), topographic variables were custom downscaled from Moore et al. (1991), and edaphic data were custom downscaled from the Global Soil Data Task Group (2000). Saxon et al. (2005) and Baker et al. (2010) provide additional details about the variables used in the MSTC analysis, including how they were downscaled. Using the MSTC approach, it is possible to assign a different weight to each of the 16 environmental variables, but we gave them all equal weight to allow for a rapid assessment of climate change pressure across the 172 species and to maintain consistency across the species.

Because MSTC can track the same clustered combination of environmental conditions at any location or date using future climatic forecasts, it has been applied to identify potential climatic refugia predicted by global shifts in environmental conditions (Baker et al., 2010; Saxon et al., 2005), to determine quantitative zones for seed transfer that take climate change into account (Potter and Hargrove, 2012), and to statistically model environmental niche envelopes to forecast suitable habitat conditions for species under altered environmental conditions such as expected under global climate change (Hargrove and Hoffman, 2005; Potter et al., 2010). In such situations, future climate projections are used, while edaphic and topographic data are held constant over time. MSTC is an appropriate tool for the assessment of the potential genetic effects of climate change on forest tree species because it is able to rapidly predict changes in suitable habitat for a large number of species, it allows for flexible occurrence data inputs, it generates relatively high-resolution results applicable at the population level, it has the ability to predict suitable habitat beyond the borders of the United States, and it incorporates pertinent environmental variables associated with plant distributions (Potter et al., 2010).

Table 1: The Multivariate Spatio-Temporal Clustering technique employed 16 spatial environmental variables, collected at a resolution of 4 km^2, to define the 30,000 quantitative global ecoregions used to predict the location and quality of current and future suitable environmental conditions for North American tree species.

Category	Spatial environmental variable
Climatic variables	Annual biotemperature (sum of monthly mean temperature where mean ≥ 5 °C)
	Growing season (number of consecutive months with mean ≥ 5 °C)
	Mean diurnal temperature range (°C)
	Mean precipitation in the coldest quarter (mm)
	Mean precipitation in the driest quarter (mm)
	Mean precipitation in the warmest quarter (mm)
	Mean precipitation in the wettest quarter (mm)
	Mean temperature in the coldest quarter (°C)
	Mean temperature in the warmest quarter (°C)
	Precipitation/potential evapotranspiration
Topographic variables	Annual potential solar insolation (kW/m^2)
	Compound topographic index (relative wetness)
Edaphic variables	Profile available water capacity (mm)
	Soil bulk density (g/cm^3)
	Total soil nitrogen (g/m^2)
	Total soil carbon (g/m^2)

Using FIA plot training occurrence data (Fig. 1), we have produced maps that predict the location and suitability of current and future environmental conditions for North American tree species using the MSTC technique (Fig. 2). We generated these maps and associated climate change pressure metrics for the ForeCASTS project (Potter et al., 2010), which aims to assess how changing climate conditions could affect the genetic integrity of forest tree species and populations. All the maps and statistics described here are available for viewing at http://www.geobabble.org/h̃nw/global/treeranges3/climate_change/. At this Web site, a page exists for each species, containing (1) maps of training occurrence locations, (2) maps of locations with currently suitable environmental conditions, (3) maps of locations expected to be suitable under multiple global circulation models (GCMs) and emissions scenarios at two time points, and (4) maps of minimum required movement under one GCM/scenario combination for 2050. When they exist, links to corresponding climate change projections from other researchers using different techniques

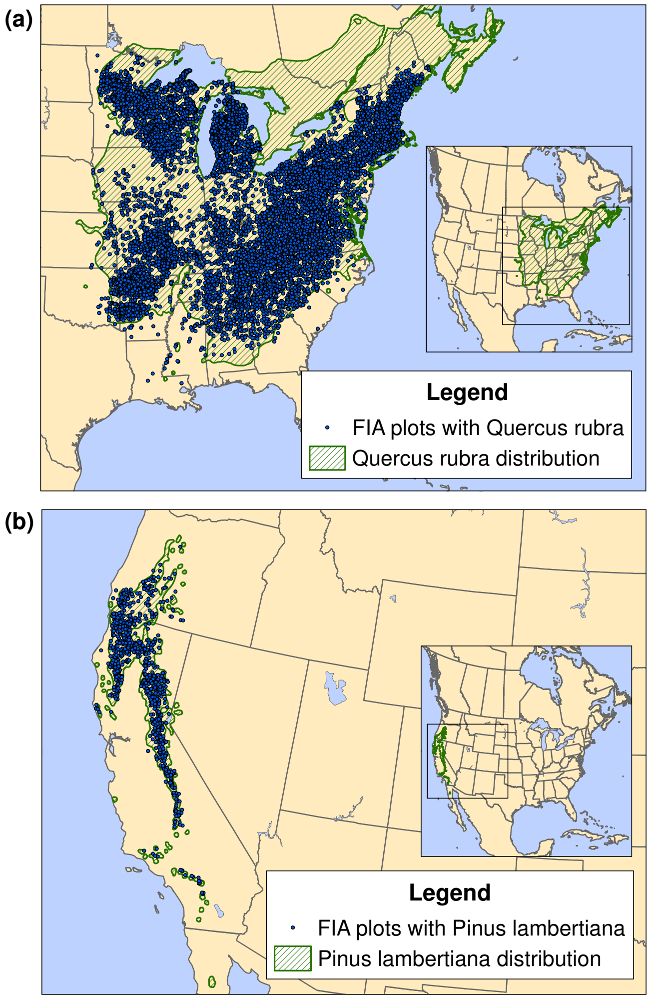

Figure 1: Forest Inventory and Analysis (FIA) plots used as Multivariate Spatio-Temporal Clustering occurrence data for (a) northern red oak (*Quercus rubra*) and (b) sugar pine (*Pinus lambertiana*). The plot locations are approximate. Species distributions are digitized versions of E.L. Little's range maps (Little, 1971; United States Geological Survey, 1999).

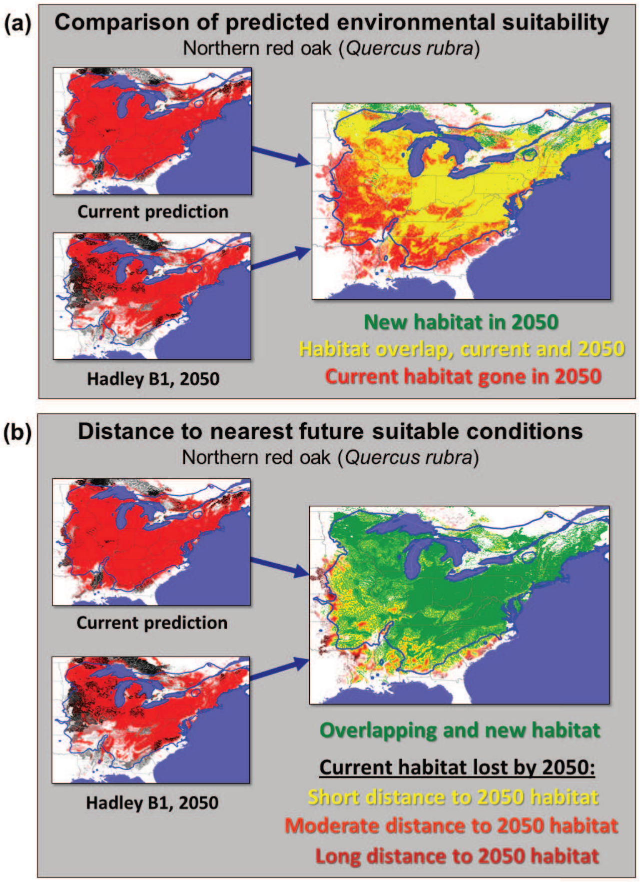

Figure 2: Multivariate Spatio-Temporal Clustering results for northern red oak (*Quercus rubra*), (a) *Q. rubra* predicted environmental suitability comparison for current conditions and for 2050 under the Hadley global circulation model, B1 emissions scenario, and (b) *Q. rubra* distance to nearest future suitable conditions under the Hadley B1 model-scenario combination.

(Crookston, 2013; Prasad et al., 2013) are included along with the ForeCASTS climate suitability maps.

To avoid overtraining the results because of relative differences in local species abundance, we selected ecoregions in the current-time suitable environmental conditions map based on the geographic distribution and commonness of the species. For very common species, an ecoregion was included as suitable when it intersected with four FIA plots containing that species. For less common species, the threshold was three occurrence plots per ecoregion, while it was two occurrence plots for uncommon species and one occurrence plot for the rarest species. Species commonness was determined by the number of ecoregions that intersect with two FIA occurrence plots containing that species; very common species encompassed 343 or more unique ecoregions, common species encompassed 49 or more and less than 343 unique ecoregions, uncommon species encompassed seven or more and less than 49 ecoregions, and rare species encompassed fewer than seven ecoregions. These training occurrence thresholds were determined by a simple first-order exponential function.

The maps of currently suitable conditions and of future predicted environmental conditions also depict areas (ecoregions) of decreasing environmental similarity to the environmental conditions currently present at the tree species training occurrence locations. Defined as the Euclidean distance in data space between the centroids of two ecoregion clusters, this ecoregion similarity is displayed on the maps as a grayscale ramp. Darker shades are given to cells belonging to ecoregions more similar to any of those that intersect with the training occurrence plots in current time, while lighter shades are given to those belonging to less similar ecoregions.

The MSTC approach assumes that trees are optimally adapted to the environmental conditions existing at their training data locations. This generally holds true for forest tree species (Johnson et al., 2004), although exceptions also exist (Mangold and Libby, 1978; Wu and Ying, 2004). It is also important to note that, with some GCM/emissions scenario combinations, the set of environmental conditions equivalent to those present in an ecoregion in current time may not exist (Fitzpatrick and Hargrove, 2009). If this happens, MSTC will not be able to predict equivalent locations for that current ecoregion on the future projection maps (Hargrove and Hoffman, 2003, 2005). However, these maps may depict future locations with environmental conditions that are similar to the original current-time ecoregion.

2.3 Metrics of projected climate change pressure

We used the MSTC mapped results to calculate, for each of the 172 tree species, four metrics of projected climate change pressure (percent change in range area over time, percent range stability over time, range shift pressure, and current realized niche occupancy). We used PROC GLM in SAS 9.2 (SAS Institute Inc., 2008) to assess whether the means of the metrics were significantly different by region and subregion, using a Tukey-Kramer test because of group size differences. We conducted a Wilcoxon signed rank test in PROC UNIVARIATE to assess to determine whether percent change in suitable habitat area over time was significantly different than 0 within each group of species (all species, regions, and subregions). We also used PROC CORR in SAS 9.2 to test for correlations between each pair of metrics, across the entire set of species and within regions. We calculated nonparametric Spearman correlations, because the variables were not typically normally distributed, and outliers were present in several cases. Pearson correlations are not likely to be robust in the presence of non-normality (Kowalski, 1972).

2.3.1 Percent change in suitable area

This measure of change over time in environmentally suitable area was determined by comparing, for each species, the percent change in area with suitable environmental conditions over time from current conditions to those projected in 2050 under the Hadley B1 GCM/emissions scenario combination.

2.3.2 Range stability over time

This measure of range stability over time was determined by calculating, for each species, the percent of currently suitable area that remains suitable over time under conditions projected in 2050 in the Hadley B1 GCM/emissions scenario combination.

2.3.3 Range shift pressure

The projected mean shift distance in suitable habitat, or "Minimum Required Movement" (MRM) distance, was determined by calculating the mean non-zero straight-line distance (measured in grid cells) from each currently suitable 4 km^2 raster cell expected to become unsuitable to the nearest expected suitable habitat cell in 2050 under the Hadley B1 GCM/emissions scenario combination.

2.3.4 Current realized niche occupancy

The breadth of niches occupied by a species is a strong predictor of extinction risk, with species having narrow niches in general being at greater risk (Brook et al., 2008; Stork et al., 2009). Since the MSTC-derived ecoregions are quantitatively defined and have fixed environmental variability, and since FIA data are sampled in a consistent and systematic fashion (Bechtold and Patterson, 2005), we used the two in combination to generate a metric of current realized niche occupancy. It is calculated as the number of unique MSTC ecoregions that intersect with two or more FIA occurrence plots containing a given species.

3 RESULTS

3.1 Percent change in suitable area

Environmentally suitable area was projected to decline by an average of 44.33% across all 172 species in the study by 2050 under Hadley B1 (Tab. 2). The decline in suitable area was projected to be twice as great in the East as in the West (50.55% compared to 23.82%); this difference was statistically significant. Northern species in the East were expected to experience a greater decline in suitable habitat area than both southern species and more generally distributed eastern species in the region, but the differences among the means were not significant. Nationally, September elm (*Ulmus serotina*) was projected to have the greatest decline in suitable area, followed by sweet crabapple (*Malus coronaria*), chalk maple (*Acer leucoderme*), Delta post oak (*Quercus similis*), and Texas ash (*Fraxinus texensis*) (Appendix A, Tab. 4). All of these, with the exception of sweet crabapple, are southern species. Only two species were projected to have an increase in suitable habitat: Great Basin bristlecone pine (*Pinus longaeva*) and dwarf live oak (*Quercus minima*). All the 170 other tree species lost projected suitable habitat. Note, however, that these results are from only one GCM/emissions scenario combination and from one time step, because our emphasis is to describe and illustrate metrics of climate change pressure rather than to present a range of potential climate change effects.

3.2 Percent range stability over time As with percent change in suitable habitat over time, the percent of currently suitable habitat expected to remain suitable was higher, on average, for western species (47.58 %) than eastern species (33.66%) (Tab. 2), a difference that was statistically significant. Range stability was projected to be greater for southern and generally distributed species in the East than for northern species, but these differences were not significant. Nationally, mean species range stability was 36.90%. Range stability values ranged from 0 percent in September elm and less than 2% in chalk maple, Delta post oak, and Kentucky coffeetree (*Gymnocladus dioicus*), to 67.93 percent in loblolly bay (*Gordonia lasianthus*), 67.9% in bigleaf maple (*Acer macrophyllum*), 69.28% in Sitka spruce (*Picea sitchensis*), and 84.82% in dwarf live oak (Appendix A, Tab. 4).

3.3 Range shift pressure Mean minimum required movement (MRM) distance, a measure of range shift pressure, was projected to be somewhat greater for species in the East than in the West (12.62 map cells compared to 8.97 map cells), although the difference in these means was not significant. The variation across species was slightly greater in the West (Tab. 2). In the East, northern species were expected to have the greatest shift pressure, and generally distributed species to have the least, with southern species intermediate between the two. Again, however, none of these differences was significant. Across all species, the mean shift pressure was 11.77 map cells. Expected range shift pressure was the greatest for September elm (94.78 map cells), Great Basin bristlecone pine (73.34 map cells) and Kentucky coffeetree (61.28 map cells), and least for winged elm (*Ulmus alata*), post oak (*Quercus stellata*), cherrybark oak (*Quercus pagoda*), and western larch (*Larix occidentalis*), all with a mean range shift pressure of approximately 3 map cells or fewer (Appendix A, Tab. 4).

3.4 Current realized niche occupancy Mean realized niche occupancy in current time was greater for eastern species than for western species (149.38 unique ecoregions compared to 85.10, with the means being significantly different) (Tab. 2). This suggests that eastern species are more likely than western species, on average, to be habitat generalists. Not surprisingly, generally distributed eastern species intersected with more unique ecoregions than either northern or southern species, with means significantly different among the subregions. Southern species had a smaller mean realized niche occupancy than northern species, but the difference was not significant. The mean across all species nationally was 134 unique ecoregions. The range across species was as low as 1 for Great Basin bristlecone pine and 2 each in Delta post oak and September elm, and as high as 502 for black cherry (*Prunus serotina*), 518 for green ash (*Prunus pennsylvanica*), 522 for American elm (*Ulmus americana*), and 635 for red maple (*Acer rubrum*) (Appendix A, Tab. 4).

3.5 Relationship among metrics Nationally, all pairs of metrics were significantly correlated (Tab. 3). The strongest correlation was between percent change in suitable area and range stability (r = 0.833). Since nearly all species were projected to experience a decrease in suitable area, this shows that species with the smallest decrease in suitable area had the greatest range stability. The relationships both between shift pressure and percent change in suitable area (r = -0.487) and between shift pressure and range stability were negative (r = -0.655); in other words, species were likely to experience less climate change shift pressure (that is, distance to the nearest suitable projected habitat for 2050 under the Hadley B1 GCM-scenario combination) with less of a projected loss of habitat and with a greater amount of habitat remaining constant over time. Current realized niche occupancy, a measure of whether a species is a habitat generalist or a habitat specialist, was positively correlated with range stability (r = 0.458), but negatively correlated with shift pressure (r = -0.505). This suggests that habitat generalists, which have been found to exist in a wider variety of environmental niches and across large geographical ranges (Fridley et al., 2007), should be able to continue to exist across a broader area while not having to move as far to reach future suitable habitat.

These general patterns existed among eastern species as well (Tab. 3), but with stronger correlations. The pattern was slightly different for western species, however. In the West, a smaller but still significant correlation existed between percent change in suitable area and range stability ($r = 0.325$). Also, the association between change in suitable area and climate change shift pressure was not significant, as it was in the eastern United States and nationally. This suggests that western species projected to lose less overall habitat may need to move greater distances from currently-suitable/future-unsuitable locations to the nearest future-suitable locations, when they do lose environmentally suitable area. This might be the result of being located on “sky islands” (McLaughlin, 1995; Warshall, 1995), which may cause populations occurring mostly at high elevations in the southern portions of their species ranges (while being

Table 2: Mean across species values of the climate change pressure metrics developed using the Multivariate Spatio-Temporal Clustering approach, nationally and by region. Percent change is significantly different than 0 for all groups. Note: EG, eastern-general; EN, eastern-north; ES, eastern-south.

		Suitable Area (km^2)			Range Stability		Shift Pressure		Niche Occupancy
Region	Species	Current	Future	% Change	Area (km^2)	%	Mean	SD	
All	172	971,470	536,995	-44.33	403,500	36.90	11.77	20.80	134.43
East	132	1,144,327	613,065	-50.55	460,407	33.66	12.62	19.41	149.38
EG	54	1,761,160	899,699	-53.06	710,863	35.24	10.26	17.91	228.30
EN	25	878,119	441,224	-56.59	289,877	25.62	16.54	25.89	123.88
ES	53	641,203	402,071	-45.14	285,663	35.85	13.16	17.89	81.00
West	40	401,336	285,962	-23.82	215,706	47.58	8.97	25.36	85.10

Table 3: Spearman correlations between climate change pressure metrics among species, nationally and by region. Correlations are significant at $p < 0.05$ except those underlined.

	% Change	Stability	Shift pressure	Niche occupancy
		All species		
% Change	.	0.833	-0.487	0.164
Stability	0.833	.	-0.655	0.458
Shift pres.	-0.487	-0.655	.	-0.505
Niche occup.	0.164	0.458	-0.505	.
		Eastern species		
% Change	.	0.903	-0. 522	0. 416
Stability	0.903	.	-0. 657	0.592
Shift pres.	-0. 522	-0.657	.	-0. 643
Niche occup.	0.416	0.592	-0.643	.
		Western species		
% Change	.	0.325	-0.058	-0.063
Stability	0.325	.	-0.462	0.643
Shift pres.	-0.058	-0.462	.	-0.427
Niche occup.	-0.063	0.643	-0.427	.

more broadly dispersed at more northerly latitudes) to have to move farther to reach an environmentally suitable location in the future.

4 DISCUSSION

Changing climatic conditions are expected to pose a threat to the viability of forest tree species, which may be forced either to adapt to new conditions or to shift their ranges to more favorable environments (Aitken et al., 2008; Davis et al., 2005). Given the limitations in funding available for species-specific management and conservation activities, it will be necessary to compare the expected impacts of these environmental changes across multiple species in a region (e.g., Barazani et al., 2008; Coates and Atkins, 2001; Gauthier et al., 2010). We describe quantitative metrics developed for such comparative assessments. These are based on climate change map products that combine estimates of species' edaphic and bioclimatic envelopes with downscaled products of climate modeling, which can predict the future spatial extent of those environmental envelopes and determine where species' ranges might exist, disappear, move, grow or shrink under changed climatic conditions (Harris et al., 2006). Using these maps, the metrics describe the existing environmental variation across the range of a species (realized current niche occupancy), the degree to which the area of suitable environmental conditions is predicted to decrease or increase over time (percent change in suitable area), the amount of currently suitable area that is expected to remain suitable (range stability over time), and the distance that tree populations currently in areas expected to become unsuitable would have to travel to reach the nearest suitable location in the future (range shift pressure).

Because the main objective of this analysis was to describe a set of predicted climate change pressure metrics, the results we present here are limited to a single global circulation model/emissions scenario combination (Hadley B1) for a single point in time (2050). Thorough assessments of risk across forest tree species should likely consider multiple GCM/scenario combinations to better account for a range of possible climate change predictions. When using downscaled climate predictions from the Hadley B1 GCM/scenario combination, we found that nearly all of the 172 species in our analysis were expected to experience a loss of overall environmental suitable area and to need to move a relatively short distance, on average, from newly unsuitable to the nearest future suitable locations (Fig. 3). Generating these metrics using other GCMs and scenarios might reveal different results.

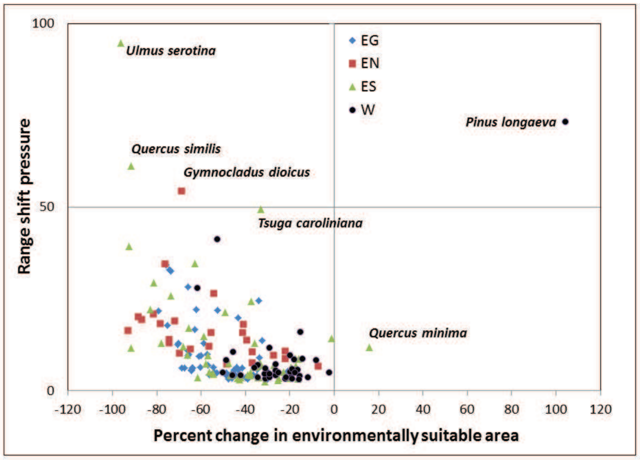

Figure 3: The 172 species included in the analysis, plotted by percent change in environmental suitable area and range shift pressure (number of grid cells), based on the Hadley B1 global circulation model/scenario combination. The labeled outlier species are discussed in the text. Note: EG, eastern-general; EN, eastern-north; ES, eastern-south; W-western.

In the current analysis, the species that are the exceptions from the pattern of suitable area loss with relatively small climate change shift pressure are perhaps the most interesting from a monitoring, management and conservation perspective. For example, Great Basin bristlecone pine (*Pinus longaeva*), an extremely long-lived species which occurs in isolated mountain ranges in California, Nevada and Utah (Hiebert and Hamrick, 1984), is expected under Hadley B1 to experience an increase in suitable area that exceeds 100 percent, while retaining about 25 percent of its existing suitable habitat. The mean distance to suitable future environmental locations, from areas expected to become unsuitable, is greater than nearly all other species, however, at about 292 km (approximately 73 4-km^2 map cells). This is because newly suitable locations for the species are projected to develop in Canada, far from its current locations, where much of its current habitat is expected to become unsuitable. At the same time, September elm (*Ulmus serotina*), a species scattered infrequently across a few southeastern states (Flora of North America Editorial Committee, 1993+), is projected to lose nearly all its currently acceptable habitat, to maintain none of its currently suitable habitat, and to need to shift an average of 379 km (approximately 95 4-km^2 map cells) to reach suitable conditions in the future. Both species clearly need to be closely monitored, and may need to be considered as candidates for facilitated migration (Pedlar et al., 2012; Vitt et al., 2010). Delta post oak (*Quercus similis*), Kentucky coffeetree (*Gymnocladus dioicus*), and Carolina hemlock (*Tsuga caroliniana*) are other species that may experience particularly intense climate change impacts. Meanwhile, dwarf live oak (*Quercus minima*), from central and northern Florida, is exceptional because, under the Hadley B1 GCM/scenario, it is projected to gain suitable area, maintain about 84 percent of its current suitable area, and need to move only a short distance from newly unsuitable to newly suitable locations.

Species in the East are projected, on average, to experience a greater loss of suitable area and a decreased level of range stability compared to species in the West under Hadley B1. Eastern species tend to occur across more FIA plots than western species and to have larger areas of current environmental suitability. Eastern species were inventoried on 2,760 FIA plots on average compared to 921 for western species, and had 1,144,237 km^2 of current suitable area compared to 401,336 km^2. These means were significantly different. Additionally, eastern species appear more likely than western species to be habitat generalists than specialists, given the greater mean realized niche occupancy in the East. Thus, greater broad-scale environmental changes may result in greater loss of suitable area for eastern species, via latitudinal displacement of species ranges (Davis and Shaw, 2001). Western species, meanwhile, are more likely to be habitat specialists and to be more limited in their current distributions, perhaps in part because of the greater topographic complexity of the West. This topographic complexity may cause current suitable environmental conditions for tree species generally to shift upward in elevation over short enough distances that grid cells remain suitable over time, rather than shifting greater distances in latitude as in the East. Interestingly, expected shift pressure on species is not significantly different between species in the two regions, despite differences in range stability and change in suitable area. Perhaps most places expected to become unsuitable for western species are those at the highest elevations, as a result of the existence of "sky islands" (McLaughlin, 1995; Warshall, 1995), from which tree species would need to traverse considerable distances to reach suitable future habitat. Though the area encompassed by such locations is smaller than that of places in the East expected to become unsuitable, it appears that species in both regions would need to span similar distances to reach future suitable environmental conditions.

It is important to note that the projected climate change pressure metrics we describe here represent only one set of inputs necessary for assessments comparing climate change risk across multiple tree species. The impact of climate change on species will vary across species based on such individualistic traits as seed dispersal mechanism and life-history strategies (Parmesan, 2006; Parmesan and Yohe, 2003), which should be incorporated into assessments of species susceptibility to climate change and other threats (Aitken et al., 2008; Myking, 2002; Sjostrom and Gross, 2006). These climate change pressure statistics, along with consideration of species' biological attributes, can allow for assessment of whether migrating species, for example, might be able to track appropriate environmental conditions over time and avoid the loss of extensive genetic variation. A loss of important adaptive genetic variation may be a concern particularly for species that have narrow habitat requirements, are located exclusively at high elevations, and/or are not able to disperse their propagules effectively across long distances. Even if not locally extirpated outright, populations of these and other species could experience significant inbreeding, genetic drift, and decreased genetic variation as a result of reduced population size. Such populations may then become more susceptible to mortality caused both by nonnative pests and pathogens and by the environmental pressures associated with climate change. This susceptibility could generate a cycle of mortality, loss of genetic variation, and inability to adapt to change that could ultimately result in population extirpation (Potter et al., 2010).

Along with the consideration of important species life-history traits and of threats other than climate change, such as pest and pathogen infestation (Dukes et al., 2009; Logan et al., 2003), we expect that the metrics we describe here will be valuable for scientists and policymakers attempting to determine which forest tree species, in the face of climate change, should be targeted for monitoring efforts and for *in situ* and *ex situ* conservation actions such as seed banking efforts, facilitated migration, and genetic diversity studies. These measures of predicted climate change pressure may be particularly helpful in multiple-species assessments across broad regional scales that take into account climate change risk to many species aggregated from relatively fine resolution projection maps.

5 ACKNOWLEDGMENTS

We thank Frank Koch for assistance with the Forest Inventory and Analysis data, Steve Norman and Carol Aubry for helpful suggestions, and Julie Canavin for data organization. Forrest Hoffman was instrumental in developing the parallel MSTC code and ran the clustering analysis. Barry Baker and Chris Zganjar prepared the input data sets used for the MSTC process. We thank the guest editors and the three anonymous reviewers for their helpful comments. This work was supported in part by the Eastern Environmental Threat Assessment Center; by the Forest Health Monitoring program of the United States Department of Agriculture (USDA) Forest Service; and by Cooperative Agreement 09-CA-11330146-078 and Research Joint Venture Agreement 10-JV-11330146-049 between the USDA Forest Service, Southern Research Station, and North Carolina State University.

REFERENCES

Aitken, S.N., S. Yeaman, J.A. Holliday, T.L. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1(1):95-111.

Aubry, C., W. Devine, R. Shoal, A. Bower, J. Miller, and N. Maggiulli. 2011. Climate Change and Forest Biodiversity: A Vulnerability Assessment and Action Plan for National Forests in Western Washington. USDA For. Serv. Pacific Northwest Region. 308 p.

Baker, B., H. Diaz, W. Hargrove, and F. Hoffman. 2010. Use of the Koppen-Trewartha climate classification to evaluate climatic refugia in statistically derived ecoregions for the People's Republic of China. Clim. Change 98(1-2):113-131.

Barazani, O., A. Perevolotsky, and R. Hadas. 2008. A problem of the rich: Prioritizing local plant genetic resources for ex situ conservation in Israel. Biol. Conserv. 141(2):596-600.

Bechtold, W.A., and P.L. Patterson. 2005. The Enhanced Forest Inventory and Analysis Program: National Sampling Design and Estimation Procedures. USDA For. Serv. Gen. Tech. Rep. SRS-GTR-80. 85 p.

Brook, B.W., N.S. Sodhi, and C.J.A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23(8):453-460.

Coates, D.J., and K.A. Atkins. 2001. Priority setting and the conservation of Western Australia's diverse and highly endemic flora. Biol. Conserv. 97(2):251-263.

Crookston, N. 2013. Research on Forest Climate Change: Potential Effects of Global Warming on Forest and Plant Climate Relationships in Western North America and Mexico. Available online at http://forest.moscowfsl.wsu.edu/climate/; last accessed June 25, 2013.

Davis, M.B., and R.G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292(5517):673-679.

Davis, M.B., R.G. Shaw, and J.R. Etterson. 2005. Evolutionary responses to changing climate. Ecology 86(7):1704-1714.

Devine, W., C. Aubry, J. Miller, K.M. Potter, and A.D. Bower. 2012. Climate change and forest trees in the Pacific Northwest: Guide to vulnerability assessment methodology. USDA For. Serv. Pacific Northwest Region. 49 p. Available online at http://ecoshare.info/projects/ccft/; last accessed Aug. 15, 2013.

Dukes, J.S., J. Pontius, D. Orwig, J.R. Garnas, V.L. Rodgers, N. Brazee, B. Cooke, K.A. Theoharides, E.E. Stange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerdau, K. Stinson, R. Wick, and M. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Can. J. For. Res. 39(2):231-248.

Fitzpatrick, M.C., and W.W. Hargrove. 2009. The projection of species distribution models and the problem of non-analog climate. Biodivers. Conserv. 18(8):2255-2261.

Flora of North America Editorial Committee. 1993+. Flora of North America North of Mexico. Available online at http://floranorthamerica.org/; last accessed June 25, 2013.

Fridley, J.D., D.B. Vandermast, D.M. Kuppinger, M. Manthey, and R.K. Peet. 2007. Co-occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. J. Ecol. 95(4):707-722.

Gauthier, P., M. Debussche, and J.D. Thompson. 2010. Regional priority setting for rare species based on a method combining three criteria. Biol. Conserv. 143(6):1501-1509.

Global Soil Data Task Group. 2000. Global Gridded Surfaces of Selected Soil Characteristics (International Geosphere-Biosphere Programme - Data and Information System [IGBP-DIS]). Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee.

Hampe, A., and R.J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8(5):461-467.

Hargrove, W.W., and F.M. Hoffman. 2003. An analytical assessment tool for predicting changes in a species distribution map following changes in environmental conditions. In Proceedings of the 4th International Conference on Integrating GIS and Environmental Modeling (GIS/EM4): Problems, Prospects and Research Needs, September 2-8, 2000, Parks, B.O., K.M. Clark, and M.P. Crane (eds.). Cooperative Institute for Research in Environmental Sciences; NOAA National Geophysical Data Center, Ecosystem Informatics; and US Geological Survey, Center for Biological Informatics, Banff, Alberta, Canada.

Hargrove, W.W., and F.M. Hoffman. 2005. Potential of multivariate quantitative methods for delineation and visualization of ecoregions. Environ. Manage. 34((Suppl. 1)):S39-S60.

Harris, J.A., R.J. Hobbs, E. Higgs, and J. Aronson. 2006. Ecological restoration and global climate change. Restor. Ecol. 14(2):170-176.

Hiebert, R.D., and J.L. Hamrick. 1984. An ecological study of bristleone pine (Pinus longaeva) in Utah and eastern Nevada. Great Basin Nat. 44(3):487-494.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25(15):1965-1978.

Hoffman, F.M., W.W. Hargrove, D.J. Erickson, and R.J. Oglesby. 2005. Using clustered climate regimes to analyze and compare predictions from fully coupled general circulation models. Earth Interact 9(10):1-27.

International Panel on Climate Change. 2007. Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 996 p.

Iverson, L.R., and D. McKenzie. 2013. Tree-species range shifts in a changing climate: detecting, modeling, assisting. Landscape Ecol. 28(5):879-889.

Iverson, L.R., A.M. Prasad, S.N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manage. 254(3):390-406.

Iverson, L.R., M.W. Schwartz, and A.M. Prasad. 2004a. How fast and far might tree species migrate in the eastern United States due to climate change? Glob. Ecol. Biogeogr. 13(3):209-219.

Iverson, L.R., M.W. Schwartz, and A.M. Prasad. 2004b. Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species. Landscape Ecol. 19(7):787-799.

Johnson, G.R., F.C. Sorensen, J.B. St Clair, and R.C. Cronn. 2004. Pacific Northwest forest tree seed zones: A template for native plants? Native Plants J. 5(2):131-140.

Kowalski, C.J. 1972. On the effects of non-normality on distribution of sample product-moment correlation coefficient. J. R. Stat. Soc. Ser. C-Appl. Stat. 21(1):1-12.

Little, E.L. 1971. Atlas of United States Trees. Volume 1. Conifers and Important Hardwoods. USDA For. Serv. Misc. Pub. 1146. 9 p., illus. [313 maps, folio].

Logan, J.A., J. Regniere, and J.A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. 1(3):130-137.

Loo, J. 2009. Ecological impacts of non-indigenous invasive fungi as forest pathogens. Biol. Invasions 11(1):81-96.

Lugo, A.E., S.L. Brown, R. Dodson, T.S. Smith, and H.H. Shugart. 1999. The Holdridge life zones of the conterminous United States in relation to ecosystem mapping. J. Biogeogr. 26(5):1025-1038.

Malmsheimer, R.W., P. Heffernan, S. Brink, D. Crandall, F. Deneke, C. Galik, E. Gee, J.A. Helms, N. McClure, M. Mortimer, S. Ruddell, M. Smith, and J. Stewart. 2008. Forest management solutions for mitigating climate change in the United States. J. For. 106(3):115-173.

Mangold, R.D., and W.J. Libby. 1978. Model for reforestation with optimal and suboptimal tree populations. Silvae Genet. 27(2):66-68.

Matthews, S.N., L.R. Iverson, A.M. Prasad, M.P. Peters, and P.G. Rodewald. 2011. Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. For. Ecol. Manage. 262(8):1460-1472.

McLaughlin, S.P. 1995. An overview of the flora of the sky islands, southeastern Arizona: Diversity, affinities, and insularity. P. 60-70 in Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico, DeBano, L.H., P.H. Ffolliott, A. Ortega-Rubio, G.J. Gottfried, R.H. Hamre, and C.B. Edminster (eds.). USDA For. Serv. Gen. Tech. Rep. RM-GTR-264. 669 p.

Moore, I.D., R.B. Grayson, and A.R. Ladson. 1991. Digital terrain modeling: A review of hydrological, geomorphological, and biological applications. Hydrol. Process. 5(1):3-30.

Myking, T. 2002. Evaluating genetic resources of forest trees by means of life history traits - a Norwegian example. Biodivers. Conserv. 11(9):1681-1696.

Neilson, R.P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecol. Appl. 5(2):362-385.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37:637-669.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918):37-42.

Pedlar, J.H., D.W. McKenney, I. Aubin, T. Beardmore, J. Beaulieu, L. Iverson, G.A. O'Neill, R.S. Winder, and C. Ste-Marie. 2012. Placing forestry in the assisted migration debate. Bioscience 62(9):835-842.

Petit, R.J., R. Bialozyt, P. Garnier-Gere, and A. Hampe. 2004. Ecology and genetics of tree invasions: From recent introductions to Quaternary migrations. For. Ecol. Manage. 197(1-3):117-137.

Potter, K.M., and W.W. Hargrove. 2012. Determining suitable locations for seed transfer under climate change: A global quantitative model. New Forest. 43(5-6):581-599.

Potter, K.M., W.W. Hargrove, and F.H. Koch. 2010. Predicting climate change extirpation risk for central and southern Appalachian forest tree species. P. 179-189 in Proceedings from the Conference on Ecology and Management of High-Elevation Forests of the Central and Southern Appalachian Mountains, Snowshoe, West Virginia, May 14-15, 2009, Rentch, J.S., and T.M. Schuler (eds.). USDA For. Serv. Gen. Tech. Rep. NRS-P-64. 242 p.

Prasad, A.M., L.R. Iverson, S. Matthews, and M. Peters. 2013. A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States. Available online at http://www.nrs.fs.fed.us/atlas/tree/tree_atlas.html; last accessed June 25, 2013.

Prentice, I.C., W. Cramer, S.P. Harrison, R. Leemans, R.A. Monserud, and A.M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. J. Biogeogr. 19(2):117-134.

Rehfeldt, G.E. 1999. Systematics and genetic structure of Ponderosae taxa (Pinaceae) inhabiting the mountain islands of the Southwest. Am. J. Bot. 86(5):741-752.

Rehfeldt, G.E., N.L. Crookston, M.V. Warwell, and J.S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. Int. J. Plant Sci. 167(6):1123-1150.

Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse, and D.A. Hamilton. 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. Ecol. Monogr. 69(3):375-407.

Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421(6918):57-60.

Russell, E.W.B. 1987. Pre-blight distribution of Castanea dentata (Marsh.) Borkh. Bull. Torrey Bot. Club 114(2):183-190.

SAS Institute Inc. 2008. The SAS System for Windows, Version 9.2. Cary, North Carolina.

Saxon, E., B. Baker, W. Hargrove, F. Hoffman, and C. Zganjar. 2005. Mapping environments at risk under different global climate change scenarios. Ecol. Lett. 8(1):53-60.

Schwartz, M.W., L.R. Iverson, A.M. Prasad, S.N. Matthews, and R.J. O'Connor. 2006. Predicting extinctions as a result of climate change. Ecology 87(7):1611-1615.

Sjostrom, A., and C.L. Gross. 2006. Life-history characters and phylogeny are correlated with extinction risk in the Australian angiosperms. J. Biogeogr. 33(2):271-290.

Smith, W.B. 2002. Forest inventory and analysis: a national inventory and monitoring program. Environ. Pollut. 116:S233-S242.

St. Clair, J.B., and G.T. Howe. 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Glob. Change Biol. 13(7):1441-1454.

Stenseth, N.C., A. Mysterud, G. Ottersen, J.W. Hurrell, K.S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297(5585):1292-1296.

Stephenson, S.L., H.S. Adams, and M.L. Lipford. 1991. The present distribution of chestnut in the upland forest communities of Virginia. Bull. Torrey Bot. Club 118(1):24-32.

Stork, N.E., J.A. Coddington, R.K. Colwell, R.L. Chazdon, C.W. Dick, C.A. Peres, S. Sloan, and K. Willis. 2009. Vulnerability and resilience of tropical forest species to land-use change. Conserv. Biol. 23(6):1438-1447.

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(6970):145-148.

United States Geological Survey. 1999. Digital representation of "Atlas of United States Trees" by Elbert L. Little Jr. Available online at http://esp.cr.usgs.gov/data/atlas/little/; last accessed June 25, 2013.

Vitt, P., K. Havens, A.T. Kramer, D. Sollenberger, and E. Yates. 2010. Assisted migration of plants: Changes in latitudes, changes in attitudes. Biol. Conserv. 143(1):18-27.

Warshall, P. 1995. The Madrean sky island archipelago: A planetary overview. P. 6-18 in Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico, DeBano, L.H., P.H. Ffolliott, A. Ortega-Rubio, G.J. Gottfried, R.H. Hamre, and C.B. Edminster (eds.). USDA For. Serv. Gen. Tech. Rep. RM-GTR-264. 669 p.

Woodall, C.W., C.M. Oswalt, J.A. Westfall, C.H. Perry, M.D. Nelson, and A.O. Finley. 2009. An indicator of tree migration in forests of the eastern United States. For. Ecol. Manage. 257(5):1434-1444.

Woudenberg, S.W., B.L. Conkling, B.M. O'Connell, E.B. LaPoint, J.A. Turner, and K.L. Waddell. 2010. The Forest Inventory and Analysis Database: Database Description and Users Manual Version 4.0 for Phase 2. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-245. 336 p.

Wu, H.X., and C.C. Ying. 2004. Geographic pattern of local optimality in natural populations of lodgepole pine. For. Ecol. Manage. 194(1-3):177-198.

Zhu, K., C.W. Woodall, and J.S. Clark. 2012. Failure to migrate: Lack of tree range expansion in response to climate change. Glob. Change Biol. 18(3):1042-1052.

APPENDIX A

Table 4: Study species, including region assignment, tree size class, number of Forest Inventory and Analysis (FIA) plots, and climate change pressure metrics developed using the Multivariate Spatio-Temporal Clustering approach (Suitable Habitat Area, Range Stability, Shift Pressure, and Niche Occupancy).

		FIA			**Suitable Habitat Area (km^2)**			**Range Stability**		**Shift Pressure**		**Niche Occ.**
Species Name	**Common Name**	**Region**	**Size**	**Plots**	**Current**	**Future**	**% Chg.**	**Area (km^2)**	**%**	**Mean (cells)**	**SD**	
Abies grandis	grand fir	W	1	1,219	561,562	452,956	-19.34	362,573	64.57	3.61	9.22	136
Abies procera	noble fir	W	1	154	81,864	60,436	-26.18	53,962	65.92	4.10	8.95	21
Acer barbatum	Florida maple	ES	1	454	746,224	237,595	-68.16	118,432	15.87	12.10	17.21	69
Acer glabrum	Rocky Mountain maple	W	2	208	163,915	112,990	-31.07	83,244	50.78	3.25	14.87	36
Acer grandidentatum	bigtooth maple	W	1	121	104,241	76,814	-26.31	42,111	40.40	5.44	12.10	24
Acer leucoderme	chalk maple	ES	1	21	116,897	8,661	-92.59	69	0.06	39.34	30.49	6
Acer macrophyllum	bigleaf maple	W	1	679	323,587	267,837	-17.23	219,802	67.93	5.48	26.61	86
Acer negundo	boxelder	EG	1	2,455	2,446,235	1,052,762	-56.96	834,034	34.09	6.94	11.83	276
Acer nigrum	black maple	EN	1	127	379,779	50,495	-86.70	22,545	5.94	19.38	23.87	28
Acer pensylvanicum	striped maple	EN	2	562	602,825	354,667	-41.17	210,179	34.87	15.82	44.12	96
Acer rubrum	red maple	EG	1	29,535	3,618,116	2,853,868	-21.12	2,251,543	62.23	5.35	13.69	635
Acer saccharinum	silver maple	EG	1	1,134	1,558,165	461,920	-70.35	364,804	23.41	12.95	21.99	168
Acer saccharum	sugar maple	EN	1	14,041	2,907,738	1,838,090	-36.79	1,377,169	47.36	7.53	14.67	473
Aesculus flava	yellow buckeye	EG	1	378	436,987	165,682	-62.09	100,284	22.95	22.16	42.54	52
Aesculus glabra	Ohio buckeye	EN	1	288	626,707	135,943	-78.31	91,114	14.54	18.23	26.06	54
Alnus rubra	red alder	W	1	1,001	291,395	233,773	-19.77	186,094	63.86	9.53	70.20	79
Amelanchier **spp.**	common serviceberry	EG	2	2,061	1,806,684	773,825	-57.17	572,602	31.69	9.92	14.24	237
Arbutus menziesii	Pacific madrone	W	2	716	232,900	197,066	-15.39	141,740	60.86	3.97	11.56	65
Asimina triloba	pawpaw	EG	3	215	551,887	136,475	-75.27	39,625	7.18	17.78	19.46	47
Betula alleghaniensis	yellow birch	EN	1	5,539	1,538,573	1,121,260	-27.12	729,094	47.39	9.65	21.25	290
Betula lenta	sweet birch	EG	1	2,655	946,112	623,769	-34.07	405,131	42.82	24.57	42.65	144
Betula nigra	river birch	EG	1	706	1,251,236	451,642	-63.90	298,893	23.89	6.14	10.16	120
Betula populifolia	gray birch	EN	1	488	443,036	345,480	-22.02	217,079	49.00	8.61	16.80	72
Calocedrus decurrens	incense-cedar	W	1	989	330,425	268,184	-18.84	177,278	53.65	3.15	8.19	86
Carpinus caroliniana	musclewood	EG	2	2,853	1,854,268	1,025,554	-44.69	872,469	47.05	4.31	8.90	218
Carya alba	mockernut hickory	EG	1	6,591	2,205,014	1,342,074	-39.14	1,200,134	54.43	3.22	6.76	292
Carya aquatica	water hickory	ES	1	455	575,403	300,701	-47.74	157,033	27.29	7.61	12.58	66
Carya cordiformis	bitternut hickory	EG	1	2,798	2,238,260	795,641	-64.45	661,385	29.55	5.50	9.75	252

Continued on next page

Table 4 – ***continued from previous page***

		FIA			Suitable Habitat Area (km^2)			Range Stability		Shift Pressure		Niche Occ.
Species Name	**Common Name**	**Region**	**Size**	**Plots**	**Current**	**Future**	**% Chg.**	**Area (km^2)**	**%**	**Mean (cells)**	**SD**	
Carya glabra	pignut hickory	EG	1	6,493	2,116,678	1,197,964	-43.40	1,011,158	47.77	5.68	9.70	273
Carya illinoinensis	pecan	EG	1	483	817,561	281,209	-65.60	135,244	16.54	10.00	17.65	86
Carya laciniosa	shellbark hickory	EN	1	347	672,521	173,063	-74.27	60,404	8.98	13.94	17.26	60
Carya ovata	shagbark hickory	EG	1	4,441	2,290,060	1,046,508	-54.30	898,319	39.23	5.14	8.12	281
Carya pallida	sand hickory	ES	1	92	289,297	76,258	-73.64	19,390	6.70	25.87	30.48	21
Carya texana	black hickory	ES	1	2,275	969,560	603,388	-37.77	317,457	32.74	5.01	6.49	128
Castanea dentata	American chestnut	EG	3	121	228,470	77,977	-65.87	39,985	17.50	28.40	65.46	27
Celtis laevigata	sugarberry	ES	1	1,501	1,289,409	689,898	-46.50	476,820	36.98	4.17	8.36	153
Celtis occidentalis	hackberry	EG	1	2,940	2,363,656	838,548	-64.52	711,293	30.09	5.61	8.89	260
Cercis canadensis	eastern redbud	EG	2	1,796	1,611,826	629,646	-60.94	427,141	26.50	9.39	15.54	178
Chamaecyparis thyoides	Atlantic whitecedar	EG	1	67	115,504	65,541	-43.26	46,390	40.16	19.90	37.87	14
Chrysolepis chrysophylla	golden chinquapin	W	2	200	156,854	109,841	-29.97	72,544	46.25	5.00	41.01	38
Cornus florida	flowering dogwood	EG	2	4,301	1,742,296	935,884	-46.28	797,791	45.79	3.48	6.51	217
***Crataegus* spp.**	hawthorn species	EG	2	1,667	2,083,660	749,207	-64.04	554,645	26.62	6.16	12.41	223
Diospyros virginiana	common persimmon	EG	1	1,636	1,490,220	766,278	-48.58	583,857	39.18	4.18	7.42	177
Fagus grandifolia	American beech	EG	1	6,795	2,411,995	1,531,651	-36.50	1,172,698	48.62	4.38	11.22	364
Fraxinus americana	white ash	EG	1	8,315	2,893,710	1,735,312	-40.03	1,429,939	49.42	3.59	6.81	438
Fraxinus caroliniana	Carolina ash	ES	1	77	163,637	105,027	-35.82	75,683	46.25	12.92	15.09	16
Fraxinus latifolia	Oregon ash	W	1	48	27,504	23,360	-15.07	8,724	31.72	15.96	74.84	6
Fraxinus nigra	black ash	EN	1	3,544	1,118,321	661,939	-40.81	394,997	35.32	18.01	30.06	183
Fraxinus pennsylvanica	green ash	EG	1	6,950	3,783,719	2,074,419	-45.18	1,715,258	45.33	5.60	10.78	518
Fraxinus profunda	pumpkin ash	ES	1	50	94,245	58,934	-37.47	48,227	51.17	24.41	41.96	9
Fraxinus quadrangulata	blue ash	EN	1	149	310,997	74,222	-76.13	19,422	6.25	34.58	34.73	25
Fraxinus texensis	Texas ash	ES	1	26	63,977	5,351	-91.64	4,688	7.33	11.59	11.91	5
Gleditsia aquatica	waterlocust	ES	1	72	125,423	46,503	-62.92	14,830	11.82	34.60	37.02	13
Gleditsia triacanthos	honeylocust	EG	1	1,209	1,690,449	549,784	-67.48	429,777	25.42	6.27	11.93	174
Gordonia lasianthus	loblolly bay	ES	1	276	219,036	180,135	-17.76	148,020	67.58	8.86	13.10	28
Gymnocladus dioicus	Kentucky coffeetree	EN	1	67	149,396	46,848	-68.64	1,889	1.26	54.35	32.27	17
Halesia caroliniana	Carolina silverbell	ES	3	22	126,007	43,134	-65.77	22,096	17.54	17.07	12.92	14

Continued on next page

Table 4 – ***continued from previous page***

		FIA			**Suitable Habitat Area (km^2)**			**Range Stability**		**Shift Pressure**		**Niche Occ.**
Species Name	**Common Name**	**Region**	**Size**	**Plots**	**Current**	**Future**	**% Chg.**	**Area (km^2)**	**%**	**Mean (cells)**	**SD**	
Ilex opaca	American holly	ES	2	2,516	1,257,475	824,553	-34.43	686,423	54.59	3.69	11.23	166
Juglans cinerea	butternut	EN	1	289	702,405	131,506	-81.28	77,655	11.06	20.89	34.78	56
Juglans nigra	black walnut	EG	1	3,589	2,112,499	717,423	-66.04	613,900	29.06	10.93	18.15	229
Juniperus monosperma	oneseed juniper	W	2	1,543	1,053,223	723,783	-31.28	546,905	51.93	4.59	12.59	168
Juniperus osteosperma	Utah juniper	W	1	3,319	1,595,135	1,195,058	-25.08	917,277	57.50	4.99	19.82	285
Juniperus scopulorum	Rocky Mountain juniper	W	2	1,585	1,366,943	740,590	-45.82	619,312	45.31	4.08	9.04	221
Juniperus virginiana	eastern redcedar	EG	1	5,575	2,680,555	1,265,599	-52.79	1,062,520	39.64	5.00	9.70	332
Larix occidentalis	western larch	W	1	962	426,800	359,398	-15.79	267,460	62.67	3.06	8.43	101
Liquidambar styraciflua	sweetgum	ES	1	13,822	1,808,686	1,447,117	-19.99	1,160,554	64.17	3.37	10.85	268
Liriodendron tulipifera	yellow-poplar	EG	1	9,802	1,785,169	1,162,744	-34.87	999,965	56.02	4.00	9.04	246
Magnolia acuminata	cucumbertree	EG	1	697	767,305	286,005	-62.73	226,473	29.52	16.75	24.20	83
Magnolia fraseri	mountain magnolia	ES	1	216	213,960	108,654	-49.22	55,911	26.13	21.45	47.29	35
Magnolia grandiflora	Southern magnolia	ES	1	407	466,563	376,023	-19.41	182,408	39.10	6.49	12.79	56
Magnolia macrophylla	bigleaf magnolia	ES	1	139	224,320	96,259	-57.09	28,515	12.71	9.52	12.20	24
Magnolia tripetala	umbrella magnolia	EG	2	45	130,364	31,461	-75.87	7,448	5.71	34.24	58.62	12
Magnolia virginiana	sweetbay	ES	1	2,115	925,510	677,888	-26.76	509,780	55.08	6.04	10.71	119
Malus angustifolia	southern crabapple	ES	2	48	154,933	26,513	-82.89	16,407	10.59	22.15	18.73	9
Malus coronaria	sweet crabapple	EN	2	40	107,523	7,700	-92.84	2,264	2.11	16.25	20.22	7
Morus rubra	red mulberry	EG	1	1,414	1,945,283	609,475	-68.67	449,358	23.10	6.21	10.36	197
Nyssa aquatica	water tupelo	ES	1	464	743,490	337,166	-54.65	213,585	28.73	4.69	10.11	77
Nyssa biflora	swamp tupelo	ES	1	2,142	930,400	567,836	-38.97	461,606	49.61	4.32	12.27	115
Nyssa ogeche	Ogeechee tupelo	ES	1	49	79,455	30,414	-61.72	25,183	31.69	3.59	5.81	8
Nyssa sylvatica	blackgum	EG	1	7,898	2,117,467	1,481,561	-30.03	1,248,716	58.97	3.44	7.13	304
Ostrya virginiana	eastern hophornbeam	EG	2	4,377	2,928,995	1,505,422	-48.60	1,170,252	39.95	5.00	8.62	392
Oxydendrum arboreum	sourwood	EG	1	3,948	1,236,347	661,396	-46.50	538,777	43.58	4.51	7.70	153
Persea borbonia	redbay	ES	2	759	544,766	456,660	-16.17	304,682	55.93	8.61	17.57	76

Continued on next page

Table 4 – ***continued from previous page***

		FIA			**Suitable Habitat Area (km^2)**			**Range Stability**		**Shift Pressure**		**Niche Occ.**
Species Name	**Common Name**	**Region**	**Size**	**Plots**	**Current**	**Future**	**% Chg.**	**Area (km^2)**	**%**	**Mean (cells)**	**SD**	
Picea rubens	red spruce	EN	1	2,274	554,807	514,999	-7.18	295,694	53.30	6.53	9.62	115
Picea sitchensis	Sitka spruce	W	1	667	180,697	166,053	-8.10	125,193	69.28	8.33	40.50	55
Pinus aristata	Rocky Mountain bristlecone pine	W	2	85	122,184	60,964	-50.10	51,836	42.42	4.90	17.00	20
Pinus attenuata	Knobcone pine	W	1	68	56,594	48,603	-14.12	18,305	32.34	8.59	61.68	16
Pinus balfouriana	foxtail pine	W	1	19	13,503	5,186	-61.59	2,324	17.21	28.04	56.65	3
Pinus echinata	shortleaf pine	ES	1	5,224	1,440,949	949,728	-34.09	723,587	50.22	3.65	10.84	197
Pinus flexilis	limber pine	W	1	573	529,426	272,864	-48.46	230,670	43.57	8.29	23.47	88
Pinus glabra	spruce pine	ES	1	252	345,237	199,612	-42.18	95,553	27.68	3.54	4.28	39
Pinus jeffreyi	Jeffrey pine	W	1	635	331,298	216,970	-34.51	145,910	44.04	3.68	12.91	71
Pinus lambertiana	sugar pine	W	1	852	276,872	215,743	-22.08	141,397	51.07	3.26	9.44	71
Pinus longaeva	Great Basin bristlecone pine	W	2	19	2,882	5,893	104.48	726	25.19	73.34	121.19	1
Pinus monticola	western white pine	W	1	499	303,642	215,201	-29.13	167,406	55.13	3.58	11.80	71
Pinus palustris	longleaf pine	ES	1	1,525	753,776	622,282	-17.44	467,259	61.99	6.71	13.18	103
Pinus ponderosa	ponderosa pine	W	1	5,670	2,193,029	1,515,092	-30.91	1,233,661	56.25	6.01	14.01	435
Pinus pungens	Table Mountain pine	EG	1	82	171,126	45,078	-73.66	26,020	15.21	32.57	66.02	19
Pinus resinosa	red pine	EN	1	2,398	909,901	551,059	-39.44	322,408	35.43	13.64	24.84	151
Pinus rigida	pitch pine	EG	1	626	669,603	316,796	-52.69	199,594	29.81	21.90	39.69	90
Pinus sabiniana	gray pine	W	1	223	133,337	111,601	-16.30	59,066	44.30	5.68	19.57	35
Pinus serotina	pond pine	ES	1	320	309,839	207,175	-33.13	165,429	53.39	6.99	26.10	35
Pinus strobus	white pine	EG	1	2,501	1,896,556	1,254,557	-33.85	854,320	45.05	9.01	17.30	316
Pinus taeda	loblolly pine	ES	1	14,223	1,511,803	1,163,362	-23.05	980,146	64.83	5.19	13.90	221
Pinus virginiana	Virginia pine	EG	1	2,558	974,682	444,750	-54.37	329,004	33.76	6.41	10.10	120
Platanus occidentalis	American sycamore	EG	1	2,014	1,838,858	803,641	-56.30	641,852	34.90	4.28	9.32	205
Populus deltoides	eastern cottonwood	EG	1	851	1,483,934	435,154	-70.68	302,336	20.37	12.68	20.64	151
Populus grandidentata	bigtooth aspen	EN	1	3,504	1,427,666	900,432	-36.93	614,141	43.02	10.48	23.13	228
Prunus americana	American plum	EG	3	200	576,666	119,111	-79.34	42,385	7.35	21.86	23.75	45
Prunus serotina	black cherry	EG	1	12,104	3,302,852	2,151,239	-34.87	1,787,825	54.13	3.93	7.65	502
Pseudotsuga menziesii	Douglas-fir	W	1	8,536	1,825,092	1,347,366	-26.18	1,150,696	63.05	7.11	18.67	429
Quercus agrifolia	California live oak	W	1	186	124,892	82,039	-34.31	35,602	28.51	7.03	12.31	26

Continued on next page

Table 4 – ***continued from previous page***

		FIA			**Suitable Habitat Area (km^2)**			**Range Stability**		**Shift Pressure**		**Niche Occ.**
Species Name	**Common Name**	**Region**	**Size**	**Plots**	**Current**	**Future**	**% Chg.**	**Area (km^2)**	**%**	**Mean (cells)**	**SD**	
Quercus alba	white oak	EG	1	15,824	2,852,292	2,000,038	-29.88	1,689,419	59.23	3.18	6.37	434
Quercus arizonica	Arizona white oak	W	1	348	237,215	168,318	-29.04	97,730	41.20	11.62	26.45	50
Quercus bicolor	swamp white oak	EN	1	392	621,260	188,560	-69.65	123,384	19.86	10.22	20.24	69
Quercus chrysolepis	canyon live oak	W	1	692	272,758	214,014	-21.54	145,150	53.22	3.69	8.23	72
Quercus coccinea	scarlet oak	EN	1	4,398	1,485,370	768,403	-48.27	557,317	37.52	7.21	11.75	195
Quercus douglasii	blue oak	W	1	327	191,613	187,290	-2.26	87,137	45.48	4.89	11.27	50
Quercus ellipsoidalis	northern pin oak	EN	1	1,146	602,713	267,878	-55.55	189,996	31.52	15.82	20.44	85
Quercus emoryi	Emory oak	W	2	226	166,441	90,748	-45.48	46,599	28.00	10.50	36.09	32
Quercus falcata	southern red oak	ES	1	5,516	1,606,804	1,203,492	-25.10	935,769	58.24	3.33	6.13	228
Quercus gambelii	Gambel oak	W	3	1,796	1,059,001	680,121	-35.78	533,744	50.40	6.22	14.72	194
Quercus garryana	Oregon white oak	W	3	313	269,240	216,182	-19.71	133,840	49.71	5.02	11.56	69
Quercus grisea	gray oak	W	3	19	33,650	15,945	-52.62	5,387	16.01	41.26	40.70	4
Quercus ilicifolia	scrub oak	EN	3	52	121,493	55,653	-54.19	10,506	8.65	26.43	68.48	12
Quercus imbricaria	shingle oak	EN	1	606	767,197	216,421	-71.79	120,711	15.73	18.87	23.28	76
Quercus incana	bluejack oak	ES	2	194	351,706	145,255	-58.70	89,869	25.55	14.88	18.35	34
Quercus kelloggii	California black oak	W	1	863	247,827	218,451	-11.85	144,739	58.40	3.62	5.89	71
Quercus laevis	turkey oak	ES	2	336	365,606	234,437	-35.88	185,415	50.71	6.40	12.15	43
Quercus laurifolia	laurel oak	ES	1	2,327	946,861	689,900	-27.14	524,184	55.36	6.90	16.15	128
Quercus lobata	California white oak	W	1	70	59,050	47,887	-18.90	16,233	27.49	5.84	24.49	15
Quercus lyrata	overcup oak	ES	1	660	754,090	425,091	-43.63	257,153	34.10	3.49	7.06	88
Quercus macrocarpa	bur oak	EN	1	2,250	1,499,070	528,839	-64.72	394,386	26.31	11.30	19.30	183
Quercus margarettiae	dwarf post oak	ES	2	175	230,203	96,953	-57.88	67,067	29.13	7.28	23.75	22
Quercus marilandica	blackjack oak	ES	1	1,216	1,159,398	526,728	-54.57	295,336	25.47	4.50	5.45	126
Quercus michauxii	swamp chestnut oak	ES	1	624	961,233	510,781	-46.86	385,502	40.10	4.39	8.92	98
Quercus minima	dwarf live oak	ES	2	102	106,951	123,742	15.70	90,712	84.82	11.84	56.53	19
Quercus muehlenbergii	chinkapin oak	EG	1	1,548	1,214,197	498,126	-58.97	280,074	23.07	13.06	17.19	139
Quercus nigra	water oak	ES	1	7,586	1,380,479	1,152,378	-16.52	861,904	62.44	3.24	10.46	207
Quercus pagoda	cherrybark oak	ES	1	1,706	1,144,016	654,250	-42.81	497,931	43.52	3.05	7.35	135
Quercus palustris	pin oak	EN	1	493	805,617	206,199	-74.40	119,471	14.83	12.92	20.43	81
Quercus phellos	willow oak	ES	1	1,692	1,208,221	693,467	-42.60	560,576	46.40	4.06	6.79	142
Quercus prinus	chestnut oak	EG	1	4,633	1,152,198	646,068	-43.93	458,812	39.82	6.33	10.61	161
Quercus rubra	northern red oak	EG	1	12,232	2,913,020	1,898,449	-34.83	1,475,575	50.65	5.93	12.00	456

Continued on next page

Table 4 – ***continued from previous page***

		FIA			Suitable Habitat Area (km^2)			Range Stability		Shift Pressure		Niche Occ.
Species Name	**Common Name**	**Region**	**Size**	**Plots**	**Current**	**Future**	**% Chg.**	**Area (km^2)**	**%**	**Mean (cells)**	**SD**	
Quercus shumardii	Shumard oak	ES	1	442	886,956	298,512	-66.34	150,534	16.97	9.81	16.87	91
Quercus similis	Delta post oak	ES	1	25	20,910	1,742	-91.67	131	0.63	61.28	31.00	2
Quercus sinuata	Durand oak	ES	1	31	45,485	8,462	-81.40	2,733	6.01	29.41	17.67	4
Quercus stellata	post oak	ES	1	6,791	1,958,086	1,460,439	-25.41	1,037,526	52.99	2.82	5.90	281
Quercus texana	Nutall oak	ES	1	270	292,539	181,896	-37.82	99,553	34.03	4.13	13.05	38
Quercus velutina	black oak	EG	1	8,807	2,533,633	1,574,952	-37.84	1,296,840	51.18	4.13	6.93	360
Quercus virginiana	live oak	ES	1	1,193	739,900	493,294	-33.33	376,968	50.95	7.63	22.45	106
Quercus wislizeni	interior live oak	W	1	253	170,049	139,851	-17.76	69,217	40.70	4.88	10.58	43
Robinia pseudoacacia	black locust	EG	1	2,160	1,567,969	625,649	-60.10	510,227	32.54	9.59	19.04	184
Salix nigra	black willow	EG	2	1,160	2,012,851	687,606	-65.84	521,829	25.92	9.61	18.48	201
Sassafras albidum	sassafras	EG	1	3,760	1,996,148	1,045,736	-47.61	833,998	41.78	3.22	5.35	259
Sequoia sempervirens	coast redwood	W	1	202	95,712	78,485	-18.00	53,958	56.38	8.54	31.25	23
Sideroxylon lanuginosum	gum bumelia	ES	2	183	372,524	82,275	-77.91	25,826	6.93	12.99	24.56	37
Taxodium distichum	baldcypress	ES	1	894	847,344	550,603	-35.02	382,509	45.14	6.58	13.63	108
Taxus brevifolia	Pacific yew	W	2	129	130,026	75,433	-41.99	57,115	43.93	4.17	35.75	28
Thuja occidentalis	northern white-cedar	EN	1	4,278	1,035,230	808,447	-21.91	516,565	49.90	10.73	40.87	206
Tilia americana	American basswood	EN	1	5,002	2,442,840	1,069,028	-56.24	767,896	31.43	12.10	19.35	326
Tilia americana* var. *caroliniana	Carolina basswood	ES	1	47	52,263	51,542	-1.38	10,167	19.45	14.22	15.02	8
Tilia americana* var. *heterophylla	white basswood	EG	1	45	67,196	17,211	-74.39	5,677	8.45	33.03	33.99	7
Tsuga canadensis	eastern hemlock	EG	1	4,485	1,537,130	1,035,442	-32.64	689,987	44.89	13.80	32.13	261
Tsuga caroliniana	Carolina hemlock	ES	1	19	44,217	29,575	-33.11	15,945	36.06	49.43	81.23	9
Tsuga mertensiana	mountain hemlock	W	1	828	311,059	220,104	-29.24	175,589	56.45	4.61	10.74	80
Ulmus alata	winged elm	ES	1	5,413	1,498,970	1,030,104	-31.28	705,746	47.08	2.52	3.93	199
Ulmus americana	American elm	EG	1	9,520	3,657,437	2,135,689	-41.61	1,744,212	47.69	6.25	13.09	522
Ulmus crassifolia	cedar elm	ES	1	414	498,412	217,252	-56.41	101,321	20.33	5.09	11.42	62
Ulmus rubra	slippery elm	EG	1	3,491	2,427,530	964,213	-60.28	824,800	33.98	6.45	11.84	277
Ulmus serotina	September elm	ES	1	16	20,300	773	-96.19	0	0.00	94.78	36.78	2
Ulmus thomasii	rock elm	EN	1	63	119,980	13,981	-88.35	10,644	8.87	20.13	29.35	9

Note: EG, eastern-general; EN, eastern-north; ES, eastern-south; W, western.