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A United States national prioritization framework for tree species vulnerability to climate change

Kevin M. Potter[1] · **Barbara S. Crane**[2] · **William W. Hargrove**[3]

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Abstract Climate change is one of several threats that will increase the likelihood that forest tree species could experience population-level extirpation or species-level extinction. Scientists and managers from throughout the United States Forest Service have cooperated to develop a framework for conservation priority-setting assessments of forest tree species. This framework uses trait data and predictions of expected climate change pressure to categorize and prioritize 339 native tree species for conservation, monitoring, management and restoration across all forested lands in the contiguous United States and Alaska. The framework allows for the quantitative grouping of species into vulnerability classes that may require different management and conservation strategies for maintaining the adaptive genetic variation of the species within each group. This categorization is based on risk factors relating to the species' (1) exposure to climate change, (2) sensitivity to climate change, and (3) capacity to adapt to climate change. We used K-means clustering to group species into seven classes based on these three vulnerability dimensions. The most vulnerable class encompassed 35 species with high scores for all three vulnerability dimensions. These will require the most immediate conservation intervention. A group of 43 species had high exposure and sensitivity, probably requiring conservation assistance, while a group of 69 species had high exposure and low adaptive capacity, probably needing close monitoring. This assessment tool should be valuable for scientists and managers determining which species and populations to target for monitoring efforts and for pro-active gene conservation and management activities.

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✉ Kevin M. Potter
kpotter@ncsu.edu

[1] Department of Forestry and Environmental Resources, North Carolina State University, 3041 Cornwallis Road, Research Triangle Park, Raleigh, NC 27709, USA

[2] Southern Region, National Forest System, USDA Forest Service, Atlanta, GA 30309, USA

[3] Eastern Forest Environmental Risk Assessment Center (EFETAC), Southern Research Station, USDA Forest Service, Asheville, NC 28804, USA

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Introduction

The ongoing warming of the Earth's climate system is unequivocal and many of the associated changes are unprecedented; at the same time, past, present and future greenhouse gas emissions will continue to alter the climate system in ways that will persist for many centuries (Intergovernmental Panel on Climate Change 2014). Climate shifts are already generating changes to the distributions of species and to ecological dynamics among them (Heller and Zavaleta 2009), increasing the likelihood that species over the next century will experience population-level extirpation or species-level extinction (Parmesan 2006). Evidence suggests that tree species are already exhibiting changes in distribution and phenology in response to climate change (Parmesan and Yohe 2003; Woodall et al. 2009; Root et al. 2003; Zhu et al. 2012). As tree species are forced to move poleward or upslope as a result of climate change, some will likely disappear or be restricted to isolated refugia, while others may expand greatly (Iverson and McKenzie 2013). The response of individual tree species to climate change will depend on their physiological tolerances, life-history strategies, and dispersal abilities, which could drive widely varying responses to potential threats. To minimize the loss of biodiversity, conservation professionals will need to identify species that are most vulnerable to climate change impacts (Pacifici et al. 2015), with vulnerability generally defined as the susceptibility of a system to negative impact (Smit et al. 2000), in this case a function of exposure to climate changes (an extrinsic factor), and of sensitivity to and ability to adapt to the changes (intrinsic factors for each species) (Foden et al. 2013; Williams et al. 2008).

In the face of the potential for climate change impacts, an important forest management goal will be to safeguard existing adaptedness within tree species and create conducive conditions for future evolution, with a focus on the conservation of variability in adaptive traits (Myking 2002). Given the stressful conditions that organisms are likely to encounter as a result of climate change and other threats, conservation efforts should explicitly consider genetic diversity and the processes that support evolutionary resilience, the ability of populations to either persist in their current state or to undergo evolutionary adaptation in response to changing environmental conditions (Sgro et al. 2011). In the context of climate change, this is especially important for species that will be unable to migrate fast enough to track rapidly changing conditions (Jump and Penuelas 2005). In fact, evolutionary adaptation can occur rapidly and can potentially help species counter stressful conditions associated with climate change; the management challenges are to understand when evolution will occur and to identify species that are likely to be evolutionary winners and losers given their life-history traits (Hoffmann and Sgro 2011).

The fundamental importance of genetic variation in forest tree species is recognized by the incorporation of genetic diversity indicators into the widely tracked Montreal Process Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests (Montréal Process Working Group 2009), which the USDA Forest Service uses as a forest sustainability assessment framework (United States Department of Agriculture Forest Service 2004, 2011). Our understanding of relevant adaptive traits or even levels or patterns of neutral genetic variation is incomplete or non-existent for many tree species, however. Several researchers have therefore proposed using ecological and life-history traits to evaluate species' genetic resources and predisposition to threats, including climate change (Sjostrom and Gross 2006; Myking 2002; Aitken et al. 2008). Maintaining genetic variation across multiple species, especially in regions with relatively high biodiversity, will require tailoring conservation, management, monitoring, and restoration efforts to species with similar traits because they will have similar vulnerabilities. Because it is impossible to conserve the genetic diversity of every species or population, conservation practitioners need to apply rational, systematic, and defensible prioritization approaches to efficiently allocate scarce conservation resources (Bottrill et al. 2008; Farnsworth et al. 2006). There is, however, no standard methodology for the assessment of species' vulnerability to climate change. Instead, the conservation goals and the availability of data will determine the most appropriate approach (Pacifici et al. 2015). A framework for assessing the climate vulnerability of species should, however, encompass the components of vulnerability, the factors determining exposure to climate change, and the potential for evolutionary and ecological responses to climate change (Williams et al. 2008).

Such priority-setting approaches will become increasingly important when conditions are rapidly changing and management needs are greater than the available capacity to respond (Millar et al. 2007). It has become increasingly clear that triage (Bottrill et al. 2008), for example, may be necessary to prioritize forest tree species and populations for conservation (St Clair and Howe 2011). The development of conservation priority lists has been applied as a successful system for identifying target species that require the allocation of scarce resources for conservation activities (Mace et al. 2007). Previous examples have been published for vascular plants in Israel (Barazani et al. 2008), New England in the United States (Farnsworth et al. 2006), western Australia (Coates and Atkins 2001), northern Spain (Jimenez-Alfaro et al. 2010), and southern France (Gauthier et al. 2010).

Species prioritization methods that make use of ecologically relevant information in a quantitative manner (often based on the assignment and summarization of point scores), rather than in a qualitative manner, have the advantage of being transparent and repeatable (Todd and Burgman 1998), characteristics that are desirable in many conservation contexts. Conservation practitioners disagree, however, about whether and how scores assigned to species should be weighted. Gauthier et al. (2010), for example, argue for the application of a simple ordinal-value scoring scheme based on a small number of criteria, in part because quantitative ranking schemes may lead to the misleading precision of ranks. Jimenez-Alfaro et al. (2010), on the other hand, assert that such quantitative ranking is an optimal approach for multi-criteria assessment, and specifically should avoid using ordinal scoring and instead use unequally weighted transformations of criteria scores based on conservation value.

In this paper, we describe and apply a data- and expert-opinion-driven hierarchical prioritization framework that uses quantitative trait data and climate change exposure predictions to categorize 339 native tree species for conservation, monitoring, management and restoration across all forested lands in the contiguous United States and Alaska. This framework applies the weighting approach of Jimenez-Alfaro et al. (2010) while addressing the concerns of Gauthier et al. (2010). Specifically, it focuses on the categorization of species—rather than their overall rank prioritization—into vulnerability classes, each with specific associated strategies for maintaining adaptive genetic variation within the context of monitoring, management, and conservation, similar to Foden et al. (2013). As such, this categorization and prioritization approach is based on risk factors relating to the species' (1) exposure to climate change, (2) sensitivity to climate change, and (3) capacity to adapt to climate change. This framework, titled Project CAPTURE (Conservation Assessment and Prioritization of Forest Trees Under Risk of Extirpation), is a cooperative effort by scientists and managers across the United States Forest Service to guide decision-making relating to tree species at threat vulnerability, and can be applied to any threat to the genetic integrity of tree species within any region.

Methods

The assessment focus was to identify and categorize forest tree species on U.S. forested lands, within the conterminous 48 States and Alaska, expected to be most vulnerable to genetic degradation in the face of climate change. Genetic degradation was defined as a significant reduction in the ability of a species to persist for the next century while maintaining sufficient genetic variation to adapt to changing environmental conditions.

We included 339 native forest tree species in this assessment. Most of these (333) were from the list inventoried by the national Forest Inventory and Analysis (FIA) program of the U.S. Forest Service within the contiguous United States and Alaska (Woudenberg et al. 2010). This number encompasses nearly all of the native trees inventoried by FIA within this area (excluding some taxa of subordinate rank within species, some species recently added to the tally list, and some taxonomically questionable hawthorn [*Crataegus*] species). The FIA program defines trees as woody perennial plants usually having a single well-defined erect stem with a more or less definitely formed crown of foliage, a stem diameter at maturity of at least 7.62 cm, and a height of at least 4.75 m at maturity, and that is not supported by vegetation or other structures (not a vine). Six rare tree or tree-like species not inventoried by FIA were also included because they are of significant conservation interest: seaside alder (*Alnus maritima*), saguaro (*Carnegiea gigantea*), Santa Cruz cypress (*Cupressus abramsiana*), Gowen cypress (*Cupressus goveniana*), Arkansas oak (*Quercus arkansana*), and Boynton oak (*Quercus boyntonii*).

Assessment framework

In March 2014, 25 USDA Forest Service resource managers and scientists from throughout the country and the agency participated in a three-day workshop to build consensus on a scientifically defensible and transparent process to categorize and prioritize tree species for conservation, monitoring, management and restoration across all forested lands in the contiguous United States and Alaska. During the workshop, participants agreed on a hierarchical and data-driven framework to achieve these goals (Fig. 1). Conceptually (Foden et al. 2013), it aims to assess the relationship among three dimensions of vulnerability: the exposure to a threat to species' adaptive genetic variation, and two intrinsic vulnerability dimensions (Sensitivity and Low Adaptive Capacity) associated with the threat (Fig. 2). *Exposure to the threat* was defined as the extent to which a threat could diminish a species' adaptive genetic variation. This represents the intensity of the climate change threat that may be experienced by individual species. *Sensitivity to the threat* was defined as the degree to which a species' total genetic resource base is susceptible to a threat. This represents the potential response of individual species to the climate change threat. *Low adaptive capacity for the threat* was defined as the extent to which a species is unable to adapt, through micro-evolutionary change and phenotypic plasticity, to a

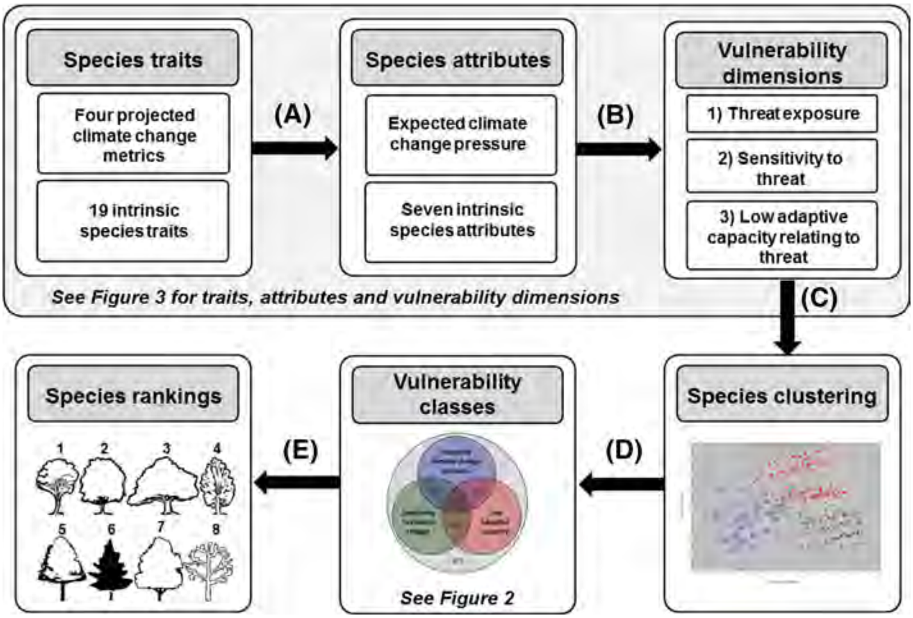


Fig. 1 The Project CAPTURE process consists of five steps: **a** assignment of particular species traits to broad species attributes, **b** assignment of species attributes to vulnerability dimensions, **c** K-means clustering of the 339 species using the vulnerability dimension data, **d** association of each cluster with a climate change vulnerability class based on Foden et al. (2013), and **e** calculation of vulnerability score and ranking within each vulnerability class

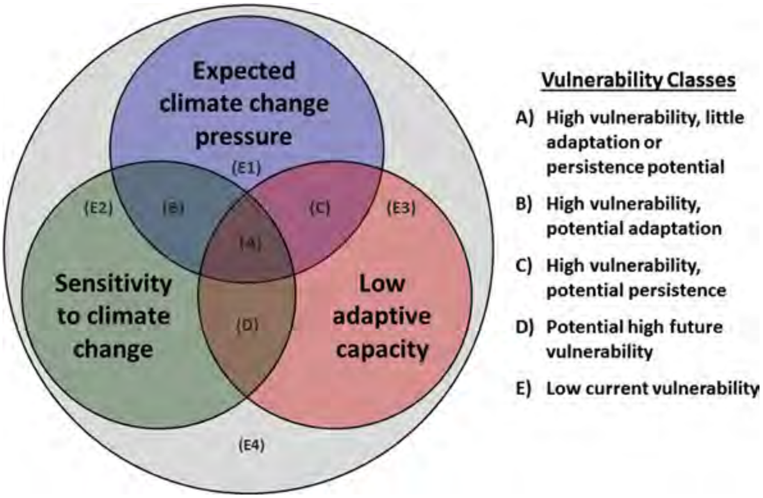


Fig. 2 Conceptual relationships among the three vulnerability dimensions (expected climate change pressure, sensitivity to climate change, and low adaptive capacity), and the description of vulnerability classes defined by those vulnerability dimensions, based on Foden et al. (2013)

specific threat. This represents the expected evolutionary resilience (Sgro et al. 2011) of the species relating to the climate change threat.

Each of the vulnerability dimensions encompassed a set of species vulnerability attributes (such as Rarity, Regeneration Capacity, and Dispersal Ability) that in turn consisted of specific species traits (Fig. 3). Before the workshop, participants completed a survey in which they assessed the proposed assignments of species traits to vulnerability attributes, and vulnerability attributes to vulnerability dimensions. The survey results were used in the current study to quantify expert agreement with these assignments. During the workshop, the participants reached general consensus about these assignments, with some changes.

Each species trait, vulnerability attribute, and vulnerability dimension was scored on a scale of 0–100, with higher scores indicating higher levels of vulnerability to genetic degradation. Many of the trait data were classified originally into ordinal categories based on vulnerability, but the use of ordinal variables can result in unpredictable weighting of criteria within a prioritization analysis (Mace et al. 2007). Therefore, all trait data were weighted using a quantile transformation to a continuous numeric scale, an approach based on the premise that conservation efforts allocated to each species should depend on the proportional number of species within each trait category (Jimenez-Alfaro et al. 2010). In this transformation, the least vulnerable category is 0 and the most vulnerable is 100, with the intermediate categories determined by the proportion of the total species included in that category plus the species in the less vulnerable categories. For example, consider a trait that encompasses four categories across 200 species, with those categories containing

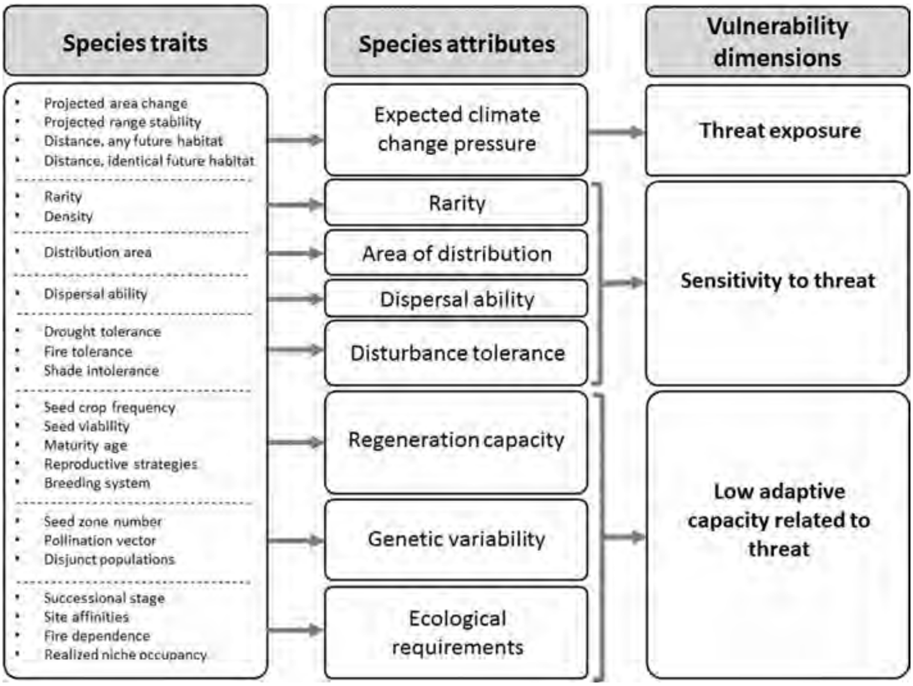


Fig. 3 The structure of the hierarchical vulnerability assessment framework. Species traits (such as seed crop frequency, pollination vector, and drought tolerance) are aggregated into species attributes (such as regeneration capacity, genetic variability, and disturbance tolerance), which are then aggregated into one of the three vulnerability dimensions

(in order of increasing conservation importance) 40, 80, 60, and 20 species. Species with lowest conservation importance (category 1) are given a weight of 0, while the others are weighted proportionally based on the number of species within that category and the lower categories, e.g. (40 + 80)/200 (0.6) for category 2, (40 + 80 + 60)/200 (0.9) for category 3, and (40 + 80 + 60 + 20)/200 (1.0) for category 4. (Each category was then rescaled to a 0–100 scale). Meanwhile, some other traits, such as species distributional area, were originally on a continuous numeric scale. To maintain consistency with the transformed ordinal traits, species were grouped into four equal-proportion weighted quantiles for the continuous traits, with species in each quantile weighted in order of conservation importance as 0, 50, 75 or 100.

Data collection

Data for species-level expected climate change pressure and for 19 intrinsic vulnerability species traits were collected for each of the species included in the assessment (Fig. 3). Most of the data were available from publicly available sources, including the FIA database, Little's species distribution maps (United States Geological Survey 1999), the Silvics of North America manual (Burns and Honkala 1990), Woody Plant Seed Manual (Bonner and Karrfalt 2008), the Fire Effects Information System (United States Department of Agriculture Forest Service 2016), the USDA PLANTS Database (U.S. Department of Agriculture Natural Resource Conservation Service 2016), the Flora of North America North of Mexico (Flora of North America Editorial Committee 1993+), and the NatureServe online data explorer (NatureServe 2016). We were able to find values for all the traits for nearly all the species. When we were not able to find a value for a trait for a species, that trait was not included in the calculation for the species' attribute score (such as the Reproductive Capacity attribute score if we were unable to find data for the age of reproductive maturity trait, for example).

Vulnerability dimension 1: Expected climate change pressure

Four metrics of predicted climate change pressure (Potter and Hargrove 2013) were calculated for each species based on Multivariate Spatio-temporal Clustering (MSTC) (Hargrove and Hoffman 2005): (1) percent change in suitable area, (2) range stability over time, (3) distance to expected future suitable habitat of any quality, (4) distance to future habitat that is identical to current. The values (within four equal-proportion quantiles) were highest for species expected to face the greatest climate change pressure. The mean across the four metrics was then calculated as the Expected Climate Change Pressure vulnerability dimension.

MSTC is a technique that employs non-hierarchical clustering to classify geographic information system (GIS) raster cells with similar current environmental conditions into "quantitative ecoregions" with roughly an equal amount of multivariate environmental heterogeneity (Potter and Hargrove 2012). It then tracks locations of those environmental combinations into the future under different climate change models and scenarios. Global in scope, MSTC incorporated 16 spatial bioclimatic, topographic and topographic environmental variables (Potter and Hargrove 2013) and generated maps using FIA (Woudenberg et al. 2010) and Global Biodiversity Information Facility (Global Biodiversity Information Facility 2016) georeferenced occurrence locations as training data. The comparisons used here are between current conditions and those projected in 2050 under the relatively moderate Hadley B1 Global Circulation Model/emissions scenario combination.

Vulnerability dimension 2: Sensitivity to climate change

The Sensitivity to Climate Change vulnerability dimension incorporated four vulnerability attributes: (1) rarity (85% agreement by workshop participants, 10% disagreement; mean confidence: 4.00 on a scale of 1–5), (2) area of distribution (80/15% agreement/disagreement; mean confidence: 3.90), (3) dispersal ability (50/35% agreement/disagreement; mean confidence: 3.80, and (4) disturbance tolerance (65/30% agreement/disagreement; mean confidence: 3.70). Higher values of the attributes indicated higher sensitivity to climate change. The overall sensitivity score for each species was the mean of its four vulnerability attributes. When attributes encompassed more than one trait, the attribute value was the mean of those traits.

Rarity

The consequences of climate change for rare species may be severe because their populations are likely to be less numerous and may be less well-connected or occur over narrow geographical regions (Jump and Penuelas 2005). We included two metrics of rarity: (1) number of plot-level occurrences of each species from a national grid of inventory plots (100% agreement by workshop participants), and (2) relative number of trees of each species per area of its distributional area in the United States (80% agreement, 20% unsure). These metrics were derived using FIA information, collected using a nationally consistent sampling protocol from approximately 140,000 forested plots across the conterminous United States and coastal Alaska, with each plot representing 2428 ha of land (Woudenberg et al. 2010; Bechtold and Patterson 2005). Given the FIA program design, these data should provide unbiased measures of frequency of occurrence.

Area of distribution

Distributional extent is likely to represent a highly important risk factor for forest tree species. The extent of a species' native range is an expression of its geographic, altitudinal and habitat tolerance, so widespread species tend to have a higher capacity to tolerate new environments given that they have already encountered a variety of climatic and habitat conditions in their evolutionary history and acquired a relatively higher phenotypic plasticity (Bradshaw et al. 2008; Friedman and Reich 2005). In fact, small geographic range is one of the best-supported empirical correlates of extinction (Stork et al. 2009; Brook et al. 2008), and range-restricted species are among the first in which entire species have gone extinct due to recent climate change (Parmesan 2006). We included a single metric of distributional area within the United States, generally based on E.L. Little's forest tree species distribution maps (United States Geological Survey 1999), although some were based on maps in the Flora of North America North of Mexico (Flora of North America Editorial Committee 1993+).

Dispersal ability

A major concern for forest tree species in the face of climate change is whether they will be able to disperse into newly available habitats quickly enough to match the rate of environmental change (Clark 1998; Cain et al. 2000). We included a single metric of dispersal ability, quantifying the relative ability of each species to disperse its propagules, using publicly available descriptions of species characteristics and based on the estimated seed dispersal distances for temperate region plants. Each dispersal type was then given a quantile weighted dispersal index score based on its likely maximum distance (Vittoz and Engler 2007), scaled from 0 to 100 from longest to shortest distance (bird- and water-dispersed: 0 wind-dispersed: 47.2; gravity- and small-animal dispersed: 100).

Disturbance tolerance

Tree species better able to survive and reproduce following natural disturbances such as drought, canopy openings (from blow-downs and other events) and fire may be less vulnerable to genetic degradation and extirpation. We included three metrics of disturbance tolerance: (1) ability to tolerate drought (90% workshop participant agreement, 5% unsure), (2) ability to tolerate fire (90% agreement, 10% unsure), and (3) ability to tolerate opening of the canopy (shade intolerance) (65% agreement, 25% unsure). Tree species with low drought tolerance are likely to have greater vulnerability to projected increases in summer temperature, especially in places where summer moisture is growth-limiting (Littell et al. 2010). Each species was assigned a weighted quantile score based on its degree of drought tolerance: high: 0, medium: 59.9, low: 95.6, none: 100. Forest tree species differ in their tolerance to wildland fire (Fischer et al. 1996), and those better able to tolerate fire may be more likely to persist on the landscape. Each species was assigned a weighted quantile score based on its degree of fire tolerance: high: 0, medium: 49.7, low: 90.4, none: 100. Meanwhile, increased stand disturbances will create gaps in closed canopies that will spur accelerated growth in shade-intolerant species (Lawson and Michler 2014). Shade tolerant species therefore may be less likely to persist in a world with an increasing frequency and extent of such disturbances. Each species was assigned a weighted quantile score based on its degree of shade tolerance: intolerant: 0, intermediate: 73.2, tolerant: 100.

Vulnerability dimension 3: Low adaptability to climate change

The Low Adaptability to Climate Change vulnerability dimension incorporated three vulnerability attributes: (1) regeneration capacity (85/10% agreement/disagreement; mean confidence: 3.95), (2) genetic variability (100% agreement; mean confidence: 4.16), and (3) ecological requirements (60/30% agreement/disagreement; mean confidence: 3.84). Higher values indicated lower adaptability to climate change; the overall score for each species was the mean of its three vulnerability attributes. The value of each attribute was calculated as the mean of the traits which it encompassed.

Regeneration capacity

Forest tree vulnerability to genetic degradation in the face of threats is likely to be influenced by several factors associated with species' ability to successfully regenerate. We included five metrics of regeneration capacity: (1) frequency of large seed crops (80% agreement, 20% not sure), (2) long-term viability of seed (added in response to participant consensus), (3) age at reproductive maturity (95% agreement, 5% not sure), (4) sexual and vegetative reproduction strategies (75% agreement, 10% not sure), and (5) breeding system

(55% agreement, 30% not sure). First, reproductive rate, or fecundity, will be critical for the successful regeneration of tree species, as measured in part by the frequency of large seed crops. Among the best-supported empirical correlates of extinction includes low fecundity (Brook et al. 2008). Each species was assigned a weighted quantile score based on its interval between large seed crops: short (more or less annually): 0, moderate (every 2–3 years): 59.8, long (every 4–6 years): 80.5, very long (more than every 7 years, or erratic/irregular): 100. Second, tree species with seeds able to remain dormant in the natural forest seed bank may be more likely to persist in the forest. Such seed dormancy is a mechanism that can prevent germination during unsuitable ecological conditions when the probability of seedling survival is low (Black et al. 2006). Each species was assigned a weighted quantile score based on whether its seeds are able to persist and successfully germinate later in a natural forest seed bank ("orthodox"): 0; whether they are dessication-intolerant ("recalcitrant"): 100; or intermediate for these characteristics ("sub-orthodox"): 75.5. Third, maturation age will influence the ability of tree species to either adapt to changing conditions, or to successfully shift their distributions in response. Specifically, delayed reproductive maturity will reduce the number of generations that can establish during any period of time (Jump and Penuelas 2005; Savolainen et al. 2004). Each species was assigned a weighted quantile score based on the age at which trees generally become reproductively mature: very early (>10 years): 0, early (10–19 years): 56.0, moderate (20–29 years): 85.1, late (30–39 years): 94.7, very late (40 or more years): 100. Fourth, tree species that have the capacity for clonal reproduction can persist in the absence of sexual reproduction for centuries or even millennia (Ally et al. 2008). The most advantageous strategy for plant species is perhaps a combination of sexual and vegetative reproduction (Farnsworth 2007). Each species was assigned a score based on the degree to which it is able to reproduce vegetatively: significant combination of sexual and clonal: 0, only sexual or only clonal, or only rare sexual or rare clonal: 100. Finally, dioecy, the breeding system in which a species has separate male and female individuals, is a factor associated with a higher risk of extinction (Vamosi and Vamosi 2005). Each species was assigned a score based on whether it consists of individuals having separate male and female flowers (monoecious) or perfect flowers (hermaphroditic): 0, or of separate male and female individuals (dioecious, mostly dioecious, or polygamodioecious): 100.

Genetic variability

Maintaining genetic diversity within plant populations and species may be important for alleviating changes in phenology as a result of climate change because this diversity influences the variation in phenological responses (Doi et al. 2010). We included three metrics quantifying the relative amount of genetic variation that exists within each species: (1) number of climatically defined seed zones intersecting each species' distribution (added in response to participant consensus), (2) pollination vector (65% agreement, 35% not sure), and (3) number of disjunct populations (85% agreement, 5% not sure). First, as an indicator of among-population adaptive variation, each species was assigned a score based on how many climatically defined provisional seed zones (Bower et al. 2014) intersected with its area of distribution. The resulting count of intersected seed zones was then converted for each species to a scale of 0–100 compared to the species with the lowest (0) and highest (100) scores (within four equal-proportion quantiles). Second, high rates and distances of pollen dispersal will contribute positively to tree species' capacity both to adapt and to migrate (Aitken et al. 2008), and wind is expected to be a more effective pollen dispersal mechanism than are animals (Govindaraju 1988). Each species was assigned a weighted quantile score based on its primary pollination vector: primarily or entirely wind: 0, significant component of both insects and wind: 67.6, and primarily or entirely insects, birds, or mammals: 100. Populations of a species that are geographic outliers should be candidates for conservation activities because they are more likely to differ genetically, and may be more vulnerable to environmental change as a result lower levels of genetic variation (Yanchuk and Lester 1996). Each species was assigned a weighted quantile score based on its number of disjunct populations, based on digitized versions of E.L. Little's range maps (United States Geological Survey 1999): no disjuncts: 0, 1–2 disjuncts: 17.1, 3–4 disjuncts: 24.2, 5 or more disjuncts, or consisting entirely of small populations (<250,000 ha): 100. Disjunct populations were defined as those that are smaller than 250,000 hectares, and were at least 50 km from the nearest population that were more than 250,000 hectares.

Ecological requirements

Tree species are more likely to be susceptible to climate change if they tend to be associated with more specific environmental conditions and processes. We included four ecological requirements metrics: (1) successional stage (80% agreement, 10% not sure), (2) site affinities (95% agreement, 5% not sure), (3) fire dependence (added in response to participant consensus), and (4) current realized broad-scale niche occupancy (75% agreement, 25% not sure). First, species associated with late stages of forest succession display more variation within populations than pioneer species (Hamrick et al. 1992), and have been considered at higher risk of vulnerability (Myking 2002). Each species was assigned a weighted quantile score based on the earliest successional stage with which it is generally associated: pioneer: 0, early: 43.4, intermediate: 68.9, late: 85.4, climax: 100. Second, species with narrower site affinities are more likely to have scattered occurrences and are expected to have less within-population variation than continuously distributed species (Hamrick et al. 1992; Myking 2002). Each species was assigned a weighted quantile score based on the breadth of the environmental conditions with which it is generally associated: wide breadth/generalist: 0, wide to moderate breadth: 49.9, moderate breadth: 63.4, moderate to narrow breadth: 84.7, narrow breadth/specialist: 100. Third, many tree species are dependent upon fire for their continued existence (Brown and Smith 2000). As a result of dramatic changes in fire regimes and fire intensities, tree species that are more dependent upon fire for their persistence, including for regeneration, may be at greater vulnerability of genetic degradation. Each species was assigned a weighted quantile score based on its degree of fire dependence: low: 0, moderate: 90.7, high: 100. Finally, narrow niche breadth is, in general, a strong predictor of extinction risk (Stork et al. 2009; Brook et al. 2008). We used the number of unique, quantitatively defined Multivariate Spatio-Temporal Clustering ecoregions (see above) that intersected with plot occurrences of each species as a metric of currently realized niche occupancy. The niche occupancy scores for the species were converted to a scale of 0–100 (within four equal-proportion quantiles), with species having the fewest niches given the highest scores.

Clustering into vulnerability classes

Species were grouped quantitatively into vulnerability classes using *K*-means clustering (Hartigan 1975) of species' climate change exposure scores and the two associated vulnerability dimension scores (Sensitivity and Low Adaptive Capacity) in Proc FASTCLUS in SAS 9.4 (SAS Institute Inc. 2013). (These scores were first standardized to a mean of 0 and a standard deviation of 1). *K*-means, one of the oldest and most widely used clustering algorithms that can be used with a wide variety of data types, is an efficient partitional clustering technique that attempts to find a user-specified number of data clusters (*K*) represented by their centroids (Tan et al. 2005). To select the number of clusters that best explains the variation in the data, we ran the *K*-means analysis for the number of clusters, *K*, from 2 to 15. The *K* that best explained variation in the data was chosen based on local peaks in two statistics, the pseudo F-statistic and the cubic clustering criterion (Milligan and Cooper 1985).

We next associated each of the clusters with one of the vulnerability classes described in the conceptual Fig. 2, based on Foden et al. (2013). Two sources of information informed this decision. First, we compared the mean vulnerability dimension scores (Expected Climate Change Pressure, Threat Sensitivity, and Low Adaptive Capacity) across the species within each cluster. Second, to aid visual interpretation of group differences, we plotted the clusters in three-dimensional space in SAS 9.4 (SAS Institute Inc. 2013) using canonical discriminant analysis, a dimension-reduction technique that derives canonical variables that are linear combinations of the quantitative variables that summarize between-class variation. We then determined how each of these canonical variables (axes) was associated with the three vulnerability dimensions.

Calculation of vulnerability score

Species were given a vulnerability rating based on the mean of their three vulnerability dimension scores. The rating was on a scale of 0–100, with higher values indicating higher external threat exposure and intrinsic threat vulnerability. The species were then ranked from most to least vulnerable within each of the vulnerability classes determined by the *K*-means clustering.

Results

Clustering into vulnerability classes

Pairwise Pearson correlations among the vulnerability attributes were either not significant ($r = -0.011$ between climate change pressure and sensitivity) or not large ($r = 0.484$ between sensitivity and low adaptive capacity, $p < 0.001$, and $r = 0.111$ between climate change pressure and low adaptive capacity, $p < 0.05$).

The Proc FASTCLUS K-means clustering analysis most strongly suggested the existence of seven clusters, since the cubic clustering criterion had a local peak at $K = 7$ (Supplementary Table 1). The canonical discriminant analysis associated each of the three vulnerability dimensions with the three canonical variables (axes) (Table 1), and the seven clusters were plotted using their scores for each of the three canonical variables (Fig. 4). Canonical variable 1, which explained 49.0% of data variation, was positively associated with all three vulnerability dimensions, most strongly with low adaptive capacity and most weakly with expected climate change pressure. Canonical variable 2, which explained 43.5% of variability, was strongly positively associated with climate change pressure, and was weakly negatively associated with the two intrinsic vulnerability dimensions. Canonical variable 3, explaining 7.6% of variation, was strongly negatively associated with

Table 1 Correlations between vulnerability dimensions and the canonical discriminant functions (canonical variables 1, 2, and 3) after controlling for group membership

	Pooled within canonical structure		
	Can1	Can2	Can3
Climate change exposure	0.4566	0.8643	−0.211
Sensitivity	0.6247	−0.4316	−0.6507
Low adaptive capacity	0.646	−0.2022	0.7361

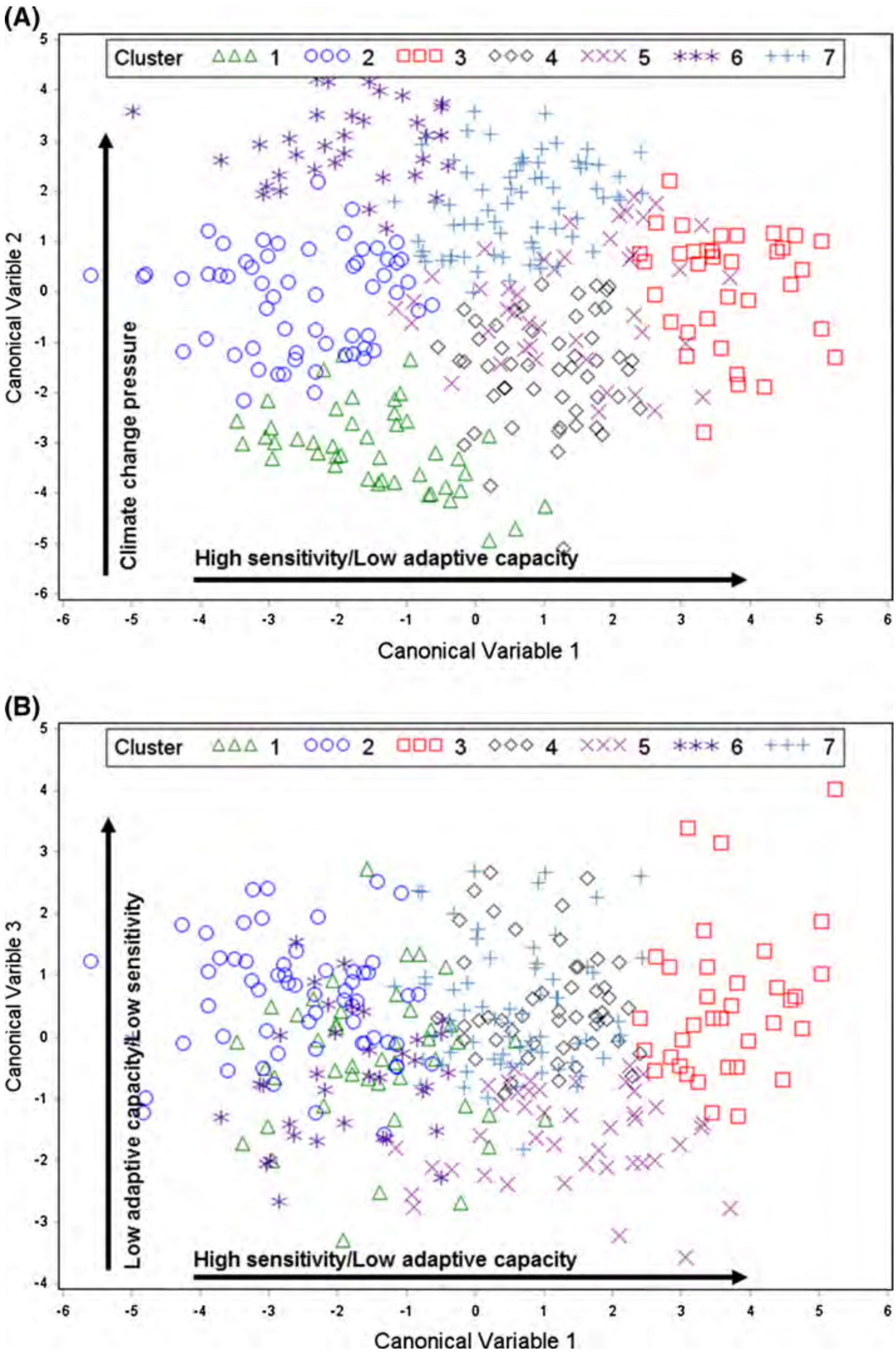
sensitivity, strongly positively associated with low adaptive capacity, and weakly negatively associated with climate change exposure.

Based on the mean vulnerability dimension scores of species within each cluster (Table 2) and the canonical discriminant analysis results (Fig. 4), we associated each cluster with a vulnerability class (Fig. 2). Cluster 3 encompassed the 35 most vulnerable species, rating highly in each of the three vulnerability dimensions, putting the species in vulnerability class A ("high vulnerability, little adaptation or persistence potential") (Table 3). The 43 species in Cluster 5 had moderate-to-high threat exposure and high sensitivity, but moderate adaptive capacity, placing them in vulnerability class B ("high vulnerability, potential adaptation") (Supplementary Table 2). The 69 species in Cluster 7 were assigned to vulnerability class C ("high vulnerability, potential persistence") because they had high threat exposure and low-to-moderate adaptive capacity, but low threat sensitivity. The 52 species in Cluster 4, meanwhile, had low threat exposure but high threat sensitivity and low adaptive capacity, which resulted in an assignment to vulnerability class D ("potential future vulnerability").

The remaining clusters had high ratings for at most one vulnerability dimension, placing them all in class E ("low current vulnerability"). For example, Cluster 6 incorporated 37 species with high threat exposure, but low sensitivity and high adaptive capacity, placing it in vulnerability class E1 (Fig. 2). Cluster 1, meanwhile, belongs in vulnerability class E2, encompassing 44 species with moderate-to-high threat sensitivity but relatively low climate change exposure and high adaptive capacity. Cluster 2, finally, belongs to vulnerability class E4, because its 59 species have low ratings for all three vulnerability dimensions. Note that not all the vulnerability classes identified in Fig. 2 will necessarily be represented in this kind of analysis. In this case, no species were categorized in vulnerability class E3, species with low adaptive capacity but relatively low predicted climate change exposure and high sensitivity to it.

Ranking of species within vulnerability classes

Vulnerability class A encompasses 35 species that have relatively high scores for all three vulnerability dimensions (threat exposure, sensitivity and low adaptive capacity). The species in this vulnerability class had among the highest mean values for all three vulnerability classes, and the highest mean low adaptive capacity score. Among these species, Rarity was the highest sensitivity attribute on average, while Genetic Variability was the most important low adaptive capacity attribute. Most of these species (24) have ranges mostly or entirely limited to the southeastern United States, while only five are from the western half of the country. The highest ranking Southeast species included water locust



(*Gleditsia aquatica* Marshall), chalk maple (*Acer leucoderme* Small), pyramid magnolia (*Magnolia pyramidata* W. Bartram), two-winged silverbell (*Halesia diptera* J. Ellis), and

◀**Fig. 4** Results of the K-means clustering and canonical discriminant analysis using scores for expected climate change pressure, sensitivity to climate change, and low adaptive capacity, across 339 North American tree species. In **a**, canonical variable 1 (x-axis) is strongly associated with low adaptability and sensitivity, and canonical variable 2 (y-axis) is most strongly associated with expected climate change pressure. In **b**, canonical variable 1 is again associated with low adaptability and sensitivity, and canonical variable 3 (y-axis) is associated negatively with threat sensitivity and positively with low adaptability. The seven clusters are related to vulnerability classes (see Fig. 2) based on their mean vulnerability dimension attributes and their locations relative to the canonical variable axes

butterbough (*Exothea paniculata* (Juss.) Radlk.).Texas walnut (*Juglans microcarpa* Berlandier) is also near the top of the list.

Vulnerability class B encompasses 43 species which have, on average, the second highest mean overall vulnerability score, along with the highest sensitivity ratings and the fourth highest adaptive capacity and threat exposure scores. Area of Distribution was the highest sensitivity attribute on average, but the mean Rarity attribute score was also high. Of these species, 22 are located in the West and 15 are in the Southeast. The species with the highest vulnerability ranks were red buckeye (*Aesculus pavia* L.), northern mountain-ash (*Sorbus decora* (Sarg.) C.K. Schneid.), Kentucky coffeetree (*Gymnocladus dioicus* (L.) K. Koch), western soapberry (*Sapindus saponaria* var. *drummondii* (Hook. & Arn.) L.D. Benson), blackbead ebony (*Ebenopsis ebano* (Berl.) Barneby & Grimes), Monterrey pine (*Pinus radiata* D. Don), and Carolina hemlock (*Tsuga caroliniana* Engelm.).

Sixty-nine species were assigned to vulnerability class C, with high threat exposure (third highest), low adaptive capacity (third highest), and moderate threat sensitivity (third lowest). These species had the third highest mean overall vulnerability score. Genetic Variability was the low adaptive capacity attribute for which these species were most vulnerable, but they were also highly vulnerable for the Ecological Requirements attribute. Most of these species (34) have widespread or primarily northern distributions, 19 are primarily Southeastern, and 16 are Western. The most highly ranked species in the vulnerability class were rock elm (*Ulmus thomasii* Sarg.), dwarf chinquapin oak (*Quercus prinoides* Willd.), pawpaw (*Asimina triloba* (L.) Dunal), southern crabapple (*Malus angustifolia* (Aiton) Michx.), black maple (*Acer nigrum* F. Michx.), and smoketree (*Cotinus obovatus* Raf.).

Vulnerability class D encompasses 52 species with the third highest mean threat sensitivity and second highest low adaptive capacity scores, but the third lowest threat exposure score. The highest sensitivity attribute was Area of Distribution and the highest adaptive capacity attributes were Ecological Requirements and Genetic Variability. Of these species, 33 had distributions primarily in the West and 15 primarily in the Southeast. Several of the most vulnerable species in this class have Western ranges, including Monterrey cypress (*Cupressus macrocarpa* (Hartw.) Bartel), four-leaf pine (*Pinus quadrifolia* Parl. ex Sudw.), Tecate cypress (*Cupressus forbesii* (Jeps.) Bartel), papershell pinyon pine (*Pinus remota* (Little) D.K. Bailey & Hawksw.), Mexican blue oak (*Quercus oblongifolia* Torr.), and drooping juniper (*Juniperus flaccida* Schltdl.).

Two vulnerability classes, meanwhile, had relatively high scores for only a single vulnerability dimension. Vulnerability class E1 encompasses species with high threat exposure only (the highest on average among the classes). Almost all of these 37 species have widespread or primarily northern distributions (89%, or 33 species). The most vulnerable of the E1 species are broadleaf hawthorn (*Crataegus dilatata* Sarg.), scarlet hawthorn (*Crataegus pedicellata* Sarg.), peachleaf willow (*Salix amygdaloides* Andersson), American plum (*Prunus americana* Marsh.), and Chickasaw plum (*Prunus angustifolia* Marshall). Vulnerability class E2 encompasses species with moderately high threat

Table 2 Cluster mean and rank for vulnerability dimension scores and overall climate vulnerability score, and assignment of each cluster to vulnerability class (see Fig. 2)

Cluster	Species	Climate				Low adaptive				Vulnerability	Class
	(n)	Exposure		Sensitivity		Capacity		Overall		Description	
		Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank		
1	44	5.44	7	51.64	4	42.31	5	33.13	6	Low current vulnerability	E2
2	59	27.14	6	28.13	7	39.29	6	31.52	7	Low current vulnerability	E4
3	35	75.49	2	63.70	2	65.64	1	68.28	1	High vulnerability, low persistence/adaptation	A
4	52	33.05	5	56.57	3	56.69	2	48.77	4	Potential high future vulnerability	D
5	43	59.58	4	64.77	1	44.53	4	56.29	2	High vulnerability, potential adaptation	B
6	37	78.77	1	28.39	6	30.49	7	45.89	5	Low current vulnerability	E1
7	69	75.18	3	39.03	5	49.00	3	54.42	3	High vulnerability, potential persistence	C

Table 3 The 40 North American tree species in vulnerability class A, ranked by climate score, which is the mean of each species' climate change exposure, sensitivity, and low adaptive capacity scores

Rank	Species name	Common name	Climate		Low adaptive capacity	Overall score
			Exposure	Sensitivity		
Vulnerability class A (cluster 3)						
1	*Gleditsia aquatica*	Water locust	100	63.09	76.36	79.81
2	*Juglans microcarpa*	Texas walnut	100	71.52	64.4	78.64
3	*Acer leucoderme*	Chalk maple	100	65.15	69.09	78.08
4	*Magnolia pyramidata*	Pyramid magnolia	100	65.69	67.63	77.77
5	*Halesia diptera*	Two-wing silver bell	91.5	70.96	65.6	76.02
6	*Exothea paniculata*	Butter bough	91.5	66.88	67.28	75.22
7	*Castanea pumila* var. *ozarkensis*	Ozark chinquapin	83.25	68.44	73.95	75.21
8	*Sabal mexicana*	Mexican palmetto	91.5	63.83	65.4	73.58
9	*Ulmus serotina*	September elm	91.5	70.22	57.87	73.2
10	*Simarouba glauca*	Paradise-tree	66	70.28	77.15	71.14
11	*Magnolia macrophylla*	Big leaf magnolia	91.5	57.19	64.7	71.13
12	*Castanea pumila*	Allegheny chinquapin	83.25	60.19	66.84	70.09
13	*Quercus arkansana*	Arkansas oak	83.25	66.54	59.6	69.8
14	*Malus coronaria*	Sweet crabapple	100	44.73	64.33	69.69
15	*Aesculus glabra*	Ohio buckeye	91.5	58.54	58.63	69.56
16	*Abies bracteata*	Bristlecone fir	58	86.8	63.19	69.33
17	*Tilia americana* var. *heterophylla*	White basswood	83.25	64.99	58.81	69.01
18	*Guapira discolor*	Beef tree	58	58.5	89.93	68.81
19	*Acer barbatum*	Florida maple	83	57.42	64.48	68.3
20	*Halesia carolina*	Carolina silver bell	74.75	68.99	59.48	67.74
21	*Aesculus flava*	Yellow buckeye	74.75	65.69	62.41	67.61
22	*Magnolia tripetala*	Umbrella magnolia	83.25	57.19	60.92	67.12
23	*Cupressus abramsiana*	Santa Cruz cypress	66.5	70.26	62.22	66.33
24	*Cladrastis kentukea*	Yellowwood	83.25	61.21	51.26	65.24
25	*Castanea dentata*	American chestnut	49.5	67.52	77.61	64.88
26	*Acoelorrhaphe wrightii*	Everglades palm	57.75	64.27	72.3	64.77
27	*Carya myristiciformis*	Nutmeg hickory	74.75	61.48	57.98	64.74
28	*Magnolia acuminata*	Cucumber tree	83	43.73	64.05	63.59

Table 3 continued

Rank	Species name	Common name	Climate		Low adaptive capacity	Overall score
			Exposure	Sensitivity		
29	*Cordia sebestena*	Longleaf geiger tree	49.75	80.03	60.36	63.38
30	*Quercus bicolor*	Swamp white oak	74.75	50.9	57.76	61.14
31	*Fraxinus caroliniana*	Carolina ash	66.25	61.55	51.8	59.86
32	*Quercus laceyi*	Lacey oak	49.5	72.77	54.2	58.82
33	*Piscidia piscipula*	Fish poison tree	41.25	53.42	77.49	57.39
34	*Lysiloma latisiliquum*	False tamarind	24.75	69.44	77.35	57.18
35	*Sideroxylon foetidissimum*	False mastic	41.25	50	75.11	55.45

For the other vulnerability classes, see supplementary Table 2

sensitivity, and consist almost entirely of species (35 of 44, or 80%) from the western half of the United States. Disturbance Tolerance and Area of Distribution were both important vulnerability attributes contributing to the high sensitivity of the species in this class. The species with the highest vulnerability ranks in this class were coast redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.), silverleaf oak (*Quercus hypoleucoides* A. Camus), Arizona alder (*Alnus oblongifolia* Torr.), dwarf live oak (*Quercus minima* (Sarg.) Small), and white oak (*Quercus alba* L.).

Finally, the 59 species in vulnerability class E4 had the lowest threat sensitivity and the second lowest values for the other two vulnerability dimensions. Many of these species (24 of the 59) occurred primarily in the western United States, including canyon live oak (*Quercus chrysolepis* Liebm.), singleleaf pinyon (*Pinus monophylla* Torr. & Frém.), and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), but several (19 and 16, respectively) had widespread distributions or occurred primarily in the Southeast, including pignut hickory (*Carya glabra* (Mill.) Sweet), black cottonwood (*Populus balsamifera* L.), red maple (*Acer rubrum* L.), sweetgum (*Liquidambar styraciflua* L.), and northern red oak (*Quercus rubra* L.).

Discussion

In an assessment of the vulnerability of the forest trees of the United States to climate change, we have applied a flexible conservation priority-setting framework that incorporates the exposure of species to threats, their sensitivity to those threats, and their capacity to adapt in response to those threats (sensu Foden et al. 2013). This Project CAPTURE framework is a cooperative effort developed with input from across the U.S. Forest Service, including from resource managers and scientists from across the agency who participated in a consensus-building workshop. It builds on previous regional National Forest System efforts to assess the vulnerability of forest tree species to climate change and other threats (Aubry et al. 2011; Devine et al. 2012; Potter and Crane 2012).

This project integrates a climate-change species distribution modeling approach with a biological trait-based vulnerability assessment to guide conservation monitoring and planning (Willis et al. 2015). By linking threat exposure, estimated using correlative climate models, with sensitivity and adaptability, evaluated using a trait vulnerability assessment, we can account for both intrinsic and extrinsic factors affecting the likelihood that species will persist in a changing world (Pacifici et al. 2015; Thomas et al. 2011). This approach was possible for the forest tree species of the conterminous United States and Alaska because relevant trait data are freely available for most of the species, and because occurrence data are collected for most tree species from tens of thousands of plots sampled in a spatially unbiased and systematic fashion across all forest land ownerships (Woudenberg et al. 2010; Bechtold and Patterson 2005). These occurrence data reliably represent the general extent of common tree species and should provide unbiased training data for species distribution modeling (e.g., Potter and Hargrove 2013). This framework also has the advantage of being applicable at a variety of regional scales (Gauthier et al. 2010).

At the same time, there are caveats and limitations related to a quantitative conservation prioritization project such as we describe here. For example, because precise vulnerability thresholds are not known for each trait, it is necessary to select arbitrary, relative thresholds for categories of higher and lower risk (Pacifici et al. 2015). While assessing conservation priorities always involves having to make arbitrary decisions (Burgman et al. 1999), we have attempted to minimize these with the use of quantile weighting for trait classifications (sensu Jimenez-Alfaro et al. 2010), which gives higher weighting based on conservation importance. Additionally, trait-based vulnerability assessments do not provide direct measures of the expected impacts on species such as extinction probability or population decline (Pacifici et al. 2015). The current project does include direct predictions of potential climate change impacts; on the other hand, it is probably not possible to accurately access vulnerability using trait data given the lack of direct information tying each of those characteristics to the likelihood of a given outcome. It also worth noting that specifically assessing extinction threat may not be possible across large groups of species for which adequate information is not available (Gauthier et al. 2010). Instead, we categorize and rank the species, relative to each other, based on their threat exposure, threat sensitivity, and adaptive capacity. Other concerns associated with prioritization include the uncertainty and misleading precision associated with summarizing criteria into a unique priority list and the possible correlation between criteria (Carter et al. 2000; Mace and Collar 2002). We address these concerns by focusing primarily on the categorization of species into like-groups using a quantitative clustering method, and making the ranking of species within these classes a secondary objective. Finally, it is worth noting that, as a species-level vulnerability assessment, this categorization and prioritization work ignores important within-species spatial variation in both traits and in potential exposure to threats such as climate change. We propose that the results of this current analysis, and subsequence analyses focused on other threats, should be used to select species for such within-species conservation prioritization assessments as described by Hastings et al. (this issue).

Applicability to management decision-making

The emphasis of the Project CAPTURE framework is the quantitative grouping of similar species into vulnerability classes that may require different management and conservation strategies for maintaining the adaptive genetic variation. The objective is to develop resilient landscapes where the evolutionary potential of species and populations can be conserved through biodiversity management and planning activities that explicitly consider genetic diversity and the processes that support ongoing evolutionary processes (Sgro et al.

2011). Advantages of this approach include its quantitative nature, its transparency, its inclusion of expert-user guidance, its ability to focus on a variety of threats (beyond climate change, for example), and its flexibility in terms of which species characteristics are included and how. Many of these characteristics led users in the U.S. National Forest System to determine that an early version of the Project CAPTURE framework was the most appropriate vulnerability assessment approach for an analysis encompassing the national forests of Washington and Oregon (Devine et al. 2012; Aubry et al. 2011).

In the current national assessment, we identified seven groups of similar species. Each of these groups may require different management and conservation strategies for maintaining the adaptive genetic variation of the species contained within it. The species at highest vulnerability are the 35 with high scores for all three vulnerability dimensions (Table 3, class A, in Fig. 2). In general, these are rare species with low genetic diversity that are located mostly in the highly species-rich Southeastern region. The greatest priority for intervention is needed for these highly climate change vulnerable species (Foden et al. 2013), such as immediate conservation planning that leads relatively quickly to systematic ex situ and in situ conservation, and potentially to assisted migration in some cases (Iverson and McKenzie 2013).

Class B (Supplementary Table 2), meanwhile, encompasses 43 “potential adapter” species that, while having high exposure and sensitivity to climate change, may be better able to adapt to the threat through microevolution, and could require some anthropogenic support to do so (Foden et al. 2013). They tend to be rare species with small distributional areas and low tolerance of disturbance, from both the West and Southeast, and may be amenable to conservation plantings (Aitken et al. 2008) and to assisted population migration, range expansion or species migration (Dumroese et al. 2015) because they tend to have relatively low dispersal ability but high genetic variation that could help them adapt to new locations. The 69 class C species are “potential persisters” that, despite having a low adaptive capacity, may be able to withstand climate change in situ, because they have low sensitivity to the threat, but will require close monitoring to verify this (Foden et al. 2013). These mostly had distributions that were widespread or limited to the Northern region, and tended to have low genetic diversity and a tendency to be environmental specialists.

Class D encompassed 52 mostly Western species that had high threat sensitivity (specifically, limited distributional areas) and low adaptive capacity (specifically, low genetic diversity and high environmental specificity), but low predicted exposure to climate change. While not currently vulnerable, they could become so beyond the 2050 timeframe of the climate projections used in the analysis. Routine monitoring will therefore be needed for these species, with a focus on quantifying a baseline of current population and stand structure conditions. Finally, the least vulnerable species were clustered into three separate groups with only one high vulnerability dimension (E1 and E2), or none (E4). These species should undergo routine long-term monitoring.

Additional threat assessment needs

Climate change is the focus of the assessment presented here. The effects of climate change, however, are occurring during a time in which species face a large number of other threats as well, such as invasive species and fragmentation (Hoffmann and Sgro 2011). Separate vulnerability assessments are likely needed that account for these threats, with results which should perhaps be combined with those relating to climate change, given that the threats may interact. Several pest and pathogen species, for example, are likely to have stronger or more widespread effects on forest composition and structure under projected climate conditions (Logan et al. 2003; Dukes et al. 2009; Sturrock et al. 2011), and the ability of native species to persist in appropriate climates is likely to be affected by new invasive species (Thomas et al. 2004).

Arguably, the potential for insect and disease infestation is a more immediate threat to the persistence and genetic integrity of tree species than is climate change. Nonnative forest pests are the only disturbance agent that has effectively eliminated entire tree species or genera from United States forests within the span of a few decades, altering ecosystem functions such as productivity, nutrient cycling and wildlife habitat (Lovett et al. 2016). A long and growing list of invasive and native insects and pathogens threaten North American forest tree species in the absence of climate change, and represent the most pervasive and important disturbance agents in North American forests (Logan et al. 2003). An effort applying the Project CAPTURE framework to pest and pathogen threats to North American tree species is currently under way. In addition to guiding in situ and ex situ conservation activities, the prioritization results of such an assessment could be applied to help select species for traditional tree improvement activities such as intra- and inter-specific resistance breeding, and for cutting-edge molecular tools such as (1) large-scale genomic mapping to identify resistance genes and (2) genetic engineering techniques (along with tree breeding) to introduce resistance genes into species highly threatened by pests or pathogens (Dumroese et al. 2015).

Additionally, stand age class structure can be used to quantify the combined effects of human and natural disturbances on the long-term sustainability of a forest (e.g., Manion and Griffin 2001; Didion et al. 2007). Stand age class structure could be used to assess within-species vulnerability based on the lack of structural sustainability at the landscape scale, accounting for the effects of management decisions, drought conditions, and fire, among other things. Specifically, the baseline and observed mortality should be comparable for a forest to be considered structurally sustainable (Cale et al. 2014). Assessing the degree to which this is not the case allows for the objective determination of the scope and direction of change in structure and composition, which in turn provides the ecological framework for objective management decisions (Cale et al. 2014).

Species-level priority assessment exercises must focus on vulnerability to one or more threats, but may also integrate other information that may be important for making conservation decisions, including economic and ecological importance, the probability of conservation success, and the availability of funds (Gauthier et al. 2010; St Clair and Howe 2011). For example, species could be given more weight in an assessment based on regional responsibility, which quantifies the degree to which a given species is associated with the region of interest (Schmeller et al. 2008). Similarly, more conservation effort may be justified for species that have high evolutionarily distinctiveness because such species may be more likely to possess unique or rare traits and ecosystem functions (Forest et al. 2007).

It is important to emphasize that a vulnerability assessment framework, including one that prioritizes species for conservation action, should be able to incorporate new information, including knowledge about the threats to species and their traits, geographic extent and conservation status (Carter et al. 2000; Millar et al. 2007; Coates and Atkins 2001). The Project CAPTURE framework is designed to enable periodic repeated categorization and prioritization assessments that incorporate new data and, in fact, to allow for expert-driven re-evaluations of the framework structure, such as whether specific life-history traits should be included and, if they are, with which vulnerability attributes they should be associated.

Conclusions

Biologists and conservation practitioners warn that anthropogenic climate change will result in the extirpation of plant species that are unable to shift their distributions to match changing conditions or that do not possess the necessary physiological and genetic adaptations that would allow them to persist in locations where conditions are changing (Giam et al. 2010; Aitken et al. 2008). In fact, climate change has the potential to overwhelm the capacity for adaptation in many plant populations and to dramatically alter their genetic composition, with resulting unpredictable changes in the presence and abundance of plant species and a reduction in their ability to resist and recover from further environmental disturbances such as pest and disease infestations (Jump and Penuelas 2005). Responding to this potentially pervasive and severe climate change threat requires an intensive multi-disciplinary, multi-scale, multi-taxon effort to identify and prioritize vulnerable species that informs governments of the seriousness of the threat and facilitates conservation adaptation and management (Williams et al. 2008).

We here present Project CAPTURE, a vulnerability framework for the prioritization and, more importantly, categorization of forest tree species for conservation action, accounting for predicted exposure to climate change, sensitivity to this threat, and adaptive capacity. In addition to the management and policy benefits of applying this framework, it should prove highly useful by integrating and guiding strategic thinking, research programs, and policy related to biodiversity and climate change, and by allowing for the identification of significant gaps in our knowledge about the species encompassed by the assessment (Williams et al. 2008). Earlier versions of the framework have been used to assist the U.S. National Forest System to prioritize tree species for conservation seed collections in the Southeast (Potter and Crane 2012), and to guide management, restoration and conservation planning in the Pacific Northwest (Devine et al. 2012; Aubry et al. 2011). We expect that future applications of Project CAPTURE will similarly guide conservation, management and restoration decision-making at a national level.

The Project CAPTURE framework is data-driven and guided by expert opinion, and is applicable to any region for which trait data and climate change projections are available. The objectives of the assessment were to identify forest tree species on U.S. forested lands, within the conterminous 48 States and Alaska, expected to be most vulnerable to genetic degradation as a result of climate change, and to quantitatively group similar species into vulnerability classes requiring different management and conservation strategies for maintaining adaptive genetic variation. The application of the framework can and should be repeated with the availability of updated climate projections for tree species, and with improved knowledge about the species' relevant life history traits. It is also being applied separately for other threats to tree species, including an ongoing assessment of the threats posed by pest and pathogen infestations, with the results of these separate assessments eventually combined in a comprehensive vulnerability evaluation.

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