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Prioritizing the conservation needs of United States tree species: Evaluating vulnerability to forest insect and disease threats

Kevin M. Potter [a], [*], Maria E. Escanferla [b], Robert M. Jetton [c], Gary Man [d], Barbara S. Crane [e]

[a] *Department of Forestry and Environmental Resources, North Carolina State University, 3041 Cornwallis Road, Research Triangle Park, NC, 27709, USA*
[b] *Department of Forestry and Environmental Resources, North Carolina State University, Campus Box 8008, Raleigh, NC, 27695, USA*
[c] *Camcore, Department of Forestry and Environmental Resources, North Carolina State University, Campus Box 8008, Raleigh, NC, 27695, USA*
[d] *Forest Health Protection, United States Department of Agriculture, Forest Service, Arlington, VA, 22209, USA*
[e] *Southern Region, National Forest System, United States Department of Agriculture, Forest Service, Atlanta, GA, 30309, USA*

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ABSTRACT

Insect and disease infestations pose major threats to several North American forest tree species. Scientists and managers from throughout the United States Forest Service developed a conservation priority-setting framework for forest tree species at risk from insects and disease and other threats. The Project CAPTURE (Conservation Assessment and Prioritization of Forest Trees Under Risk of Extirpation) framework is data-driven and guided by expert opinion, allowing the quantitative grouping of species into vulnerability classes that may require different management and conservation strategies. We applied this framework to categorize and prioritize 419 native North American tree species for conservation, monitoring, and management using trait data and insect and disease threat data for each host tree species. The categorization is based on vulnerability factors relating to each tree species' (1) insect and disease threat severity, (2) sensitivity to insect and disease infestation, and (3) capacity to adapt to insect and disease infestation. We used K-means clustering to group species into 11 classes based on these vulnerability dimensions. The three most vulnerable classes encompassed 15 species which require the most immediate conservation intervention. Two additional classes face less severe insect and disease threats and may be good candidates for resistance breeding efforts. Other groups had traits associated with high sensitivity and/or low adaptive capacity to potential future insect and disease threats, suggesting that these species need close monitoring. This assessment tool should be valuable for decision-makers determining which species and populations to target for monitoring efforts and for pro-active gene conservation and management activities.

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* Corresponding author.
E-mail address: kpotter@ncsu.edu (K.M. Potter).

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1. Introduction

Harmful diseases and insects, both introduced and native, pose the most pervasive and important threat to North American forests (Logan et al., 2003). Epidemics of exotic insects (Aukema et al., 2011; Brockerhoff and Liebhold, 2017; Gandhi and Herms, 2010), diseases (Ghelardini et al. 2016, 2017; Loo, 2009; Wingfield et al., 2017), and symbiotic complexes of both (Wingfield et al., 2017) cause extensive ecological damage and billions of dollars of economic impacts. Significantly, no other disturbance agent has effectively eliminated forest tree species, or even genera, from forests in the United States as quickly as forest pests, sometimes within only a few decades (Lovett et al., 2016).

It is extremely important to conserve the irreplaceable genetic resources of tree species threatened by nonnative insects and diseases (Sniezko and Koch, 2017). The most imperiled tree species are vulnerable to functional extirpation and to the associated widespread loss of important adaptive genetic variation. The unfortunate reality, however, is that both time and resources are limited for the urgent work needed to conserve tree species and populations. In fact, resources for forest management are declining even as forests increase in value and become more challenging to effectively manage (Ayres and Lombardero, 2018). It is necessary, therefore, to efficiently allocate scarce conservation resources using species-level prioritization approaches that are rational, systematic, and defensible (Bottrill et al., 2008; Farnsworth et al., 2006). These approaches should emphasize safeguarding existing genetic adaptiveness within tree species and the processes that allow for evolutionary resilience, which is the ability of populations to persist in their current state or to adapt to changing environmental conditions (Myking, 2002; Sgro et al., 2011).

A conservation framework, titled Project CAPTURE (Conservation Assessment and Prioritization of Forest Trees Under Risk of Extirpation), is a data- and expert-driven effort by scientists and managers in the United States Forest Service to both categorize and prioritize native tree species based on their vulnerability to losing adaptive genetic variation as a result of multiple threats. This framework recently was applied to categorize the vulnerability of United States tree species to climate change (Potter et al., 2017). The application of this framework to insects and diseases is perhaps even more urgent, given the immediacy of several disease and insect threats. Vulnerability in this framework follows the characterization of Foden et al. (2013) as a function of three dimensions: the tree species' exposure to an extrinsic threat, their sensitivity to the threat, and their ability to adapt to it. In this case, the severity of the most serious insect and disease agents for tree species (Potter et al., 2019) is used to determine that species' insect and disease threat exposure. The sensitivity and adaptive capacity vulnerability dimensions, meanwhile, are based on species characteristics, arranged in a hierarchical fashion to reflect expert opinion. Such species characteristics, including life-history traits (e.g., Barrett et al., 2008; Giraud et al., 2010), influence the frequency and severity of infestation (Ghelardini et al., 2017). The tree species included in the assessment are then quantitatively grouped into vulnerability classes of species that may require similar conservation and management strategies and actions for maintaining their adaptive genetic variation (Potter et al., 2017).

The need to apply this categorization and prioritization framework to United States tree species is critical because the most serious exotic insect and disease invaders have the potential to functionally extirpate their tree hosts (Gandhi and Herms, 2010). Already, at least a half dozen nonnative fungal diseases have seriously impacted important North American tree species. For example, the loss of American chestnut (*Castanea dentata* (Marsh.) Borkh.), following infestation by chestnut blight (*Cryphonectria parasitica* (Murrill) Barr), fundamentally changed forest ecosystems across much of eastern North America (Loo, 2009). Similarly, the unfolding decimation of several ash (*Fraxinus*) species in parts of eastern North America by the emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) is creating a cascade of ecological impacts in forest communities (Klooster et al., 2018). The changes in forest structure and species composition that result from such effective extirpations of host species, or the loss of individuals in larger size classes, can alter important natural ecosystem functions, such as productivity, nutrient cycling and wildlife habitat, and urban tree services, including shading, pollutant uptake, and property value enhancement (Lovett et al., 2016; Tobin, 2015). These impacts may be subtle but still long-lasting and broad in their extent (Garnas et al., 2011; Loo, 2009).

A flexible framework is therefore needed to categorize and prioritize the 419 native North American tree species based on their vulnerability to the loss of adaptive genetic variation as a result of mortality caused by insect and disease infestation. We here describe such a framework that is hierarchical and guided by expert opinion, and that incorporates insect and disease threat severity for each tree species host in addition to 12 species traits. The framework, a cooperative effort by scientists and managers from across the United States Forest Service, categorizes host tree species into vulnerability classes based on the three vulnerability dimensions. The vulnerability classes are then associated with different sets of conservation, management and monitoring strategies for maintaining adaptive genetic variation within species.

2. Materials and methods

2.1. Assessment framework

The aim of this assessment was to categorize 419 United States forest tree species based on their expected vulnerability to genetic degradation as a result of mortality caused by insect and disease infestations, and then to prioritize species within these vulnerability classes based on conservation need. We defined genetic degradation as a significant reduction in the genetic variation necessary for a species to adapt to changing environmental conditions over the next century.

The assessment was based on a framework that encompasses three dimensions of vulnerability (sensu Foden et al., 2013): **(1)** severity of insect and disease threats, **(2)** sensitivity to insect and disease threats, and **(3)** low adaptive capacity relative to insect and disease threats. The first of these is the extent of mortality likely to occur as a result of insect and disease infestation for each species and represents the intensity of the threat. The second is the degree to which the genetic resource base of each species is susceptible to insect and disease infestation, and thus represents the potential response of a species to insects and diseases. The third is the degree to which a species is unable to adapt to the threat of insect and disease infestations, either as a result of phenotypic plasticity or evolutionary change.

Conceptually, the degree of vulnerability for each species depends on the degree to which it has high values for each of the three vulnerability dimensions (Fig. 1). For example, any species with high insect and disease threat severity (A1-A4 in Fig. 1) is currently imperiled by one or more insect or disease threats, but species that also have high sensitivity (A2) or low adaptive capacity (A3), or both (A1), are probably more immediately at risk of widespread genetic degradation or even extirpation. Meanwhile, a species with high sensitivity and low adaptive capacity, but low current insect and disease threat severity (B), may be particularly at risk from future insects or diseases introduced from overseas. Finally, a species with low values for all three vulnerability dimensions (E) has relatively low vulnerability to current or future insect or disease infestation.

The vulnerability framework has a hierarchical structure (Fig. 2), with the Sensitivity and Adaptive Capacity vulnerability dimensions each consisting of two vulnerability attributes: Rarity and Area of Distribution (for Sensitivity), and Regeneration Capacity and Genetic Variability (for Adaptive Capacity). These attributes, in turn, encompass several specific traits. In early 2017, 34 natural resource professionals from a variety of disciplinary backgrounds, including forest health, forest management, forest genetics and forest ecology, completed a survey to evaluate proposed assignments of species traits to vulnerability attributes, and vulnerability attributes to vulnerability dimensions. The experts were chosen to represent variation in disciplinary background, geographic location, and employment (government agency, university, and nongovernmental organization). Results from the survey are included below to quantify expert agreement with the structure of the hierarchical framework.

2.2. Tree species included in the assessment

This vulnerability assessment includes 419 forest tree species native to the contiguous 48 United States and Alaska. We adopted the definition of trees used by the national Forest Inventory and Analysis (FIA) program of the United States Forest Service (Woudenberg et al., 2010): woody perennial plants that usually have 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 are not vines. The foundation of the assessment list was the set of 362 native tree species inventoried by FIA in the contiguous United States and Alaska, with native status defined by the USDA PLANTS database (U.S. Department of Agriculture Natural Resource Conservation Service, 2019). (We excluded species of hybrid or exotic origin.) We also included an additional 57 species that also occur in the continental United States but are not inventoried by FIA because they

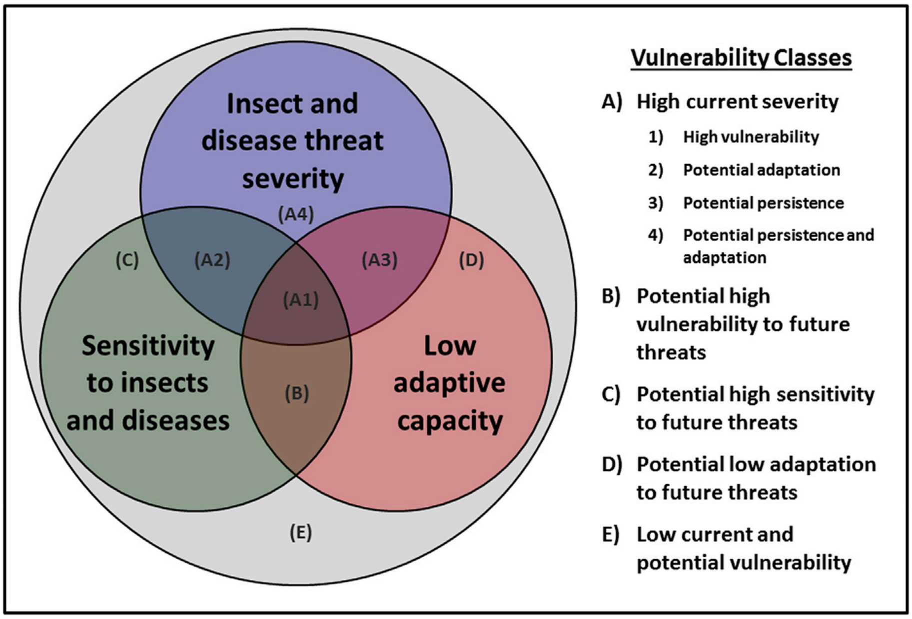

Fig. 1. Conceptual relationships among the three vulnerability dimensions (insect and disease threat severity, sensitivity to insects and diseases, and low adaptive capacity), and the description of vulnerability classes defined by those vulnerability dimensions, based on Foden et al. (2013).

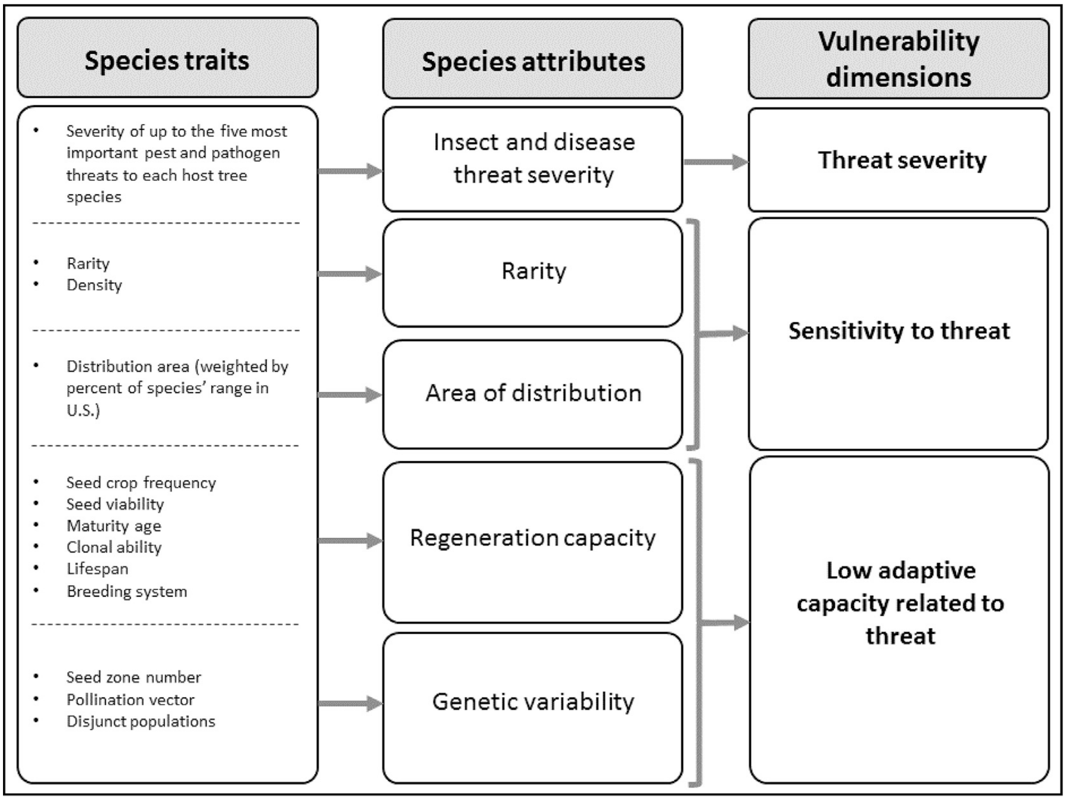

Fig. 2. The structure of the hierarchical vulnerability assessment framework. Based on the results of an expert survey, species traits (such as seed crop frequency and pollination vector) are aggregated into species attributes (such as regeneration capacity and genetic variability), which are then aggregated into one of the three vulnerability dimensions.

are rare and/or limited in their distributions. These were woody plant species that generally meet the FIA definition of a tree and were listed in a series of United States Forest Service publications describing the distributions of the forest trees and shrubs of the United States (Little, 1971, 1976a,b; Viereck and Little, 1975).

2.3. Insect and disease threats and severity ratings

Evaluating the severity of insect and disease threats, one of the three vulnerability dimensions in the assessment framework, required listing as many as five of the most serious insect and disease threats for each of the 419 tree species and then assigning a severity rating for each host and insect/disease combination, as described by Potter et al. (2019). Both introduced and native insect and disease species are included in the list because both can have significant impacts on native tree species. These are actual or known potential insect and disease threats for each tree species; other insect and disease agents could cause problems as a result of long-distance transport through international trade (Leung et al., 2014), but we are not able to predict with certainty which agents may be a threat to any particular tree species. The threat severity ratings are as follows (Potter et al., 2019):

- Near complete mortality of all mature trees, or inability to reproduce sexually = 10
- Near complete mortality in a congeneric species = 9 (sensu Gilbert and Webb, 2007)
- Significant mortality of mature trees = 8
- Moderate mortality of mature trees = 5
- Moderate mortality in association with other threats = 3
- Minor mortality, usually of already-stressed trees = 1

Each of these severity ratings was transformed using an exponential function to reflect the nonlinear increase in severity across the rating group. The transformed values of each species' insect and disease agents were then summed, with the threat sums standardized across tree species so the species with the highest total threat severity had a score of 100, and the one with the lowest total threat severity had a score of 0.

2.4. Tree species attributes

The vulnerability assessment framework incorporates two vulnerability dimensions in addition to insect and disease Threat Severity: Sensitivity to insect and disease threats, and Low Adaptive Capacity relative to insect and disease threats. As noted above, each of these, in turn, consists of two species attributes (Fig. 2). The inclusion of these attributes in the dimensions was guided by the results of the expert survey, as was the assignment of each of a series of specific traits to the four attributes. (For more information about the calculation of species trait values, see Appendix 1). Because the species information applied in the framework is relative to all the species included in the assessment, the species trait, attribute and vulnerability dimension data were scored on a scale of 0—100, with higher scores associated with higher vulnerability.

2.4.1. Sensitivity to insect and disease threats

The Sensitivity to Insect and Disease Threats vulnerability dimension incorporated two species attributes: **1)** rarity (77.4 percent agreement by survey participants, 9.7 percent disagreement; mean confidence: 3.97 on a scale of 1—5), and **2)** area of distribution (70/16.7 percent agreement/disagreement; mean confidence: 3.90). Each species' overall sensitivity dimension score was the mean of the two attributes. The attributes, meanwhile, consisted of one (for area of distribution) or two (for rarity) metrics. Table 1 provides citations supporting the inclusion of these metrics in the vulnerability framework while reporting the level of support among the surveyed experts for including the two rarity metrics. Appendix 1 explains the calculation of the metrics included in the rarity and area of distribution attributes.

2.4.2. Low adaptive capacity to insect and disease threats

The Low Adaptive Capacity to Insect and Disease Threats vulnerability dimension incorporated two species attributes: **1)** regeneration capacity (80.1 percent agreement by survey participants, 12.9 percent disagreement; mean confidence: 4.13 on a scale of 1—5), and **2)** genetic variability (90.3/3.2 percent agreement/disagreement; mean confidence: 4.16). Each species' overall adaptive capacity dimension score was the mean of the two attributes. The attributes, meanwhile, consisted of six (regeneration capacity) or three (genetic variability) metrics. Table 1 reports the level of support among the surveyed experts for including the metrics within these two attributes, and Appendix 1 explains how we calculated these metrics.

2.5. Clustering into vulnerability classes

We applied *K*-means clustering (Hartigan, 1975) in Proc FASTCLUS in SAS 9.4 (SAS Institute Inc. 2013) to group the 419 species into vulnerability classes based on their scores for the three vulnerability class scores (for insect and disease Threat Severity, Sensitivity, and Low Adaptive Capacity) after these had been standardized to a mean of 0 and standard deviation of 1. *K*-means is an efficient partitional clustering technique that returns a user-specified number of data clusters (*K*) represented by their centroids (Tan et al., 2005). Users run the clustering for a variety of values of *K* to find the value that best explains the

Table 1
Traits included within each species attribute, expert survey results about whether to include each trait within the attribute, and citations supporting the inclusion of the trait in an assessment of tree species vulnerability to insect and disease infestation.

Attribute/Trait	Survey Results				Citations
	N	% Agree	% Disagree	% Unsure	
Rarity (Sensitivity)					
Plot level occurrences[a]	31	83.87	6.45	9.68	Budde et al. (2016), Gaston (2008)
Density[a]	32	81.25	6.25	12.5	McKinney (1997)
Distribution (Sensitivity)					
Area of distribution[a]	–	–	–	–	Bradshaw et al. (2008), Leao et al. (2014)
Regeneration Capacity (Low Adaptive Capacity)					
Large seed crop frequency	31	93.54	0	6.45	McKinney (1997)
Long-term viability of seed	32	93.75	3.13	3.13	Black et al. (2006), Estrada et al. (2015)
Age at reproductive maturity	32	93.75	3.13	3.13	Jump and Peñuelas (2005)
Sexual and asexual reproductive strategies	31	70.97	12.9	16.13	Godefroid et al. (2014)
Typical lifespan	31	64.52	19.35	16.13	McKinney (1997), Jump and Peñuelas (2005)
Breeding system	32	75	12.5	12.5	Vamosi and Vamosi (2005)
Genetic Variability (Low Adaptive Capacity)					
Number of seed zones[a]	31	70.97	22.58	6.45	Bower et al. (2014), Prasad (2015)
Pollination vector	30	56.67	3.33	40	Budde et al. (2016), Godefroid et al. (2014)
Number of disjunct populations	30	90	0	10	Jump and Peñuelas (2005), Kuhn et al. (2016)

[a] Continuous data converted to quantiles.

variation in a dataset. Here, we ran the analysis for $K = 2$ to $K = 15$. We chose the appropriate K based on two metrics, peaks in the pseudo F-statistic and the cubic clustering criterion (Milligan and Cooper, 1985).

We next determined which of the insect and disease vulnerability classes (Fig. 1, sensu Foden et al., 2013) were most closely associated with each of the clusters from the analysis of the selected K. To do this, we first calculated the mean vulnerability dimension scores across the species within each of the clusters. Second, to visually interpret differences among the clusters, we plotted them in three-dimensional space in SAS 9.4 (SAS Institute Inc, 2013) using canonical discriminant analysis. This dimension-reduction technique derives canonical variables that are linear combinations of the quantitative variables that summarize between-class variation. We ascertained how each of these canonical variables (axes) related to the three vulnerability dimensions.

Finally, we calculated an overall vulnerability rating for each species with the three vulnerability dimensions given weights as determined by the 34 survey respondents. These experts had been asked to allocate weights totaling 100 among the dimensions; on average, these were 37 for Threat Severity, 33 for Sensitivity, and 30 for Low Adaptive Capacity. The vulnerability rating was therefore calculated as

$$V = \frac{(\mathrm{T} * 37) + (\mathrm{S} * 33) + (\mathrm{A} * 30)}{100}$$

where V is the overall vulnerability rating, T is Threat Severity, S is Sensitivity and A is Low Adaptive Capacity. The species were then ranked by this overall vulnerability rating within each of the vulnerability classes defined by the K-means clustering analysis.

3. Results

3.1. Assignment to vulnerability classes

The insect and disease Threat Severity vulnerability dimension was not significantly correlated with either of the other vulnerability dimensions ($r = 0.005$ and $p = 0.924$ with Sensitivity and $r = 0.005$ and $p = 0.923$ for Low Adaptive Capacity). Sensitivity and Low Adaptive Capacity were significantly correlated ($p < 0.0001$), but relatively weakly ($r = 0.221$).

The results of the K-means clustering analysis indicated that 11 clusters best explain the variation in the species-level vulnerability dimension data, given peaks in both the cubic clustering criterion and the pseudo F-statistic at $K = 11$ (Supplementary Table 1). Each of the three vulnerability dimensions was strongly associated with one of the three canonical variables (axes) that explain the cluster membership of species (Table 2). Canonical variable 1, which explained 57.4 percent of the variation, was strongly and positively related to insect and disease Threat Severity. Canonical variable 2, meanwhile, was most strongly linked with Sensitivity and explained 28.5 percent of data variability, while canonical variable 3 explained 14.1 percent of variation and was most positively associated with Low Adaptive Capacity.

All the species, with their cluster assignments, were plotted using their scores for the three canonical variables (Fig. 3). This information was combined with the mean vulnerability dimension scores for the species in each cluster (Table 3) to generally associate each cluster with a vulnerability class (Fig. 4). All but one cluster fit neatly into a single vulnerability class. Cluster 11 encompassed species that all had similar scores for Sensitivity and Low Adaptive Capacity, but which spanned low to moderate Threat Severity. This cluster was therefore split into two groups for tree species with low (<10) and moderate (>10) Threat Severity, hereafter Cluster 11a and Cluster 11b.

Three of the clusters consisted of species with high insect and disease Threat Severity (5, 6, and 9). The five species in Cluster 9 had high severity, high sensitivity, and low to moderate adaptive capacity, and were therefore placed in vulnerability class A1 ("high current vulnerability") (Table 3). Cluster 5 incorporated six species with high threat severity, moderate sensitivity, and high adaptive capacity, and was assigned to vulnerability class A2 ("high current vulnerability, potential adaptation"). Another set of four species in Cluster 6 had high severity but relatively low sensitivity and high adaptive capacity, placing it in vulnerability class A4 ("high current vulnerability, potential persistence/adaptation"). Meanwhile, two

Table 2
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
Threat Severity	0.9991	0.0097	−0.0397
Sensitivity	−0.0039	0.9250	−0.3799
Low Adaptive Capacity	0.0122	0.3948	0.9187

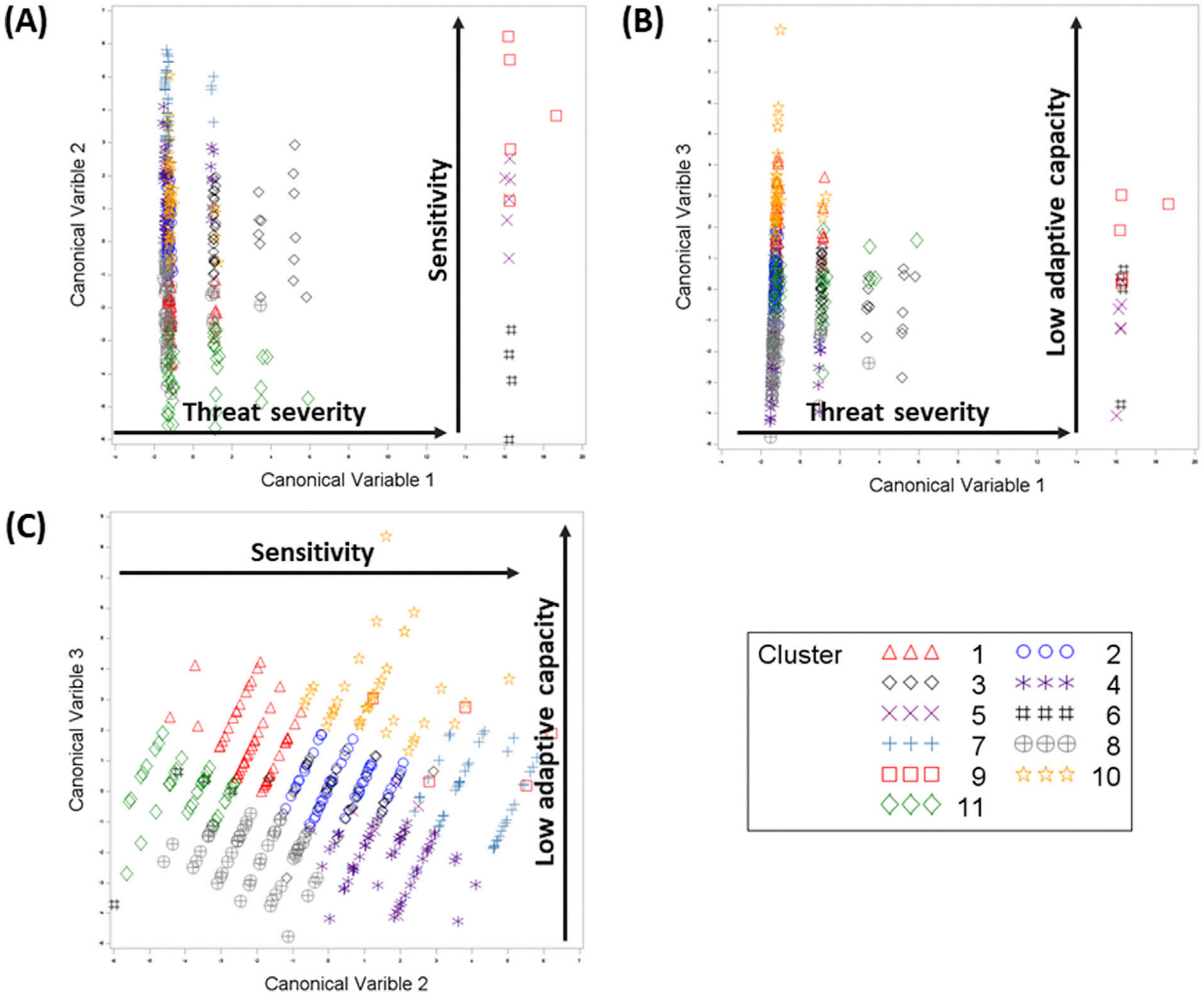

Fig. 3. Results of the K-means clustering and canonical discriminant analysis using scores for insect and disease threat severity, sensitivity to insect and disease threats, and low adaptive capacity, across 419 North American tree species. In (A), canonical variable 1 (x-axis) is strongly associated with insect and disease threats, and canonical variable 2 (y-axis) is most strongly associated with sensitivity. In (B), canonical variable 1 is again associated with insect and disease threats, and canonical variable 3 (y-axis) is associated with low adaptive capacity. In (C), canonical variable 2 is associated with sensitivity, and canonical variable 3 is associated with low adaptive capacity. The 11 clusters are related to vulnerability classes (see Fig. 1) based on their mean vulnerability dimension attributes (Table 3) and their locations relative to the canonical variable axes.

additional clusters encompassed species with moderate Threat Severity (3 and 11a). The 41 species in Cluster 3 were categorized with both moderate threat severity and sensitivity along with high adaptive capacity. As a result, this group is best classified in vulnerability class A2, but with a lower overall vulnerability than the species in cluster 2 (also classified as A2, but with higher threat severity). Similarly, the 18 species in Cluster 11a were classified as A4, as was Cluster 6, but with lower overall vulnerability.

Two clusters, 2 and 7, were assigned to vulnerability class B ("potential high vulnerability to future threats") because they both had relatively low insect and disease Threat Severity along with relatively high Sensitivity and relatively Low Adaptive Capacity (Supplementary Table 2). The 47 species in Cluster 7 (B.1), however, had a much higher mean Sensitivity score, the highest of any cluster, and a higher Low Adaptive Capacity score than the 62 species in Cluster 2 (B.2) (Table 3). Similarly, two clusters were associated with vulnerability class D ("potential low adaptation to future threats"). Cluster 10, incorporating 43 species, had the highest mean Low Adaptive Capacity score, while the 59 Cluster 1 species also had Low Adaptive Capacity that was relatively high. The insect and disease Threat Severity and Sensitivity scores of each were low. Cluster 4 (58 species) was categorized in vulnerability class C ("potential high sensitivity to future threats") because its species have relatively high Sensitivity and relatively low severity and high adaptive capacity.

The remaining Cluster 8, of 55 species, and Cluster 11b, of 21 species, were assigned to vulnerability class E ("low current and potential vulnerability") with low values for all three of the vulnerability dimensions.

Table 3
Cluster mean and rank for vulnerability dimension scores and overall insect and disease vulnerability score, and assignment of each cluster to vulnerability class (see Fig. 1).

Cluster	Species (n)	Insect and Disease Severity		Sensitivity		Low Adaptive Capacity		Overall		Vulnerability	
		mean	rank	mean	rank	mean	rank	mean	rank	Description	Class
1	59	1.9	6	24.3	9	51.9	4	24.3	9	Potential low adaptation to future threats	**D.2**
2	62	0.3	12	52.7	6	50.4	5	32.6	8	Potential high vulnerability to future threats	**B.2**
3	41	17.5	4	53.7	5	48.7	6	38.8	5	Moderate current severity, potential adaptation	**A2.2**
4	58	1.7	8	74.1	3	39.0	9	36.8	7	Potential high sensitivity to future threats	**C**
5	6	88.4	3	66.4	4	45.4	7	68.2	2	High current severity, potential adaptation	**A2.1**
6	4	88.5	2	14.4	11	35.3	11	48.1	3	High current severity, potential persistence/adaptation	**A4.1**
7	47	1.2	10	89.0	1	57.4	3	47	4	Potential high vulnerability to future threats	**B.1**
8	55	1.8	7	38.8	8	30.9	12	22.7	11	Low current and potential vulnerability	**E.1**
9	5	90.7	1	79.7	2	68.4	2	80.4	1	High current vulnerability	**A1**
10	43	1.2	9	50.1	7	69.4	1	37.8	6	Potential low adaptation to future threats	**D.1**
11a	18	16.4	5	15.1	10	39.2	8	22.8	10	Moderate current severity, potential persistence/adaptation	**A4.2**
11b	21	0.6	11	11.8	12	38.1	10	15.5	12	Low current and potential vulnerability	**E.2**

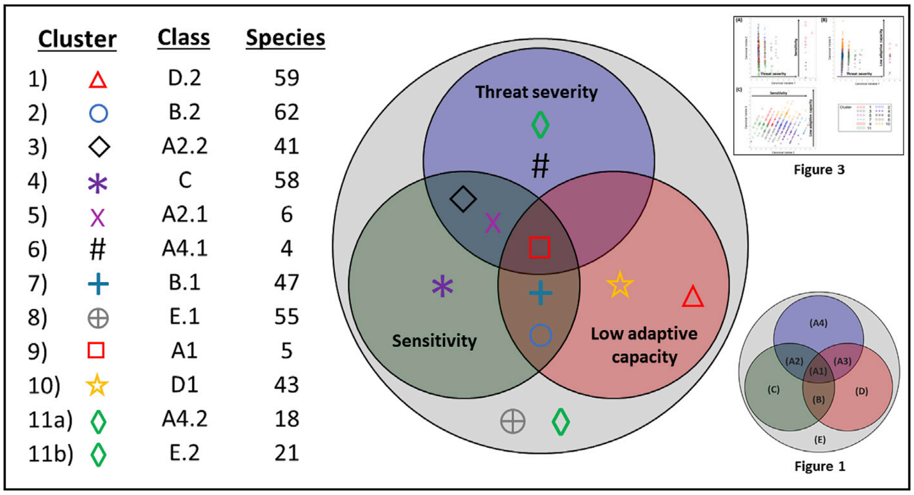

Fig. 4. The results of the K-means clustering (top right and Fig. 3) were combined with the mean vulnerability dimension scores for each cluster (Table 3) to generally associate the cluster with a vulnerability class (bottom right and Fig. 1).

3.2. *Composition of vulnerability classes*

The five species placed within vulnerability class A1 had the highest mean Insect and Disease Severity vulnerability dimension scores, and the second highest Sensitivity and Low Adaptive Capacity scores (Table 3). The species are Florida torreya (*Torreya taxifolia* Arn.), American chestnut (*Castanea dentata* (Marshall) Borkh.), Allegheny chinquapin (*Castanea pumila* (L.) Mill.), Ozark chinquapin (*C. pumila* (L.) Mill. *var. ozarkensis* (Ashe) Tucker), and redbay (*Persea borbonia* (L.) Spreng.) (Table 4). All are imperiled by devastating diseases. All have relatively to highly restricted distributions, and all but redbay are relatively rare within their distributions. All have moderate to low regeneration capacity and relatively low genetic variation as defined by the metrics used in the framework (Appendix 1).

The two species clusters assigned to vulnerability class A2 (clusters 5 and 3) differed in having high versus moderate Insect and Disease Severity. Both had relatively high mean Sensitivity and high mean adaptive capacity. Class A2.1 encompassed only six species that face severe insect and disease threats (Carolina ash [*Fraxinus caroliniana* Mill.], pumpkin ash [*Fraxinus profunda* (Bush) Bush], Carolina hemlock [*Tsuga caroliniana* Engelm.], Port-Orford-cedar [*Chamaecyparis lawsoniana* (A. Murray) Parl.], tanoak [*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon & S.H. Oh], and butternut [*Juglans cinerea* L.]) (Table 4). The 41 species in class A2.2 (Supplementary Table 2) face less severe, though generally still important, insect and disease threats. These include sugar pine (*Pinus lambertiana* Douglas), Fraser fir (*Abies fraseri* [Pursh] Poir.), California black oak (*Quercus kelloggii* Newberry), and several ash (*Fraxinus*) species that have not yet been infested by EAB but

Table 4
The 15 North American tree species in vulnerability class A facing the highest insect and disease severity, ranked within each class by the species' overall insect and disease vulnerability score. For the other vulnerability classes, see Supplementary Table 2.

Rank	Species name	Common name	Insect and Disease Severity	Sensitivity	Low Adaptive Capacity	Overall Score	Overall Rank
Vulnerability Class A1 (Cluster 9)							
1	Torreya taxifolia	Florida torreya	88.0	100.0	75.6	88.2	1
2	Castanea pumila var. ozarkensis	Ozark chinquapin	88.7	100.0	64.0	85.0	2
3	Castanea dentata	American chestnut	100.0	74.5	74.7	84.0	3
4	Castanea pumila var. pumila	Allegheny chinquapin	88.7	74.5	58.1	74.8	4
5	Persea borbonia	redbay	88.0	49.5	69.7	69.8	7
Vulnerability Class A2.1 (Cluster 5)							
1	Fraxinus profunda	pumpkin ash	88.7	74.8	52.7	73.3	5
2	Fraxinus caroliniana	Carolina ash	88.7	66.0	55.5	71.2	6
3	Tsuga caroliniana	Carolina hemlock	88.1	83.0	30.7	69.2	8
4	Chamaecyparis lawsoniana	Port-Orford-cedar	88.6	66.5	45.1	68.3	9
5	Lithocarpus densiflorus	tanoak	88.0	58.3	47.2	65.9	10
6	Juglans cinerea	butternut	88.6	49.8	40.9	61.5	11
Vulnerability Class A4.1 (Cluster 6)							
1	Fraxinus americana	white ash	88.7	24.8	42.7	53.8	14
2	Tsuga canadensis	eastern hemlock	88.1	16.5	43.0	50.9	24
3	Fraxinus nigra	black ash	88.7	8.3	42.5	48.3	36
4	Fraxinus pennsylvanica	green ash	88.7	8.3	13.1	39.5	109

eventually may experience extensive mortality because of it. Species in the A2.1 vulnerability class also tend to be rarer than the generally more common A2.2 species, resulting in a somewhat higher mean Sensitivity score.

The four species in vulnerability class A4.1 had the second highest mean Insect and Disease Severity score, but the second lowest Sensitivity and Low Adaptive Capacity scores (Table 3). These species are all facing extensive decline as a result of insect or disease infestations but have the potential advantage of being widespread and common with relatively high genetic variation and regeneration capacity. These species are eastern hemlock (*Tsuga canadensis* (L. Carriere) and three species of ash: white (*Fraxinus americana* L.), black (*F. nigra* Marshall), and green (*F. pennsylvanica* Marshall) (Table 4). Meanwhile, the 18 species in class A4.2 have a moderately high mean Insect and Disease Severity score (the fifth highest), and among the lowest Sensitivity and Low Adaptive Capacity scores. It includes species, such as whitebark pine (*Pinus albicaulis* Engelm.), American elm (*Ulmus americana* L.), and American beech (*Fagus grandifolia* Ehrh.) (Supplementary Table 2), that are facing insect and disease agents that are serious but not the most devastating.

Two clusters of tree species were classified in class B, with low Insect and Disease Severity, relatively high Sensitivity, and relatively high adaptive capacity. Vulnerability class B.1 encompasses 47 species that have the highest mean Sensitivity score across all clusters and the third highest mean Low Adaptive Capacity score. Many of these species are rare to uncommon, have small distributions, and have low genetic variability, although they have relatively high regeneration capacity (Supplementary Table 2). Meanwhile, the 62 species categorized in vulnerability class B.2 had the sixth highest mean Sensitivity and the fifth highest mean Low Adaptive Capacity score. These are mostly species that are more common and have larger distributions than B.1 species, and that have moderate regeneration capacity and relatively low genetic variability.

Three vulnerability classes had relatively high scores for only one of the three vulnerability dimensions. Vulnerability Class C encompasses 58 species with the third highest mean Sensitivity score, but among the lowest severity and Low Adaptive Capacity mean scores. In general, these are uncommon species occurring across relatively limited extents, but that have relatively high regeneration capacity and genetic variability. At the same time, vulnerability classes D.1 and D.2 consist of species having low or relatively low adaptive capacity scores while having low threat severity and relatively low sensitivity. The 43 species in vulnerability class D.1, in fact, had the highest mean Low Adaptive Capacity score in large part because they have low genetic variability and, to a lesser degree, low regeneration capacity. The 59 species in Vulnerability Class D.2, meanwhile, had the fourth highest Low Adaptive Capacity mean score because of their generally moderate regeneration capacity and genetic variability.

Finally, 54 species in vulnerability class E.1 had the lowest mean Low Adaptive Capacity scores and among the lowest Insect and Disease Severity and Sensitivity scores. These were relatively common species with large ranges and relatively high reproductive capacity and genetic variability (Supplementary Table 2). The 21 species in vulnerability class E.2, meanwhile, had the lowest mean Sensitivity score and among the lowest severity and low adaptive capacity scores. These were mostly common species with large ranges and with relatively high regeneration and genetic variability.

4. Discussion

Nonnative insect and disease agents have been, and will almost certainly continue to be, particularly devastating to tree species that have limited or nonexisting defenses because of the absence of coevolutionary history with the introduced pests (Gandhi and Herms, 2010), resulting in major ecological consequences and altered forest landscapes (Tobin, 2015). The extensive mortality and selection pressures experienced by the host tree species are likely to result in the loss of genetic diversity (Altizer et al., 2003), which in turn may reduce the capacity of the host species to adapt to other subsequent environmental changes (Loo, 2009). We categorized and prioritized 419 North American tree species for conservation, monitoring, management and restoration based on their expected vulnerability to genetic degradation as a result of insect and disease infestation. Similar to an effort focusing on the potential effects of climate change on U.S. tree species (Potter et al., 2017), this assessment applied a hierarchical data- and expert-opinion driven framework incorporating species-based information relating both to the severity of insect and disease threats and to characteristics associated with the sensitivity and adaptive capacity to these threats. This effort was driven by the need of the United States Forest Service for a systematic approach that identifies at-risk tree species and informs decisions about which species to target for gene conservation activities.

This assessment is designed to be flexible and transparent, both in the set of host species it encompasses, and in its application of expert opinion in constructing the framework hierarchy. Its emphasis is on the quantitative categorization of species into classes with similar insect and disease threat severity, sensitivity and adaptive capacity, rather than on the generation of a conservation priority list that may potentially suggest a misleading level of precision associated with summarizing species attribute data into a unique ranking (Carter et al., 2000; Mace and Collar, 2002). Our ranking of species within vulnerability classes is therefore a secondary objective to the assignment of species to those classes, each of which may require different monitoring and conservation strategies for sustaining adaptive genetic variation within the species.

4.1. Conservation assessment within categories

The current assessment identified 11 groups of United States forest tree species with similar types and degrees of vulnerability to insect and disease infestations. Three of these vulnerability classes (A1, A2.1 and A4.1) encompass the 15 species that have the highest levels of vulnerability to current insect and disease threats (Table 4). Each of these species is threatened by one or more serious nonnative insects or pathogens. An additional 59 tree species in two vulnerability classes (A2.2 and A4.2) are also vulnerable but face less devastating insect and disease threats.

Arguably, each of the 15 most vulnerable species, and several of the other 59, should be the focus of both a comprehensive gene conservation program and a genetic resistance screening and development effort. The goal of gene conservation, especially in species that are imperiled, is to maintain genetic integrity and natural levels of genetic diversity within species (Maunder et al., 2004; Rajora and Mosseler, 2001). In particular, conservation efforts such as seed collection and banking can serve as an insurance policy against extinction (FAO, 2014) and as a source of material for research and the eventual reintroduction of species (Holsinger and Vitt, 1997; Maunder et al., 2004). A critical line of research for this *ex situ* germplasm relates to the potential resistance of the host tree species to the insect or disease. Although resistance in host populations is often too rare in the initial phase of an epidemic to substantially reduce its mortality effects (Prospero and Cleary, 2017; Sniezko and Koch, 2017), the evolutionary potential of tree species to respond to pests and pathogens should not be underestimated (Budde et al., 2016). This is because a small number of resistant individuals may be present even in the host tree species that are most susceptible, and this resistance can be harnessed to produce genetic diversity and resistant populations for restoration and reforestation (Sniezko, 2006). For a resistance development program to be successful, it must include research, tree breeding and restoration components, which may be expedited with the careful implementation of new genomic technologies as long as they are well-integrated with traditional breeding efforts (Sniezko and Koch, 2017). Such host resistance programs can enable the long-term conservation of affected tree species and forest ecosystems when the programs are integrated into an ecologically informed management response framework and when substantial investments in resistance development are made as soon as eradication of the nonnative agent is deemed impossible (Showalter et al., 2018). Specifically, earlier and more focused efforts to find, evaluate and implement the development of resistance would hasten the establishment of applied breeding programs, and therefore should not be constrained while other approaches such as eradication and containment of the disease or insect are the main focus (Sniezko and Koch, 2017).

Both gene conservation and the development of resistance are essential for the five species in vulnerability class A1 (Cluster 9). These species are particularly at risk because, in addition to experiencing extensive mortality from exotic diseases, they are highly sensitive to these diseases because of their rarity and/or relatively restricted distributions. They also have a reduced ability to adapt to these threats as a result of relatively low regeneration capacity and genetic variation. The conservation needs of these species, therefore, are urgent and immediate. Fortunately, efforts are under way to facilitate resistance in most of these species and/or to preserve their genetic variation. For example, American chestnut has been the focus of decades-long projects to breed for resistance to chestnut blight and to transform the species with a resistance-conferring transgene (followed by conventional breeding) (Steiner et al., 2017). Additionally, work is under way to locate persistent redbay survivor trees and to identify and test clones tolerant to laurel wilt disease (Smith and Jokela, 2016), which has killed hundreds of millions of redbay trees since the early 2000s (Hughes et al., 2017). Finally, Florida torreya, a rare species that has declined precipitously as the result of a canker disease (Smith et al., 2011), has been the focus of efforts to expand an *ex situ* gene conservation program (Smith et al., 2014) and to develop a somatic embryogenesis tissue culture system for cryogenic storage of the species and later plant regeneration (Ma et al., 2012). Efforts to enhance resistance to chestnut blight in Allegheny chinquapin and Ozark chinquapin are currently nascent (e.g., Mellano et al., 2012), but could possibly benefit from the extensive resistance breeding and transgenetic work completed on their congener, American chestnut.

The 10 species in vulnerability classes A2.1 and A4.1 (Clusters 5 and 6) are those for which conservation and the facilitation of resistance are the next most pressing, given the severity of the insect and disease threats which they face. Members of the A2.1 group (pumpkin ash, Carolina ash, Port-Orford-cedar, Carolina hemlock, butternut, and tanoak) are generally more sensitive to their threats because they have small distributions and/or are rare within those areas. Gene conservation or resistance screening and breeding programs are in varying degrees of development for each. A cooperative genetic resource conservation program between the United States Forest Service and the Camcore international tree breeding and conservation program at North Carolina State University focuses on *ex situ* seed collections from pumpkin and Carolina ash, among other members of the genus susceptible to EAB (Jetton and Whittier, 2016). A long-term screening and breeding program for Port-Orford-cedar has made significant progress in selecting for root disease (*Phytophthora lateralis* Tucker & Milbrath) resistance (Sniezko et al., 2017a). For Carolina hemlock, which is being decimated by the exotic hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) (Havill et al., 2011), an *ex situ* gene conservation project has collected seed from throughout its range and established seedlings at four conservation plantings inside and outside the United States (Jetton et al., 2013). An effort is ongoing across 17 states in the United States and two Canadian provinces to establish *ex situ* germplasm collections and to screen for tolerance to butternut canker (*Sirococcus clavigignenti-juglandacearum*) (Coggeshall et al., 2017). Finally, tanoak, which has experienced a large-scale decline as a result of a *Phytophthora ramorum* epidemic (Cobb et al., 2012), has been the subject of a multi-year common garden study of seedling resistance that revealed variable resistance with significant heritability (Hayden et al., 2010).

Meanwhile, members of the A4.1 group (eastern hemlock and white, black and green ash) are also facing severe threats from HWA (Havill et al., 2011) and EAB (Herms and McCullough, 2014), respectively. These four species, however, may have some extra breathing room because of their extensive distributions and commonness and relatively higher regeneration capacity and genetic variability. At the same time, it is important to underscore the importance of maintaining large populations of tree species threatened by insects and diseases, through silvicultural practices and long-term land-use planning if possible, to reduce the chance of inbreeding and reduced intraspecific genetic diversity by maximizing gene flow at the landscape level (Budde et al., 2016). This will increase the likelihood that species will retain fitness relative to a wide variety of environmental pressures beyond the infestation, as well as the evolutionary potential to adapt to new conditions. The maintenance of such intraspecific diversity is also an important consideration for the restoration of tree species to ensure that they will survive and reproduce (Thomas et al., 2014) following the successful enhancement of insect or disease resistance. Conservation efforts are ongoing for each of the four A4 species. As with Carolina hemlock, seeds have been collected from across much of the range of eastern hemlock, with some reserved in germplasm repositories and others planted in a seed orchard conservation bank (Jetton et al., 2013). Additionally, biological control (Onken and Reardon, 2011) and chemical control (Cowles et al., 2006) measures have been developed and employed to lessen the impacts of HWA, while research proceeds on effective silvicultural treatments (Brantley et al., 2017; Jetton and Mayfield, 2018) and the enhancement of host resistance (Oten et al., 2014). For the three widespread ashes, recent work includes investigating levels of resistance to emerald ash borer within species (Tanis and McCullough, 2015), chemical control (Tanis et al., 2012), and biological control (Duan et al., 2018). Additionally, thousands of seed lots, mostly of white and green ash, have been collected for long-term germplasm storage and research (Karrfalt, 2017).

The 41 species in vulnerability class A2.2 have moderately high threat severity, sensitivity, and adaptive capacity scores on average. In addition to gene conservation efforts, many of these should be strong candidates for relatively intensive efforts to develop genetic resistance, especially given their potential for adaptation. Six of these are ash species that have not yet been infested by emerald ash borer and that could shift into a higher vulnerability class if they experience severe mortality once exposed to EAB. These species are in addition to blue ash (*Fraxinus quadrangulata* Michx.), which appeared to be more resistant to EAB than white, green and black ash in a controlled plantation study (Tanis and McCullough, 2015). The Camcore/United States Forest Service ash genetic resource conservation program includes seed collections for blue ash and Texas ash (*Fraxinus albicans* Buckley) (Jetton and Whittier, 2016). Six other A2.2 species are five-needle pines that face a serious exotic disease threat (white pine blister rust, *Cronartium ribicola* J.C. Fisch., WPBR) and a native bark beetle threat (mountain pine beetle, *Dendroctonus ponderosae* Hopkins). These pines have been the target of conservation measures, including WPBR genetic resistance identification (Kinloch et al., 1999; Schoettle et al., 2014), screening (Kinloch et al., 2008), breeding (Sniezko, 2006), and mapping (Liu et al., 2016); *ex situ* conservation (Sniezko et al., 2017b); and a regeneration for resilience framework (Schoettle et al., 2018). Finally, the A2.2 vulnerability class also encompassed 14 oak (*Quercus*), three maple (*Acer*), and two fir (*Abies*) species (Table 4). Meanwhile, the A4.2 vulnerability class contained several tree species that, while generally less at risk than other species, have been the focus of resistance breeding efforts because of important insect or disease threats (Supplementary Table 2).

Most species belonging to other vulnerability classes are unlikely to need the same degree of conservation attention, with some exceptions. For example, the 47 species in vulnerability class B.1 and the 62 species in vulnerability class B.2 do not currently face severe insect and disease threats, but they have high sensitivity and low adaptive capacity relative to future insect and disease threats. For example, several are rare across limited geographical distributions and exhibit low genetic variability. Monitoring the development of future threats is important for such species, as is assessing existing *in situ* conservation and the extent and representativeness of *ex situ* seed collections in case these are needed for future resistance screening and breeding programs. A similar approach seems appropriate for the 58 species in vulnerability class C, because these are also mostly rare and limited-distribution species that are potentially sensitive to future insect and disease threats. These may prove more adaptable, however, so *ex situ* collections may be less important, and *in situ* conservation more important, than for the B.1 and B.2 species. Meanwhile, the 43 species in vulnerability class D.1 and the 59 species in vulnerability class D.2 may be less able to adapt to future insect and disease threats but are likely to be less sensitive to them because they are relatively common and widespread. Pre-emptive conservation measures are not as critical for these species, although it may be important to warehouse germplasm that is broadly representative of locally adapted genotypes. Finally, the 76 species in vulnerability classes E.1 and E.2, which are mostly common and widespread with high genetic variability and regeneration capacity, should be subject to routine monitoring of demographic trends broadly and at smaller scales that correspond with seed transfer areas.

4.2. Additional assessment needs

This assessment effort accounts only for insect and disease threat agents that are currently present in the United States, as it is difficult to accurately predict the identity and impacts of future invasive species introductions. At the same time, most countries have a limited capacity to prevent invasions, which will continue to be facilitated by globalization and climate change (Early et al., 2016). U.S. policymakers and managers therefore should be prepared for the introduction of several new exotic pest species in the relatively near future (Leung et al., 2014), perhaps in keeping with the recent trend of increased detections of phloem-feeding and wood-boring insects (Aukema et al., 2010). We therefore strongly recommend regularly updating the inventory of insect and disease agents affecting native host tree species in the United States, and their associated severities, as well as repeating the vulnerability assessment described here as new data become available.

It is important to note that this assessment does not address the ecological or socio-economic effects associated with the loss or reduction of host tree species. Ecological impacts encompass changes in the dynamics associated with canopy gaps, coarse woody debris, biochemical cycling and interactions among terrestrial and aquatic organisms, all with accompanying effects on forest composition, structure and function (Gandhi and Herms, 2010). Socio-economic impacts, though difficult to value monetarily, include the costs associated with insect and disease detection and containment programs; with tree treatment, removal and replacement; and with the loss of residential property values (Aukema et al., 2011; Epanchin-Niell, 2017).

Finally, integrating tree species' exposure to multiple threats would offer a fuller picture of the overall vulnerability of these species to the loss of adaptive genetic capacity or extirpation in parts of or throughout their distributions. Specifically, climate warming is expected to influence the forest impacts of insects and diseases by affecting the abundance and distribution of these disturbance agents; the ability of trees to defend against or tolerate attacks by insects and diseases; and the interactions between insects and pathogens and their competitors, natural enemies and mutualists (Weed et al., 2013). Changes in climatic conditions are likely to consequently alter the disturbance regimes of many forest insects and diseases in North America, often through complex interactions that vary by the type of agent (e.g., Kolb et al., 2016) and that are in some cases uncertain because of inadequate data about some insect and disease agents and because some depend on complex relationships that are not well understood (Dukes et al., 2009). A comprehensive assessment of North American tree species will encompass multiple threats, so a future objective of the United States Forest Service Project CAPTURE conservation framework will be to combine the results of this tree host-level analysis of vulnerability to insects and diseases with a tree species-level climate vulnerability assessment (Potter et al., 2017).

5. Conclusions

A goal of several government agencies and nonprofit organizations is the preservation of the adaptive genetic diversity of the host tree species devastated by nonnative insects and diseases and the eventual restoration of these tree species to the forest. We here describe a data-driven conservation assessment framework, guided by expert opinion and developed to identify the most vulnerable forest tree species. This framework is therefore geared toward better enabling the efficient use of limited resources for the prevention of their widespread genetic degradation and the identification and development of genetic resistance to nonnative insects and diseases. The emphasis of the effort is to assign native tree species to vulnerability classes which may need different conservation and management approaches, with the ranking of species within those classes a secondary objective.

Nearly all the most highly vulnerable tree species are the current or recent focus of at least minimal efforts to conserve their genetic variation and/or to screen for and improve genetic resistance. These efforts are uneven, however, and species are at different stages in these areas. Given the high probability that more destructive invaders will be introduced in the near future (Aukema et al., 2011), it will be critical to advance these efforts rapidly and, to the extent possible, lay the foundations for gene conservation and resistance development programs for tree species that could be particularly vulnerable to future exotic insects and diseases. The ultimate objective is the maintenance, and establishment through restoration if necessary (Sniezko and Koch, 2017), of resistant self-sustaining populations that retain adequate genetic diversity to adapt to future environmental challenges.

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Appendix 1. Calculations of Tree Trait Values and Attributes

The Project CAPTURE (Conservation Assessment and Prioritization of Forest Trees Under Risk of Extirpation) assessment framework is both hierarchical and expert-driven. The highest level of the hierarchy consists of the three dimensions of vulnerability of tree species to insects and disease infestation (sensu Foden et al., 2013): **(1)** the severity of the insect and disease threats, **(2)** sensitivity to the threats, and **(3)** low adaptive capacity relative to the threats (Fig. 1). Guided by expert opinion, we defined a tree species' sensitivity as consisting of two attributes, rarity and area of distribution, and we defined low adaptive capacity as encompassing two different attributes, regeneration capacity and genetic variability (Fig. 2). Each of these attributes contains a set of specific characteristics, from publicly available data sources or publications, that are included to account for differences in species' relevant life history characteristics and occurrence patterns that may affect their ability to tolerate and adapt in response to insect and disease threats.

Calculation of Species Trait Values

Some species traits were initially classified into ordinal classes based on vulnerability, such as “Short”, “Moderate” and “Long” for tree species lifespan or “Wind”, “Wind and Insects” and “Insects” for pollination vector. Such traits were converted to a continuous numeric scale using quantile transformation based on the premise that the conservation efforts allotted for species should reflect the proportional number of species within each category of a trait (Jimenez-Alfaro et al., 2010). This approach assigns a value of 100 to the most vulnerable category within a species trait and a value of 0 to the least vulnerable category, with the values of the intermediate categories calculated as the proportion of the total species in the category plus the species in all the categories that are less vulnerable. For example, a set of 200 species could have categorical data related to their typical lifespan, with 40 species having a short lifespan, 100 a medium lifespan, and 60 a long lifespan. Since species with a short lifespan have the lowest conservation concern, those 40 species can be given a weight of 0. Species of medium lifespan can be given a weight of 70 ($(40 + 100)/200 = 0.7$; transformed to 70 on a 0–100 scale), while those with a long lifespan would be given a weight of 100 ($(40 + 100+60)/200 = 1.0$; transformed to 100).

Meanwhile, other trait data, such as the number of plots in a systematic national grid on which a species was inventoried, were continuous. To maintain consistency with the transformed ordinal traits, species for these continuous traits were grouped into four equal-proportion weighted quantiles, with an equal number of species in each quantile given scores of 0, 33, 66 or 100 in increasing conservation importance.

Calculation of Sensitivity Attributes

Rarity

Rare species are among the most vulnerable to a variety of threats (Lavergne et al., 2005; Mace et al., 2008) in part because they encompass fewer individuals or populations than more common species (Jump and Peñuelas, 2005) and often exhibit a reduced ability to adapt to environmental change (Willi et al., 2006). For this assessment, the large majority of experts surveyed agreed (Table 1) that the rarity attribute should include two species characteristics: **1)** the number of plot-level occurrences from a national grid of inventory plots, and **2)** the density of inventoried trees per area of species' distributional area in the United States. The rarity attribute was calculated as the mean of these two metrics. For most species, these metrics were derived using FIA information, collected using a nationally consistent sampling protocol from approximately 135,000 forested plots across the conterminous United States and coastal Alaska, with each plot representing 2,428 ha of land (Bechtold and Patterson, 2005; Woudenberg et al., 2010). Given the FIA program design, these data should provide unbiased measures of frequency of occurrence. For most species, distributional area is from E.L. Little's forest tree species distribution maps (United States Geological Survey, 1999), although some information was from maps in the Flora of North America North of Mexico (Flora of North America Editorial Committee, 1993+). For species not inventoried by FIA, we included only an occurrence density score, using georeferenced occurrence data from the Global Biodiversity Information Facility (Global Biodiversity Information Facility, 2018).

Area of Distribution

The extent of tree species' distribution is an important factor in their sensitivity to threats. Plant species with restricted geographic ranges, for example, are more susceptible to threats because they tend to have narrower habitat tolerances (Bradshaw et al., 2008; Stork et al., 2009). On the other hand, large populations of native tree species are more likely to allow natural selection to operate with sufficient intensity to ensure mechanisms of resistance and tolerance to develop over time (Loo, 2009). This assessment incorporates a measure of each tree species' range area within the United States. As noted above, the distributional areas of most tree species were from a set of range maps originally published by the USDA Forest Service (United States Geological Survey, 1999), while some tree species distributions were based on maps in the Flora of North America North of Mexico (Flora of North America Editorial Committee, 1993+). The species areas were multiplied by the percent of each species' range that occurs within the United States; this concept of "regional responsibility" (Gauthier et al., 2010) avoids inflating the appropriate conservation efforts allocated to species that are rare within the country but more common globally.

Calculation of Low Adaptive Capacity Attributes

Regeneration Capacity

The adaptive capacity of species depends in part on their ability to reproduce successfully, with genetic degradation from threats such as insects and disease more likely for species that are unable to regularly and frequently regenerate. The regeneration capacity attribute in this assessment is calculated as the mean of six metrics that the surveyed experts agreed should be included (Table 1): **1)** frequency of large seed crops, **2)** long-term viability of seed, **3)** age at reproductive maturity, **4)** sexual and vegetative reproduction strategies, **5)** typical lifespan, and **6)** monoecious vs. dioecious breeding system. An additional metric, growth rate, was not incorporated because a majority of the surveyed experts did not agree that it should be included (34.5 percent disagreed and 20.7 percent were unsure). For the frequency of large seed crops, species were assigned weighted quantile scores: short interval between seed crops (more or less annually): 0, moderate interval (every 2–3 years): 64.7, long interval (every 4–6 years): 78.5, and very long interval (more than every 7 years, or erratic/irregular): 100. For long-term seed viability, species were assigned weighted quantile scores based on whether their seeds are able to persist and successfully germinate in a natural forest seed bank ("orthodox"): 0; whether they are dessication-intolerant ("recalcitrant"): 100; or intermediate for these characteristics ("sub-orthodox"): 75.4. For age of reproductive maturity, there were five weighted quantile scores: very early (>10 years): 0, early (10–19 years): 57.4, moderate (20–29 years): 85.0, late (30–39 years): 95.0, very late (40 or more years): 100. For sexual and clonal reproductive strategies, species were assigned one of two scores based on the degree to which they are able to reproduce vegetatively: significant combination of sexual and clonal: 0, only sexual or only clonal, or only rare sexual or rare clonal: 100. Species were assigned three weighted quantile scores based on the typical lifespan of mature trees: short (<~75 years): 0, moderate (~75–~150 years): 49.3, or long (>150 years): 100.0. Finally, species were assigned scores based on whether they consist 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

Tree species are long-lived and immobile life forms that require high levels of genetic diversity to adapt to changing environmental influences (FAO, 2014), with genetic variation conveying option value that is important to the survival of tree species in the face of severe stresses (Jump et al., 2009; Schaberg et al., 2008), including widespread epidemics (Altizer et al., 2003). For example, intraspecific genetic diversity of trees offers insurance against invasive diseases through the likelihood that some hosts will possess or develop effective mechanisms to resist or minimize the damage caused by the disease (Prospero and Cleary, 2017). We calculated the genetic variability attribute as the mean of three metrics recommended for inclusion by the surveyed experts (Table 1): **1)** number of climatically defined seed zones intersecting each species' distribution, **2)** pollination vector, and **3)** number of disjunct populations. As a surrogate for environmental conditions that could be associated with adaptive variation across species' distributions, the species were assigned scores based on how many of the climatically defined seed zones, as described by Bower et al. (2014), were contained within their distributional ranges. These scores were grouped into four equal-proportion quantiles (<9 = 100, 9–16 = 66, 17–25 = 33, >25 = 0). For pollination vector, each species was assigned a weighted quantile score given its primary vector of pollination: by wind: 0; by both wind and insects/animals: 65.4; by insects, birds or mammals: 100. The number of disjunct populations was determined using digitized versions of E.L. Little's range maps (United States Geological Survey, 1999), with disjunct populations defined as those smaller than 250,000 ha and at least 50 km from the nearest population greater than 250,000 ha. Tree species were grouped into weighted quantile classes based on the number of disjuncts across their U.S. distributions: no disjuncts: 0; 1–2 disjuncts: 18.6; 3–4 disjuncts: 26.0; 5 or more disjuncts, or consisting entirely of small populations (none >250,000 ha): 100.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00622.

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