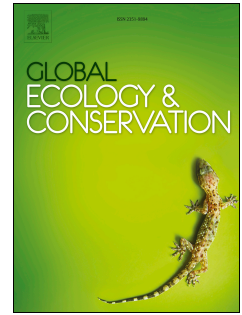


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1 **Prioritizing the Conservation Needs of United States Tree Species: Evaluating**
2 **Vulnerability to Forest Insect and Disease Threats**

3
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22 **Abstract**

23 Insect and disease infestations pose major threats to several North American forest tree species.
24 Scientists and managers from throughout the United States Forest Service developed a
25 conservation priority-setting framework for forest tree species at risk from insects and disease
26 and other threats. The Project CAPTURE (Conservation Assessment and Prioritization of Forest
27 Trees Under Risk of Extirpation) framework is data-driven and guided by expert opinion,
28 allowing the quantitative grouping of species into vulnerability classes that may require different
29 management and conservation strategies. We applied this framework to categorize and prioritize
30 419 native North American tree species for conservation, monitoring, and management using
31 trait data and insect and disease threat data for each host tree species. The categorization is based
32 on vulnerability factors relating to each tree species' (1) insect and disease threat severity, (2)
33 sensitivity to insect and disease infestation, and (3) capacity to adapt to insect and disease
34 infestation. We used K-means clustering to group species into 11 classes based on these
35 vulnerability dimensions. The three most vulnerable classes encompassed 15 species which
36 require the most immediate conservation intervention. Two additional classes face less severe
37 insect and disease threats and may be good candidates for resistance breeding efforts. Other
38 groups had traits associated with high sensitivity and/or low adaptive capacity to potential future
39 insect and disease threats, suggesting that these species need close monitoring. This assessment
40 tool should be valuable for decision-makers determining which species and populations to target
41 for monitoring efforts and for pro-active gene conservation and management activities.

42 **Keywords**

- 43 gene conservation; forest health; insects and disease; invasive species; genetic resistance;
- 44 threatened species

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45 **1. Introduction**

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

54 It is extremely important to conserve the irreplaceable genetic resources of tree species
55 threatened by nonnative insects and diseases (Sniezko and Koch 2017). The most imperiled tree
56 species are vulnerable to functional extirpation and to the associated widespread loss of
57 important adaptive genetic variation. The unfortunate reality, however, is that both time and
58 resources are limited for the urgent work needed to conserve tree species and populations. In
59 fact, resources for forest management are declining even as forests increase in value and become
60 more challenging to effectively manage (Ayres and Lombardero 2018). It is necessary, therefore,
61 to efficiently allocate scarce conservation resources using species-level prioritization approaches
62 that are rational, systematic, and defensible (Bottrill et al. 2008; Farnsworth et al. 2006). These
63 approaches should emphasize safeguarding existing genetic adaptiveness within tree species and
64 the processes that allow for evolutionary resilience, which is the ability of populations to persist
65 in their current state or to adapt to changing environmental conditions (Myking 2002; Sgro et al.
66 2011).

67 A conservation framework, titled Project CAPTURE (Conservation Assessment and
68 Prioritization of Forest Trees Under Risk of Extirpation), is a data- and expert-driven effort by
69 scientists and managers in the United States Forest Service to both categorize and prioritize
70 native tree species based on their vulnerability to losing adaptive genetic variation as a result of
71 multiple threats. This framework recently was applied to categorize the vulnerability of United
72 States tree species to climate change (Potter et al. 2017). The application of this framework to
73 insects and diseases is perhaps even more urgent, given the immediacy of several disease and
74 insect threats. Vulnerability in this framework follows the characterization of Foden et al. (2013)
75 as a function of three dimensions: the tree species' exposure to an extrinsic threat, their
76 sensitivity to the threat, and their ability to adapt to it. In this case, the severity of the most
77 serious insect and disease agents for tree species (Potter et al. 2019) is used to determine that
78 species' insect and disease threat exposure. The sensitivity and adaptive capacity vulnerability
79 dimensions, meanwhile, are based on species characteristics, arranged in a hierarchical fashion to
80 reflect expert opinion. Such species characteristics, including life-history traits (e.g., Barrett et al.
81 2008; Giraud et al. 2010), influence the frequency and severity of infestation (Ghelardini et al.
82 2017). The tree species included in the assessment are then quantitatively grouped into
83 vulnerability classes of species that may require similar conservation and management strategies
84 and actions for maintaining their adaptive genetic variation (Potter et al. 2017).

85 The need to apply this categorization and prioritization framework to United States tree
86 species is critical because the most serious exotic insect and disease invaders have the potential
87 to functionally extirpate their tree hosts (Gandhi and Herms 2010). Already, at least a half dozen
88 nonnative fungal diseases have seriously impacted important North American tree species. For
89 example, the loss of American chestnut (*Castanea dentata* (Marsh.) Borkh.), following

90 infestation by chestnut blight (*Cryphonectria parasitica* (Murrill) Barr), fundamentally changed
91 forest ecosystems across much of eastern North America (Loo 2009). Similarly, the unfolding
92 decimation of several ash (*Fraxinus*) species in parts of eastern North America by the emerald
93 ash borer (EAB, *Agrilus planipennis* Fairmaire) is creating a cascade of ecological impacts in
94 forest communities (Klooster et al. 2018). The changes in forest structure and species
95 composition that result from such effective extirpations of host species, or the loss of individuals
96 in larger size classes, can alter important natural ecosystem functions, such as productivity,
97 nutrient cycling and wildlife habitat, and urban tree services, including shading, pollutant uptake,
98 and property value enhancement (Lovett et al. 2016; Tobin 2015). These impacts may be subtle
99 but still long-lasting and broad in their extent (Garnas et al. 2011; Loo 2009).

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

109

110 **2. Materials and Methods**

111 *2.1 Assessment framework*

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

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

127 Conceptually, the degree of vulnerability for each species depends on the degree to which
128 it has high values for each of the three vulnerability dimensions (Figure 1). For example, any
129 species with high insect and disease threat severity (A1-A4 in Figure 1) is currently imperiled by
130 one or more insect or disease threats, but species that also have high sensitivity (A2) or low
131 adaptive capacity (A3), or both (A1), are probably more immediately at risk of widespread
132 genetic degradation or even extirpation. Meanwhile, a species with high sensitivity and low

133 adaptive capacity, but low current insect and disease threat severity (B), may be particularly at
134 risk from future insects or diseases introduced from overseas. Finally, a species with low values
135 for all three vulnerability dimensions (E) has relatively low vulnerability to current or future
136 insect or disease infestation.

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

148

149 *2.2 Tree species included in the assessment*

150 This vulnerability assessment includes 419 forest tree species native to the contiguous 48
151 United States and Alaska. We adopted the definition of trees used by the national Forest
152 Inventory and Analysis (FIA) program of the United States Forest Service (Woudenberg et al.
153 2010): woody perennial plants that usually have a single well-defined erect stem with a more or

154 less definitely formed crown of foliage, a stem diameter at maturity of at least 7.62 cm, and a
155 height of at least 4.75 m at maturity, and that are not vines. The foundation of the assessment list
156 was the set of 362 native tree species inventoried by FIA in the contiguous United States and
157 Alaska, with native status defined by the USDA PLANTS database (U.S. Department of
158 Agriculture Natural Resource Conservation Service 2019). (We excluded species of hybrid or
159 exotic origin.) We also included an additional 57 species that also occur in the continental United
160 States but are not inventoried by FIA because they are rare and/or limited in their distributions.
161 These were woody plant species that generally meet the FIA definition of a tree and were listed
162 in a series of United States Forest Service publications describing the distributions of the forest
163 trees and shrubs of the United States (Little 1971, 1976a, b; Viereck and Little 1975).

164

165 *2.3 Insect and disease threats and severity ratings*

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

- 176 • Near complete mortality of all mature trees, or inability to reproduce sexually =
177 10
- 178 • Near complete mortality in a congeneric species = 9 (sensu Gilbert and Webb
179 2007)
- 180 • Significant mortality of mature trees = 8
- 181 • Moderate mortality of mature trees = 5
- 182 • Moderate mortality in association with other threats = 3
- 183 • Minor mortality, usually of already-stressed trees = 1

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

189

190 *2.3 Tree species attributes*

191 The vulnerability assessment framework incorporates two vulnerability dimensions in
192 addition to insect and disease Threat Severity: Sensitivity to insect and disease threats, and Low
193 Adaptive Capacity relative to insect and disease threats. As noted above, each of these, in turn,
194 consists of two species attributes (Figure 2). The inclusion of these attributes in the dimensions
195 was guided by the results of the expert survey, as was the assignment of each of a series of
196 specific traits to the four attributes. (For more information about the calculation of species trait

197 values, see Appendix 1). Because the species information applied in the framework is relative to
198 all the species included in the assessment, the species trait, attribute and vulnerability dimension
199 data were scored on a scale of 0 to 100, with higher scores associated with higher vulnerability.

200

201 2.3.1 Sensitivity to insect and disease threats

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

211

212 2.3.2 Low adaptive capacity to insect and disease threats

213 The Low Adaptive Capacity to Insect and Disease Threats vulnerability dimension
214 incorporated two species attributes: **1**) regeneration capacity (80.1 percent agreement by survey
215 participants, 12.9 percent disagreement; mean confidence: 4.13 on a scale of 1 to 5), and **2**)
216 genetic variability (90.3/3.2 percent agreement/disagreement; mean confidence: 4.16). Each

217 species' overall adaptive capacity dimension score was the mean of the two attributes. The
218 attributes, meanwhile, consisted of six (regeneration capacity) or three (genetic variability)
219 metrics. Table 1 reports the level of support among the surveyed experts for including the
220 metrics within these two attributes, and Appendix 1 explains how we calculated these metrics.

221

222 *2.3 Clustering into vulnerability classes*

223 We applied *K*-means clustering (Hartigan 1975) in Proc FASTCLUS in SAS 9.4 (SAS
224 Institute Inc. 2013) to group the 419 species into vulnerability classes based on their scores for
225 the three vulnerability class scores (for insect and disease Threat Severity, Sensitivity, and Low
226 Adaptive Capacity) after these had been standardized to a mean of 0 and standard deviation of 1.
227 *K*-means is an efficient partitional clustering technique that returns a user-specified number of
228 data clusters (*K*) represented by their centroids (Tan et al. 2005). Users run the clustering for a
229 variety of values of *K* to find the value that best explains the variation in a dataset. Here, we ran
230 the analysis for $K=2$ to $K=15$. We chose the appropriate *K* based on two metrics, peaks in the
231 pseudo F-statistic and the cubic clustering criterion (Milligan and Cooper 1985).

232 We next determined which of the insect and disease vulnerability classes (Figure 1, sensu
233 Foden et al. 2013) were most closely associated with each of the clusters from the analysis of the
234 selected *K*. To do this, we first calculated the mean vulnerability dimension scores across the
235 species within each of the clusters. Second, to visually interpret differences among the clusters,
236 we plotted them in three-dimensional space in SAS 9.4 (SAS Institute Inc. 2013) using canonical
237 discriminant analysis. This dimension-reduction technique derives canonical variables that are

238 linear combinations of the quantitative variables that summarize between-class variation. We
239 ascertained how each of these canonical variables (axes) related to the three vulnerability
240 dimensions.

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

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

246
247 where V is the overall vulnerability rating, T is Threat Severity, S is Sensitivity and A is Low
248 Adaptive Capacity. The species were then ranked by this overall vulnerability rating within each
249 of the vulnerability classes defined by the K -means clustering analysis.

250

251 **3. Results**

252 *3.1 Assignment to vulnerability classes*

253 The insect and disease Threat Severity vulnerability dimension was not significantly
254 correlated with either of the other vulnerability dimensions ($r=0.005$ and $p=0.924$ with

255 Sensitivity and $r=0.005$ and $p=0.923$ for Low Adaptive Capacity). Sensitivity and Low Adaptive
256 Capacity were significantly correlated ($p<0.0001$), but relatively weakly ($r=0.221$).

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

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

274 Three of the clusters consisted of species with high insect and disease Threat Severity (5,
275 6, and 9). The five species in Cluster 9 had high severity, high sensitivity, and low to moderate
276 adaptive capacity, and were therefore placed in vulnerability class A1 (“high current
277 vulnerability”) (Table 3). Cluster 5 incorporated six species with high threat severity, moderate

278 sensitivity, and high adaptive capacity, and was assigned to vulnerability class A2 (“high current
279 vulnerability, potential adaptation”). Another set of four species in Cluster 6 had high severity
280 but relatively low sensitivity and high adaptive capacity, placing it in vulnerability class A4
281 (“high current vulnerability, potential persistence/adaptation”). Meanwhile, two additional
282 clusters encompassed species with moderate Threat Severity (3 and 11a). The 41 species in
283 Cluster 3 were categorized with both moderate threat severity and sensitivity along with high
284 adaptive capacity. As a result, this group is best classified in vulnerability class A2, but with a
285 lower overall vulnerability than the species in cluster 2 (also classified as A2, but with higher
286 threat severity). Similarly, the 18 species in Cluster 11a were classified as A4, as was Cluster 6,
287 but with lower overall vulnerability.

288 Two clusters, 2 and 7, were assigned to vulnerability class B (“potential high
289 vulnerability to future threats”) because they both had relatively low insect and disease Threat
290 Severity along with relatively high Sensitivity and relatively Low Adaptive Capacity
291 (Supplementary Table 2). The 47 species in Cluster 7 (B.1), however, had a much higher mean
292 Sensitivity score, the highest of any cluster, and a higher Low Adaptive Capacity score than the
293 62 species in Cluster 2 (B.2) (Table 3). Similarly, two clusters were associated with vulnerability
294 class D (“potential low adaptation to future threats”). Cluster 10, incorporating 43 species, had
295 the highest mean Low Adaptive Capacity score, while the 59 Cluster 1 species also had Low
296 Adaptive Capacity that was relatively high. The insect and disease Threat Severity and
297 Sensitivity scores of each were low. Cluster 4 (58 species) was categorized in vulnerability class
298 C (“potential high sensitivity to future threats”) because its species have relatively high
299 Sensitivity and relatively low severity and high adaptive capacity.

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

303

304 3.2 Composition of vulnerability classes

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

314 The two species clusters assigned to vulnerability class A2 (clusters 5 and 3) differed in
315 having high versus moderate Insect and Disease Severity. Both had relatively high mean
316 Sensitivity and high mean adaptive capacity. Class A2.1 encompassed only six species that face
317 severe insect and disease threats (Carolina ash [*Fraxinus caroliniana* Mill.], pumpkin ash
318 [*Fraxinus profunda* (Bush) Bush], Carolina hemlock [*Tsuga caroliniana* Engelm.], Port-Orford-
319 cedar [*Chamaecyparis lawsoniana* (A. Murray) Parl.], tanoak [*Notholithocarpus densiflorus*
320 (Hook. & Arn.) P.S. Manos, C.H. Cannon & S.H. Oh], and butternut [*Juglans cinerea* L.]
321 (Table 4). The 41 species in class A2.2 (Supplementary Table 2) face less severe, though

322 generally still important, insect and disease threats. These include sugar pine (*Pinus lambertiana*
323 Douglas), Fraser fir (*Abies fraseri* [Pursh] Poir.), California black oak (*Quercus kelloggii*
324 Newberry), and several ash (*Fraxinus*) species that have not yet been infested by EAB but
325 eventually may experience extensive mortality because of it. Species in the A2.1 vulnerability
326 class also tend to be rarer than the generally more common A2.2 species, resulting in a somewhat
327 higher mean Sensitivity score.

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

340 Two clusters of tree species were classified in class B, with low Insect and Disease
341 Severity, relatively high Sensitivity, and relatively high adaptive capacity. Vulnerability class
342 B.1 encompasses 47 species that have the highest mean Sensitivity score across all clusters and
343 the third highest mean Low Adaptive Capacity score. Many of these species are rare to

344 uncommon, have small distributions, and have low genetic variability, although they have
345 relatively high regeneration capacity (Supplementary Table 2). Meanwhile, the 62 species
346 categorized in vulnerability class B.2 had the sixth highest mean Sensitivity and the fifth highest
347 mean Low Adaptive Capacity score. These are mostly species that are more common and have
348 larger distributions than B.1 species, and that have moderate regeneration capacity and relatively
349 low genetic variability.

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

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

366 adaptive capacity scores. These were mostly common species with large ranges and with
367 relatively high regeneration and genetic variability.

368

369 **4. Discussion**

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

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

396

397 *4.1 Conservation assessment within categories*

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

405 Arguably, each of the 15 most vulnerable species, and several of the other 59, should be
406 the focus of both a comprehensive gene conservation program and a genetic resistance screening

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

429 programs, and therefore should not be constrained while other approaches such as eradication
430 and containment of the disease or insect are the main focus (Sniezko and Koch 2017).

431 Both gene conservation and the development of resistance are essential for the five
432 species in vulnerability class A1 (Cluster 9). These species are particularly at risk because, in
433 addition to experiencing extensive mortality from exotic diseases, they are highly sensitive to
434 these diseases because of their rarity and/or relatively restricted distributions. They also have a
435 reduced ability to adapt to these threats as a result of relatively low regeneration capacity and
436 genetic variation. The conservation needs of these species, therefore, are urgent and immediate.
437 Fortunately, efforts are under way to facilitate resistance in most of these species and/or to
438 preserve their genetic variation. For example, American chestnut has been the focus of decades-
439 long projects to breed for resistance to chestnut blight and to transform the species with a
440 resistance-conferring transgene (followed by conventional breeding) (Steiner et al. 2017).
441 Additionally, work is under way to locate persistent redbay survivor trees and to identify and test
442 clones tolerant to laurel wilt disease (Smith and Jokela 2016), which has killed hundreds of
443 millions of redbay trees since the early 2000s (Hughes et al. 2017). Finally, Florida torreyia, a
444 rare species that has declined precipitously as the result of a canker disease (Smith et al. 2011),
445 has been the focus of efforts to expand an *ex situ* gene conservation program (Smith et al. 2014)
446 and to develop a somatic embryogenesis tissue culture system for cryogenic storage of the
447 species and later plant regeneration (Ma et al. 2012). Efforts to enhance resistance to chestnut
448 blight in Allegheny chinquapin and Ozark chinquapin are currently nascent (e.g., Mellano et al.
449 2012), but could possibly benefit from the extensive resistance breeding and transgenetic work
450 completed on their congener, American chestnut.

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

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

495 biological control (Duan et al. 2018). Additionally, thousands of seed lots, mostly of white and
496 green ash, have been collected for long-term germplasm storage and research (Karrfalt 2017).

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

518 Most species belonging to other vulnerability classes are unlikely to need the same
519 degree of conservation attention, with some exceptions. For example, the 47 species in
520 vulnerability class B.1 and the 62 species in vulnerability class B.2 do not currently face severe
521 insect and disease threats, but they have high sensitivity and low adaptive capacity relative to
522 future insect and disease threats. For example, several are rare across limited geographical
523 distributions and exhibit low genetic variability. Monitoring the development of future threats is
524 important for such species, as is assessing existing *in situ* conservation and the extent and
525 representativeness of *ex situ* seed collections in case these are needed for future resistance
526 screening and breeding programs. A similar approach seems appropriate for the 58 species in
527 vulnerability class C, because these are also mostly rare and limited-distribution species that are
528 potentially sensitive to future insect and disease threats. These may prove more adaptable,
529 however, so *ex situ* collections may be less important, and *in situ* conservation more important,
530 than for the B.1 and B.2 species. Meanwhile, the 43 species in vulnerability class D.1 and the 59
531 species in vulnerability class D.2 may be less able to adapt to future insect and disease threats but
532 are likely to be less sensitive to them because they are relatively common and widespread. Pre-
533 emptive conservation measures are not as critical for these species, although it may be important
534 to warehouse germplasm that is broadly representative of locally adapted genotypes. Finally, the
535 76 species in vulnerability classes E.1 and E.2, which are mostly common and widespread with
536 high genetic variability and regeneration capacity, should be subject to routine monitoring of
537 demographic trends broadly and at smaller scales that correspond with seed transfer areas.

538

539 *4.2 Additional assessment needs*

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

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

560 Finally, integrating tree species' exposure to multiple threats would offer a fuller picture
561 of the overall vulnerability of these species to the loss of adaptive genetic capacity or extirpation
562 in parts of or throughout their distributions. Specifically, climate warming is expected to
563 influence the forest impacts of insects and diseases by affecting the abundance and distribution
564 of these disturbance agents; the ability of trees to defend against or tolerate attacks by insects and
565 diseases; and the interactions between insects and pathogens and their competitors, natural
566 enemies and mutualists (Weed et al. 2013). Changes in climatic conditions are likely to
567 consequently alter the disturbance regimes of many forest insects and diseases in North America,
568 often through complex interactions that vary by the type of agent (e.g., Kolb et al. 2016) and that
569 are in some cases uncertain because of inadequate data about some insect and disease agents and
570 because some depend on complex relationships that are not well understood (Dukes et al. 2009).
571 A comprehensive assessment of North American tree species will encompass multiple threats, so
572 a future objective of the United States Forest Service Project CAPTURE conservation
573 framework will be to combine the results of this tree host-level analysis of vulnerability to
574 insects and diseases with a tree species-level climate vulnerability assessment (Potter et al.
575 2017).

576

577 *4.3 Conclusions*

578 A goal of several government agencies and nonprofit organizations is the preservation of
579 the adaptive genetic diversity of the host tree species devastated by nonnative insects and
580 diseases and the eventual restoration of these tree species to the forest. We here describe a data-
581 driven conservation assessment framework, guided by expert opinion and developed to identify

582 the most vulnerable forest tree species. This framework is therefore geared toward better
583 enabling the efficient use of limited resources for the prevention of their widespread genetic
584 degradation and the identification and development of genetic resistance to nonnative insects and
585 diseases. The emphasis of the effort is to assign native tree species to vulnerability classes which
586 may need different conservation and management approaches, with the ranking of species within
587 those classes a secondary objective.

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

598

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616

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873

874 **Table 1** Traits included within each species attribute, expert survey results about whether to include each trait within the attribute, and citations
 875 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)					
<i>Plot level occurrences*</i>	31	83.87	6.45	9.68	Budde et al. (2016), Gaston (2008)
<i>Density*</i>	32	81.25	6.25	12.5	McKinney (1997)
Distribution (Sensitivity)					
<i>Area of distribution*</i>	--	--	--	--	Bradshaw et al. (2008), Leao et al. (2014)
Regeneration Capacity (Low Adaptive Capacity)					
<i>Large seed crop frequency</i>	31	93.54	0	6.45	McKinney (1997)
<i>Long-term viability of seed</i>	32	93.75	3.13	3.13	Black et al. (2006), Estrada et al. (2015)
<i>Age at reproductive maturity</i>	32	93.75	3.13	3.13	Jump and Peñuelas (2005)
<i>Sexual and asexual reproductive strategies</i>	31	70.97	12.9	16.13	Godefroid et al. (2014)
<i>Typical lifespan</i>	31	64.52	19.35	16.13	McKinney (1997), Jump and Peñuelas (2005)
<i>Breeding system</i>	32	75	12.5	12.5	Vamosi and Vamosi (2005)
Genetic Variability (Low Adaptive Capacity)					
<i>Number of seed zones*</i>	31	70.97	22.58	6.45	Bower et al. (2014), Prasad (2015)
<i>Pollination vector</i>	30	56.67	3.33	40	Budde et al. (2016), Godefroid et al. (2014)
<i>Number of disjunct populations</i>	30	90	0	10	Jump and Peñuelas (2005), Kuhn et al. (2016)

* Continuous data converted to quantiles.

876
877 **Table 2** Correlations between vulnerability dimensions and the canonical discriminant functions
878 (canonical variables 1, 2, and 3) after controlling for group membership.
879

	<i>Pooled within canonical structure</i>		
	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

880

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

883

Cluster	Species (n)	Insect and Disease Severity		Sensitivity		Low Adaptive Capacity		Overall		Vulnerability Description	Classes
		mean	rank	mean	rank	mean	rank	mean	rank		
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

884

885

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888 **Table 4** The 15 North American tree species in vulnerability class A facing the highest insect and disease severity, ranked within each
 889 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	<i>Torreya taxifolia</i>	Florida torreya	88.0	100.0	75.6	88.2	1
2	<i>Castanea pumila</i> var. <i>ozarkensis</i>	Ozark chinquapin	88.7	100.0	64.0	85.0	2
3	<i>Castanea dentata</i>	American chestnut	100.0	74.5	74.7	84.0	3
4	<i>Castanea pumila</i> var. <i>pumila</i>	Allegheny chinquapin	88.7	74.5	58.1	74.8	4
5	<i>Persea borbonia</i>	redbay	88.0	49.5	69.7	69.8	7
Vulnerability Class A2.1 (Cluster 5)							
1	<i>Fraxinus profunda</i>	pumpkin ash	88.7	74.8	52.7	73.3	5
2	<i>Fraxinus caroliniana</i>	Carolina ash	88.7	66.0	55.5	71.2	6
3	<i>Tsuga caroliniana</i>	Carolina hemlock	88.1	83.0	30.7	69.2	8
4	<i>Chamaecyparis lawsoniana</i>	Port-Orford-cedar	88.6	66.5	45.1	68.3	9
5	<i>Lithocarpus densiflorus</i>	tanoak	88.0	58.3	47.2	65.9	10
6	<i>Juglans cinerea</i>	butternut	88.6	49.8	40.9	61.5	11
Vulnerability Class A4.1 (Cluster 6)							
1	<i>Fraxinus americana</i>	white ash	88.7	24.8	42.7	53.8	14
2	<i>Tsuga canadensis</i>	eastern hemlock	88.1	16.5	43.0	50.9	24
3	<i>Fraxinus nigra</i>	black ash	88.7	8.3	42.5	48.3	36
4	<i>Fraxinus pennsylvanica</i>	green ash	88.7	8.3	13.1	39.5	109

890

891 **Figure captions**

892

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

896

897

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

901

902

903 **Figure 3** Results of the K-means clustering and canonical discriminant analysis using scores for insect and disease threat severity,
904 sensitivity to insect and disease threats, and low adaptive capacity, across 419 North American tree species. In (A), canonical variable
905 1 (x-axis) is strongly associated with insect and disease threats, and canonical variable 2 (y-axis) is most strongly associated with
906 sensitivity. In (B), canonical variable 1 is again associated with insect and disease threats, and canonical variable 3 (y-axis) is
907 associated with low adaptive capacity. In (C), canonical variable 2 is associated with sensitivity, and canonical variable 3 is associated
908 with low adaptive capacity. The 11 clusters are related to vulnerability classes (see Figure 1) based on their mean vulnerability
909 dimension attributes (Table 3) and their locations relative to the canonical variable axes.

910

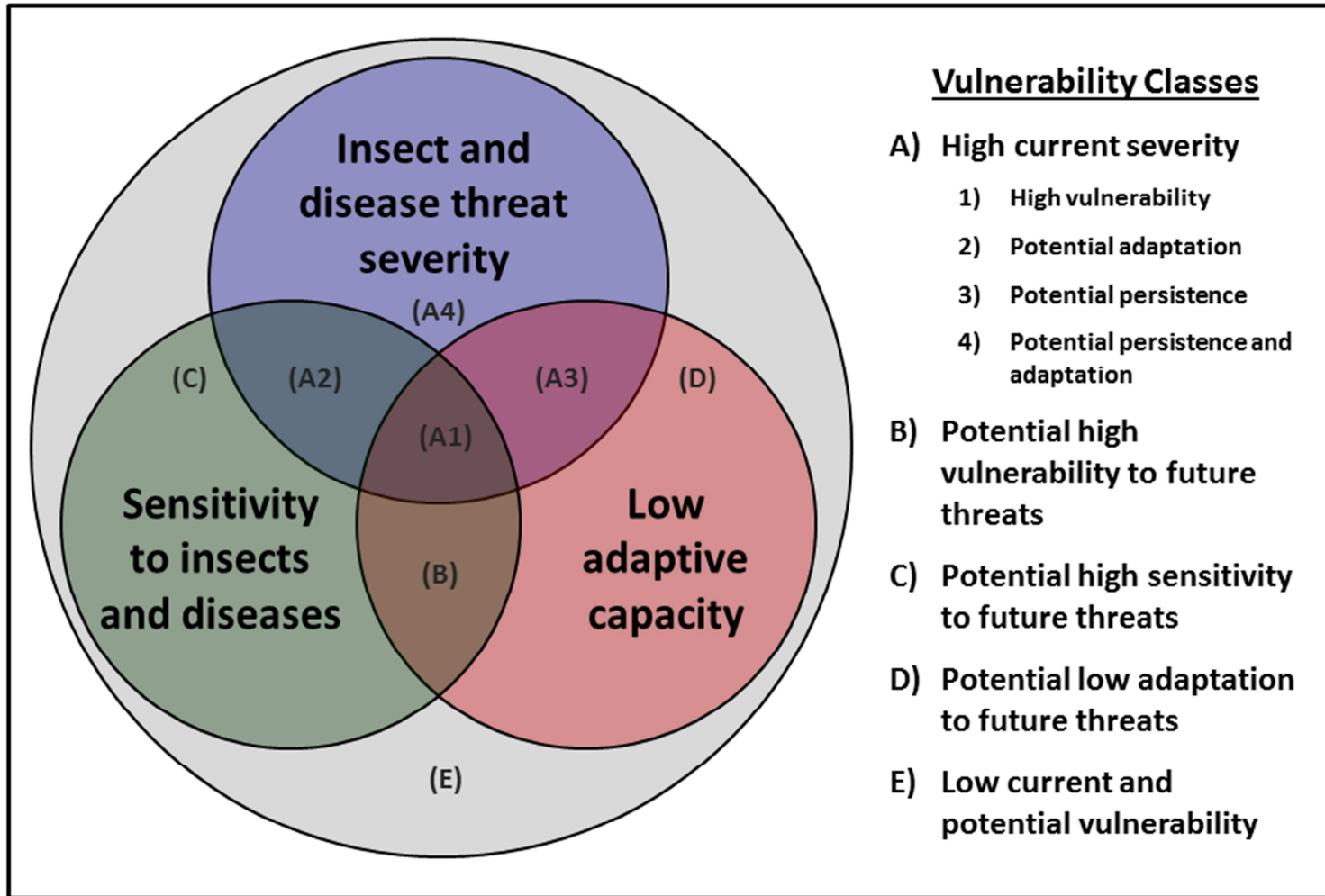
911

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

914

915 **Figure 1**

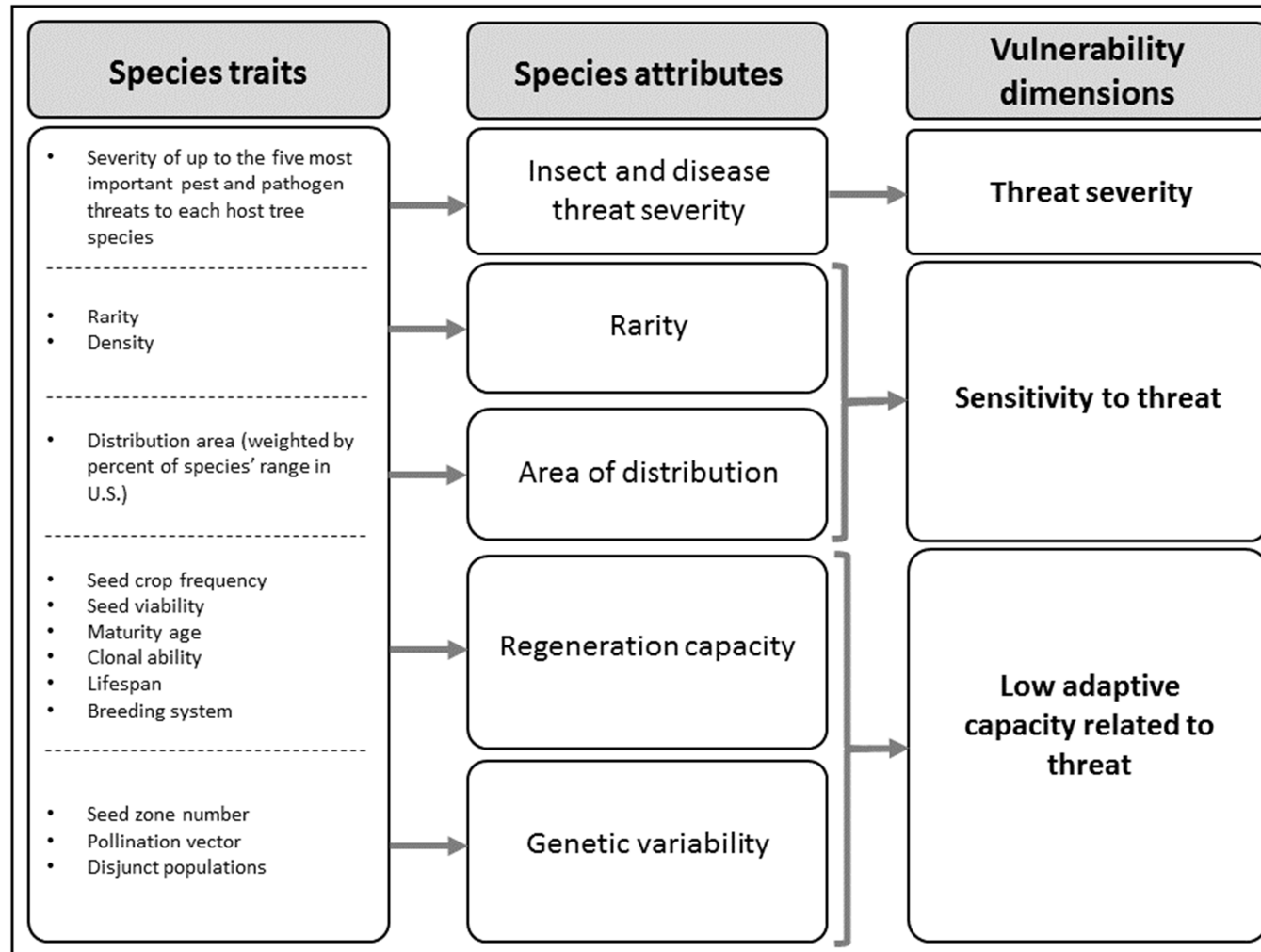
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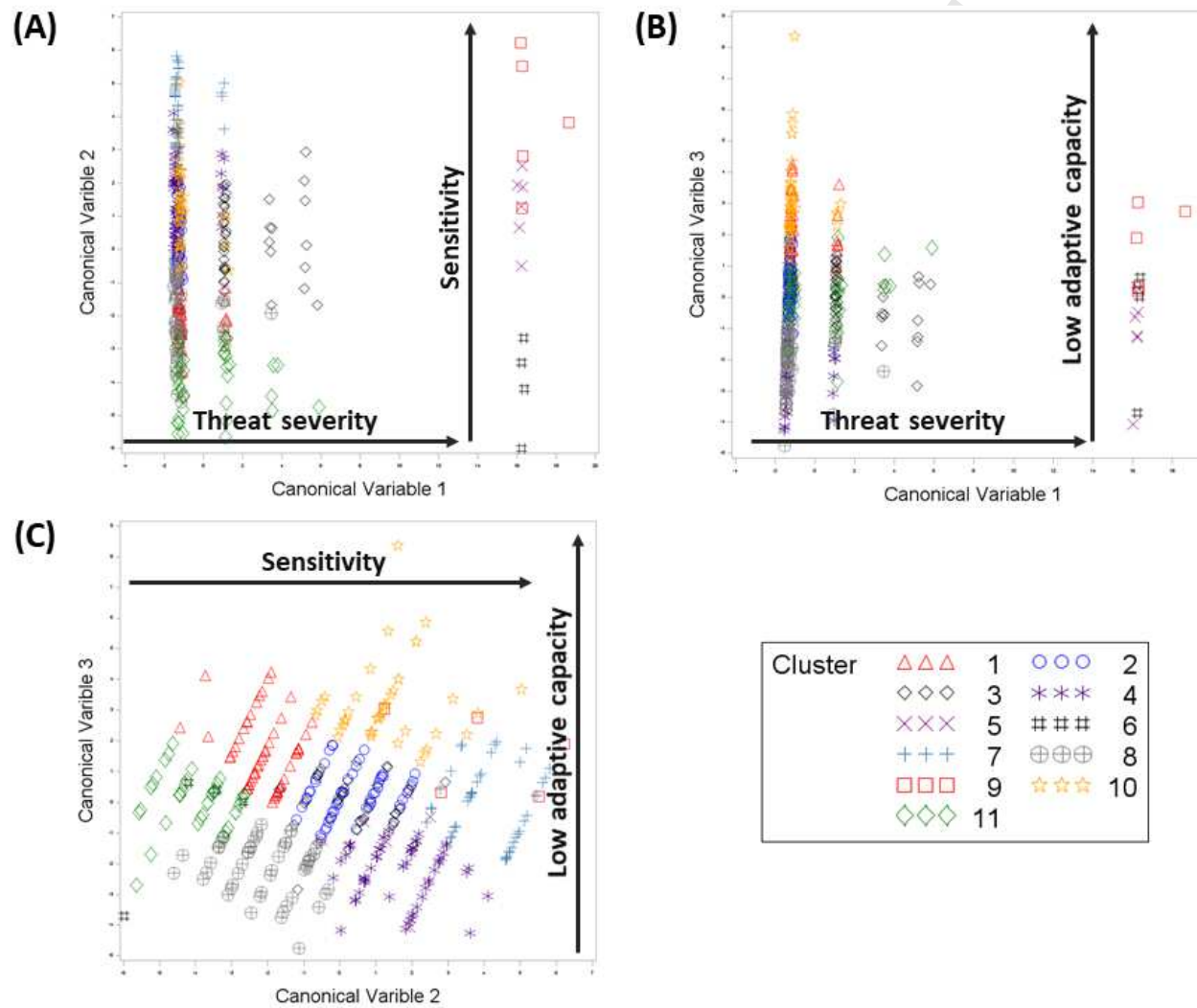
918 **Figure 2**

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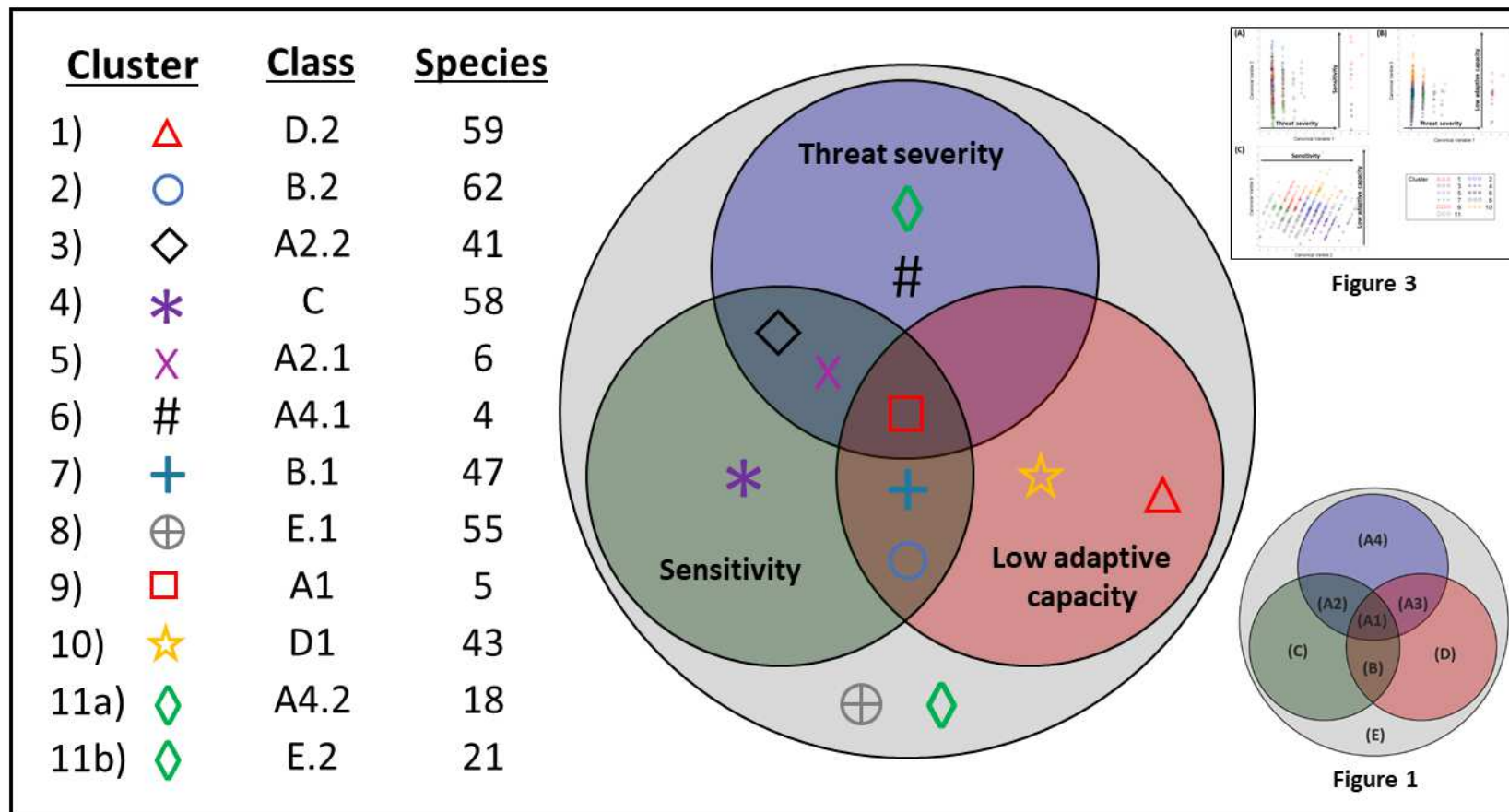
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921 **Figure 3**
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924 **Figure 4**
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Appendix 1: Calculations of Tree Trait Values and Attributes

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 (Figure 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 (Figure 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 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 desiccation-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 hectares and at least 50 kilometers from the nearest population greater than 250,000 hectares. 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.

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Highlights:

- U.S. tree species separate into 11 groups based on insect and disease vulnerability
- Three groups encompassed 15 vulnerable species requiring immediate intervention
- Efforts to conserve the genetic diversity of these most vulnerable species are uneven
- Two groups face less severe threats and would benefit from resistance breeding
- Two other groups are vulnerable to future threats and therefore need close monitoring