Biological Conservation 224 (2018) 34–46

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Do United States protected areas effectively conserve forest tree rarity and evolutionary distinctiveness?

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ARTICLE INFO

Keywords:
Biodiversity
Biogeography
Conservation biology
Evolution
Prioritization
Protected areas

ABSTRACT

Because forest tree species face serious threats including insect and disease epidemics, climate change, and forest fragmentation and conversion, prioritizing species and forests for conservation is an essential management goal. This paper describes a species prioritization approach that incorporates both the rarity of species, because of the increased vulnerability associated with rare species, and their evolutionary distinctiveness (ED), a measure of evolutionary originality. Rarity and ED scores, and scores for the two combined, were calculated for 352 North American forest tree species. A weak but significant phylogenetic signal was associated with species rarity. The scores were used to weight species importance values on approximately 130,000 forest inventory plots across the conterminous United States. The resulting plot-level estimates of conservation value were employed to identify geographic hotspots of forests with high conservation value, and to assess whether forests with protected status effectively conserve rarity and ED. Rarity hotspots were detected in California, the Southwest, central Texas, and Florida. Hotspots of ED included locations along the Pacific Coast, in the Northern Rockies, and in scattered eastern locations. Protected forest areas across the United States effectively conserve ED, but not rarity. In fact, rarity was lowest in areas with the highest protection, and highest in areas with no or unknown protected status. Multiple-use protected areas had higher ED, but not rarity, than restricted-use protected areas. Protected area effectiveness varied across the country. Such spatially explicit assessment approaches can help determine which forests to target for monitoring efforts and pro-active management activities.

1. Introduction

The need to conserve forests and their constituent tree species is acute, widespread, and increasingly urgent. Globally, species extinction rates currently exceed the background rate of extinction by approximately 1000 times (Pimm et al., 2014), and are coupled with an alarming trend of population declines and extirpations (Ceballos et al., 2017). Several factors threaten the future integrity of forest tree populations, including forest fragmentation and conversion (Asner et al., 2009; Riitters et al., 2016), drought and other changing climatic conditions (Fettig et al., 2013; van Mantgem et al., 2009; Woudenberg et al., 2010), nonnative insect and disease infestations (Dukes et al., 2009; Ramsfield et al., 2016), and changes in wildfire intensity and frequency (Nowacki and Abrams, 2008). Trees and other plants provide numerous essential ecosystem services, such as water catchment sustainability, carbon sequestration, and erosion control, and deliver many economic, cultural, scientific, and social benefits (FAO, 2014b; Millennium Ecosystem Assessment, 2005). These underscore the necessity of securing the conservation and sustainable use of trees and other plants (Sharrock, 2012). The funding, personnel and time needed to enable the effective conservation of tree species will almost certainly be insufficient to respond to all conservation needs, however. Rational, systematic, and defensible methods are therefore required to prioritize species for conservation (Bottrill et al., 2008; Millar et al., 2007).

Because conservation resources are scarce, conservation practitioners have been successful in developing priority lists of species most in need of those resources (Mace et al., 2007). The process of prioritizing vascular plant species varies both in complexity and in the number of factors that efforts encompass to reflect different conservation objectives (e.g., Barazani et al., 2008; Coates and Atkins, 2001; Farnsworth et al., 2006; Gauthier et al., 2010; Jimenez-Alfaro et al., 2010; Larkin et al., 2016; Potter et al., 2017a). The current paper proposes a prioritization approach that incorporates the geographic rarity of species and their evolutionary distinctiveness, two factors that are highly useful for informing conservation prioritization efforts at biogeographic scales (Cadotte and Davies, 2010; Jetz et al., 2014; Rosauer et al., 2009; Tucker et al., 2012; Veron et al., 2017). The first of these serves as a proxy for extinction risk, while the second is a measurement of the evolutionary originality of a species, and thus may reflect the potential for species to possess rare traits and to provide

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https://doi.org/10.1016/j.biocon.2018.05.007
Received 15 September 2017; Received in revised form 30 April 2018; Accepted 11 May 2018

unusual or unique ecosystem services (Faith, 1992; Pavoine et al., 2005; Vane-Wright et al., 1991). Additionally, evolutionary originality and rare traits may contribute to the adaptive potential of natural communities in the face of environmental change (Cadotte and Davies, 2010; Forest et al., 2007). In this paper, geographic rarity and evolutionary distinctiveness are combined with a national network of systematically sampled forest plots to assess whether forests in protected areas of the United States are representative of rarity and evolutionary distinctiveness across all forests.

While many traits may contribute to tree species' vulnerability to extinction or extirpation (Myking, 2002; Potter et al., 2017a; Sjostrom and Gross, 2006), rarity is widely understood to correlate strongly with extinction risk (Gaston, 2008; Lavergne et al., 2005; Mace et al., 2008). It is important to note, however, that rarity encompasses multiple facets that vary across scales, from geographic range size at the broadest scale, to habitat specificity at medium scale, and to local density at the finest scale (Hartley and Kunin, 2003; Rabinowitz, 1981). Relying on only one of these facets, such as range size, may provide misleading information on the conservation status of species (Bland et al., 2015; Rondinini et al., 2006). Rarity at different scales, meanwhile, is associated with different extinction processes (Hartley and Kunin, 2003). Broad-scale rarity for example, is a greater concern in the face of broad-scale threats such as climate change; geographic distribution, in fact, is a strong predictor of extinction probability (Stork et al., 2009), including in response to changing climatic conditions (Brook et al., 2008; Parmesan, 2006). At medium to small scales, rare species by definition encompass fewer individuals and/or fewer populations than common species (Jump and Penuelas, 2005), which means that a greater proportion of individuals within the species may be susceptible to elimination by localized random events. They also tend toward lower genetic diversity and gene flow, and therefore a reduced ability to adapt to environmental change (Willi et al., 2006). Range restricted tree species, in particular, are more likely than other plant species to be threatened because they are more likely to have a narrow habitat tolerance (Bradshaw et al., 2008; Stork et al., 2009). The loss of rare species is a concern because both theoretical and experimental studies indicate that rare species play an important role in ecosystem functioning (Gascon et al., 2015). Rare species often possess the most distinct combinations of traits both locally and regionally, thus disproportionally increasing the variety of potential ecosystem functions across spatial scales and underscoring their conservation importance (Mouillot et al., 2013). A national, high-intensity inventory of species occurrences can lay the foundation for an assessment of the multiple rarity facets of individual species. The Forest Inventory and Analysis network of approximately 140,000 plots, coordinated and maintained by the United States Department of Agriculture (USDA) Forest Service, is such an inventory, with a standard plot design and an unbiased spatial sample at a relatively high intensity across the conterminous United States (Bechtold and Patterson, 2005; Woudenberg et al., 2010).

In addition to taxonomic rarity, greater conservation priority is also justified for species with higher evolutionary distinctiveness, a measure of evolutionary originality of species that is determined by partitioning the branch lengths of a phylogenetic supertree among the constituent species based on their location on the tree (Isaac et al., 2007; Redding and Mooers, 2006). Species with high evolutionary distinctiveness (ED) may be more likely to possess unique or rare morphological or ecological traits and provide unusual ecosystem functions (Faith, 1992; Gascon et al., 2015; Vane-Wright et al., 1991), although this is not always the case (Grandcolas et al., 2014). The ecological impact of the loss of species from older and species-poor clades therefore may be higher than that of younger species in clades containing many species (Mace et al., 2003). At the same time, the loss of younger and more common species also may have important ecological impacts (Gaston, 2008), although closely related species are more likely to possess redundancy of the same or similar traits. Prioritizing the preservation of ED, while considering other criteria such as species vulnerability (Larkin et al., 2016), is therefore one strategy for allowing ecosystems to adapt and diversify in a changing and uncertain future (Cadotte and Davies, 2010; Veron et al., 2017).

These species-level taxonomic rarity and ED metrics should be valuable for guiding decisions about which species may need conservation attention. At the same time, these metrics also can inform conservation management within a spatial context when intersected with standardized inventory data collected from species assemblages across broad regions. Specifically, information about the relative dominance of each species in a community can be combined with rarity and ED metrics to generate plot-level conservation-weighted importance values, which, when summed for each plot, can then be utilized in broad-scale conservation assessments. This approach should be useful, for example, to evaluate the degree to which protected areas conserve the full range of biodiversity in a region (Gaston et al., 2008; Margules and Pressey, 2000). In the context of assessing biodiversity representativeness, conservation-weighted importance values can be applied to test whether the rarity and evolutionary distinctiveness of tree species encompassed within the protected areas of a region approximate these features of forests outside of protection.

The effective preservation of forest tree species will require coordinated on-site (in situ) conservation activities, such as reserve establishment and management, because they are the most likely to maintain the full range of species' of genetic diversity while allowing for the dynamic unfolding of evolutionary processes within species (Rajora and Mosseler, 2001), although off-site (ex situ) efforts such as conservation seed collections and botanical garden plants also should play a role. In situ conservation also allows for the simultaneous conservation of multiple species while maintaining the ecological, cultural and aesthetic values of those species (FAO, 2014b). Reflecting the importance of in situ conservation, the Food and Agricultural Organization (FAO) of the United Nations has determined that a strategic priority in its Global Plan of Action for the Conservation, Sustainable Use and Development of Forest Genetic Resources should be strengthening the contribution of primary forests and protected areas to in situ conservation (FAO, 2014a). It is uncertain, however, whether existing in situ reserves adequately protect tree species and are sufficient for future conservation needs (Potter et al., 2017b). Another important knowledge gap is the relative ecological performance of protected areas with differing levels of protection and kinds of management (Gaston et al., 2008). Given that the United States has one of the oldest and most sophisticated systems of protected areas in the world, as well as relatively high levels of resources potentially available for conservation, one would expect that it has effectively conserved its biodiversity (Jenkins et al., 2015).

This paper proposes a spatially explicit assessment of whether protected forest reserves in the conterminous 48 United States effectively conserve forest tree rarity and evolutionary distinctiveness. Tree rarity and ED are defined using a species prioritization approach applied to 352 native North American forest tree species, with resulting species-level scores that are used in combination with a national network of standardized inventory plots to conduct the assessments. Specifically, the paper describes the use of a species-level Rarity Index (RI), Evolutionary Distinctiveness (ED), and a Rarity-Evolutionary Distinctiveness Index (REDI) that combines RI and ED. These indices are used to weight species importance values on tens of thousands of Forest Inventory and Analysis (FIA) plots across the conterminous 48 United States. When summed on each plot, these weighted importance values represent an estimate of the plot's conservation importance. The plot estimates are then used to identify statistically significant geographic hotspots and coldspots of forest conservation value. They also are employed to determine whether protected forests conserve greater rarity and ED than do unprotected forests, by testing whether mean plot-level conservation-weighted importance values (RI_p, ED_p, and $REDI_p$) are significantly higher or lower on protected plots. A similar analysis was conducted to assess whether restricted use protected areas, such as national parks and wilderness areas, conserve greater rarity and ED than protected areas that allow multiple, and potentially extractive uses, such as National Forest System (NFS) and Bureau of Land Management (BLM) general public lands.

2. Materials and methods

2.1. Tree occurrence data

The Forest Inventory and Analysis (FIA) Program is the primary source of information about the extent, condition, status and trends in United States forest resources across all ownerships (Smith, 2002). FIA data are an unparalleled source of tree location information in the United States because the FIA program maintains a national network of approximately 135,000 fixed-area forested plots (each approximately 0.067 ha) from which tree inventory data are collected in a consistent manner and on a regular basis (Woudenberg et al., 2010). The FIA national sample intensity is approximately one plot per 2428 ha (Bechtold and Patterson, 2005), encompassing accessible forest land across the conterminous 48 United States and southeastern Alaska. Given this design, FIA data should provide unbiased measures of tree occurrence frequency across broad scales, and should avoid the sparse intensity and spatial bias issues often associated with species point occurrence data (Rondinini et al., 2006). Because FIA plots are based on an unbiased spatial sample and are not at an extremely fine sampling intensity (Bechtold and Patterson, 2005; Woudenberg et al., 2010), they are unlikely to encompass the rarest of tree species. This could be considered an omission error, but, given the robust statistical design of the plot network, these missed species can be categorized as the rarest of the rare by virtue of the fact they are not encountered on any plots. FIA field crews have a list of 352 native tree species and varieties they are asked to inventory on each plot; of these, 32 species (9.1%) were not recorded on any plot.

Each FIA plot includes four 7.2-m-fixed-radius circular subplots in a triangular arrangement with one plot in the center, and with plot centers spaced 36.6 m apart (Woudenberg et al., 2010). Field crews collect data on a wide variety of variables, including the species, size and condition of all trees with a diameter of at least 12.7 cm on forested subplots (Smith, 2002; Woudenberg et al., 2010). Inventory data are publicly available. Initial annual inventory plots were established between 1999 and 2005, with plots remeasured every five to seven years in the eastern United States and every 10 years in the West. The FIA program defines tree species as 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 supported by vegetation or other structures (i.e., not vines). It generally follows the taxonomy of the United States Department of Agriculture's PLANTS database (U.S. Department of Agriculture Natural Resource Conservation Service, 2017).

The current assessment encompasses 133,802 FIA plots for which the most recent data were available in early 2017, with approximately 74% of the plots inventoried during the timeframe of 2010 through 2015. The analyses described here assess the relative rarity and evolutionary distinctiveness of each of 352 native United States tree species and varieties inventoried by the FIA program, and a combined index of rarity and ED. The Rarity Index (RI), Evolutionary Distinctiveness (ED) and Rarity/Evolutionary Distinctiveness Index (REDI) scores for each species were then used to assess plot-level forest conservation value across the FIA plots. Briefly, the index values for each species were scaled from 0 to 100, with 100 being the highest conservation score and 0 the lowest, and were multiplied by each species' plot-level importance value (on a scale of 0–1), a measure of its dominance within a community. These species' conservation-weighted importance values were then summed for each plot to calculate plot-level measures of conservation value, RI_p, EDI_p, and $REDI_p$. (The plot-level statistics are described in detail below.) These were applied to identify geographic hotspots of forest conservation value, and to assess whether there are significant differences in plot-level conservation-weighted importance values between protected and unprotected forests.

2.2. Calculating rarity

In her classification of rarity, Rabinowitz (1981) focused on three aspects that are each broadly related to a different scale of analysis: geographic range size (broad), habitat specificity (medium), and local density (fine), with different scales associated with different extinction processes (Hartley and Kunin, 2003). For this assessment, a Rarity Index (*RI*) was determined for each of the 352 tree species, incorporating national area of distribution (A) as a broad-scale indicator of rarity, national rarity of occurrence (R_N) as a medium-scale indicator of habitat specificity, and local rarity (R_L) as a fine-scale indicator of species density. The index was calculated for each species as the mean of A and R_N, each weighted by endemicity (E), and R_L:

$$RI = \frac{(E(A + R_N)) + R_L}{3}$$

A was calculated as the area of each tree species' occurrence in the United States, based on E.L. Little's forest tree species distribution maps (United States Geological Survey, 1999) or based on digitized versions of in the Flora of North America North of Mexico (Flora of North America Editorial Committee 1993 +) when such maps did not exist from Little. These maps estimate the distributions of species North America, Central America, and the Caribbean. R_N was calculated as the percent of the total FIA plots on which each species was inventoried (its relative frequency nationally). R_L was calculated as the mean number of stems of a given tree species on the FIA plots on which that species occurs, with saplings (between 2.54 and 12.7 cm diameter at breast height) given a weight of 0.5. All three scores were converted to a scale of 0 to 100 so the most common or widespread species had a score of 0 and the least common or least widespread a score of 100. The A and R_N values (each a measurement at the national scale) were weighted by endemicity (E), determined by the percent of each species' range that occurs within the United States. Endemicity, also called “regional responsibility”, is often incorporated in conservation assessments because it allocates the appropriate amount of conservation effort for a species based on the degree to which it is associated with a region of interest (Gauthier et al., 2010; Kricsfalusy and Trevisan, 2014; Schmeller et al., 2008). Because R_L is a local metric, it was not similarly weighted.

2.3. Quantifying evolutionary distinctiveness

Evolutionary Distinctiveness (*ED*) was determined for each of the 352 species. *ED* was quantified using the fair-proportion method of Isaac et al. (2007), which calculates the evolutionary originality of species by partitioning to them the sum of the branch lengths of a phylogenetic supertree encompassing all the species in the assessment (the total phylogenetic diversity represented by all the species). Specifically, each branch length in the supertree was given a value equal to its length divided by the number of species subtending the branch; each species' *ED* was calculated as the sum of these values for all branches from which it is descended, to the root of the phylogeny (Isaac et al., 2007). The *ED* metric, therefore, does not double-count any of the phylogenetic diversity represented in the supertree. It was calculated in the package picante (Kembel et al., 2010) in R version 3.3.0, using a hypothesized phylogenetic supertree of the North American forest tree species included in the assessment (Fig. 1). This reference phylogeny, with branch lengths measured in millions of years, was constructed based on a review of 189 molecular systematics and paleobotanical studies (Appendix 1, 2).

Pearson correlations among the indices, and among the components of the Rarity Index, were calculated across species using the CORR

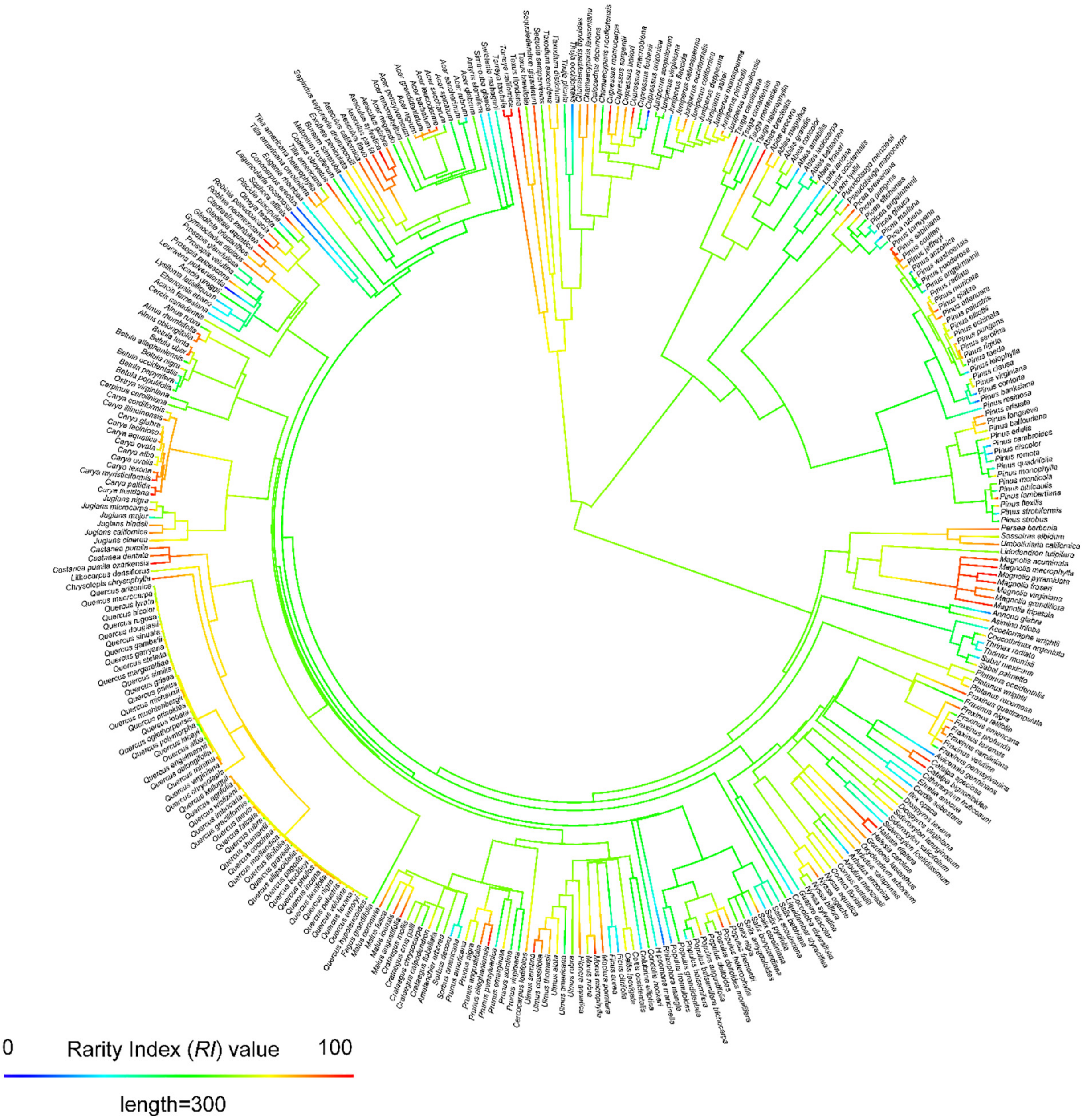

Fig. 1. The phylogenetic supertree of 352 native North American forest tree species included in the assessment, with branch lengths measured in millions of years. The colors depict Rarity Index (*RI*) scores for each species interpolated throughout the branches of the tree.

procedure in SAS 9.4 (SAS Institute Inc., 2013). Using the R package picante (Kembel et al., 2010), Blomberg's K statistic of phylogenetic signal (Blomberg et al., 2003) was calculated for the Rarity Index and its components. The statistical significance of the phylogenetic signal was assessed by comparing observed values to null values obtained when shuffling taxa labels across the tips of the phylogeny. The R package phytools (Revell, 2012) displayed the traits on the phylogenetic supertree encompassing the 352 species in the assessment.

A Rarity and Evolutionary Distinctiveness Index (*REDI*) of conservation value was calculated for each species as the product of *RI* and *ED*, so that, similar to Redding and Mooers (2006), it represents the potential loss of evolutionary history associated with each species, measured in millions of years:

$$REDI = \left(\frac{RI}{100}\right) * ED$$

ED and REDI were rescaled to 0 to 100, with 100 equating to the highest evolutionary diversity and 0 the lowest, for plot-level assessments of conservation value (below). Species ED and REDI were not rescaled.

2.4. Assessing forest conservation value

It was next possible to assess plot-level forest conservation value, for each of 132,673 plots, using all three metrics by first calculating the importance value (IV) of each species on a given plot. IV is a measure of a species' dominance within a community that often incorporates the number and size of the trees of that species within the community (Smith and Smith, 2001). Here, it is calculated as the mean of the species' abundance and basal area on the plot (each on a scale of 0 to 1) relative to the abundance and basal area of all species on the plot. Each species' IV was then weighted separately by its *RI*, *ED*, or *REDI* scores. The species' conservation-weighted importance values were then summed for each plot to calculate plot-level measures of conservation

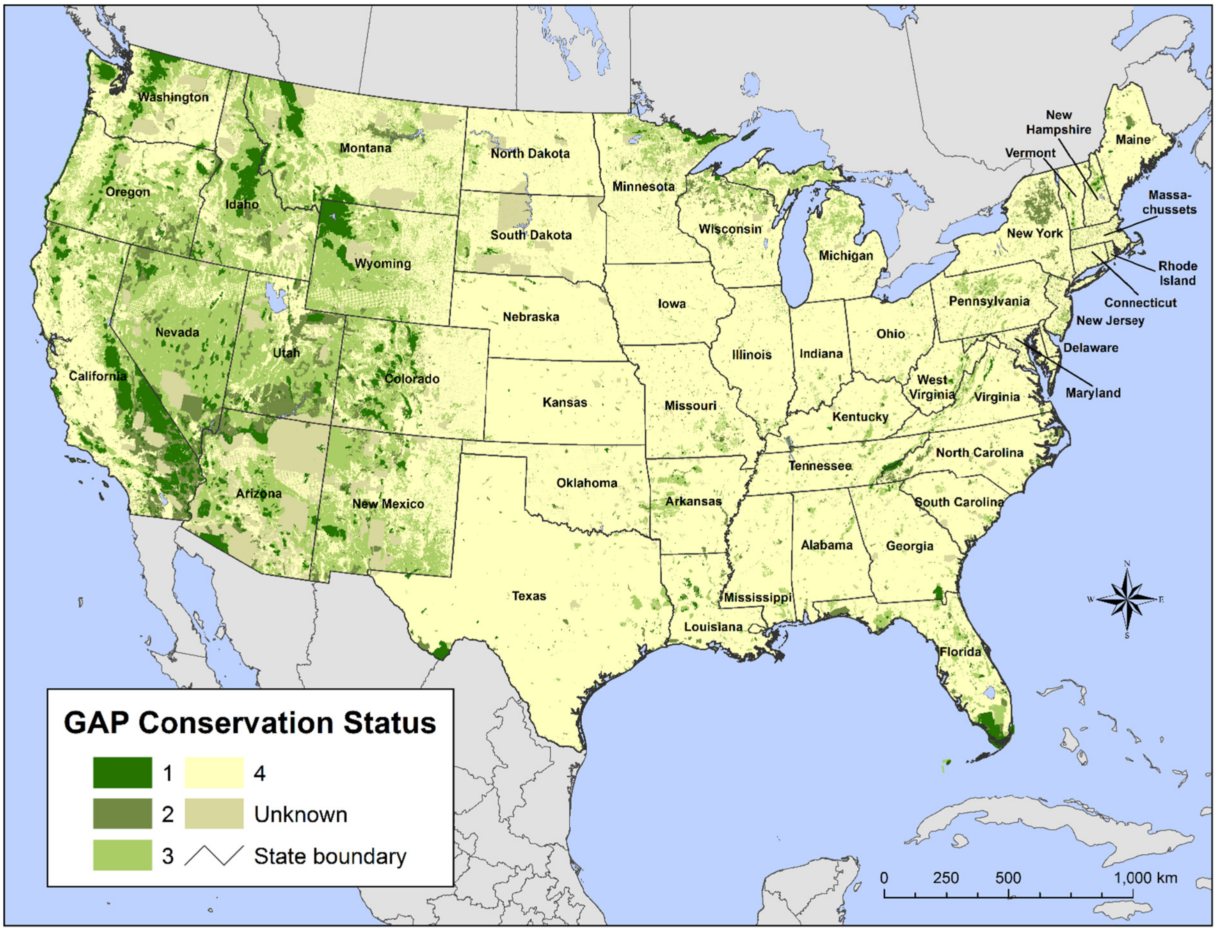

Fig. 2. Map of United States Gap Analysis Program (GAP) conservation status. (Data from the Conservation Biology Institute, 2016).

value:

$$RI_p = \sum_{i=1}^{n_p} \left(RIS_i * \left(\frac{RA_{ip} + RBA_{ip}}{2} \right) \right)$$

$$ED_p = \sum_{i=1}^{n_p} \left(EDS_i * \left(\frac{RA_{ip} + RBA_{ip}}{2} \right) \right)$$

$$REDI_p = \sum_{i=1}^{n_p} \left(REDIS_i * \left(\frac{RA_{ip} + RBA_{ip}}{2} \right) \right)$$

where

n_p = the number of species on plot p

RI_p = the summed rarity index weighted importance values for the species on plot p

ED_p = the summed evolutionary distinctiveness weighted importance values for the species on plot p

$REDI_p$ = the summed rarity and evolutionary distinctiveness index weighted importance values for the species on plot p

RIS_i = rarity index score for species i, scaled across species from 0 to 100

EDS_i = evolutionary distinctiveness score for species i, after scaling across species from 0 to 100

$REDIS_i$ = rarity-evolutionary distinctiveness index score for species i, after scaling across species from 0 to 100

RA_{ip} = the relative abundance for species i on FIA plot p, calculated as $RA_i = \frac{TPA_i}{TPA_{total}}$, where TPA_i is the trees per acre represented by the species on the plot, and TPA_{total} is the total trees per acre represented by the plot

RBA_{ip} = the relative basal area of species i on FIA plot p, calculated as $RBA_i = \frac{BA_i}{BA_{total}}$, where BA_i is the basal area of the species on the plot, and BA_{total} is the total basal area present on the plot

The plot RI_p, ED_p, and $REDI_p$ values, with each scaled from 0 to 100, were used to identify areas in the conterminous 48 States with higher or lower plot-level forest conservation values than expected by chance using the Spatial Association of Scalable Hexagons (SASH) analytical approach (Potter et al., 2016). This method divides the region of interest into equal-area hexagonal cells optimal for spatial neighborhood analysis, aggregates data into these cells, and then employs a Getis-Ord (G_i*) hotspot analysis (Getis and Ord, 1992) in ArcMap® 10.1 (ESRI, 2014) to identify locations with higher- or lower-than-expected values of an indicator of interest. In this case, the mean plot-level conservation metrics were calculated for each of 6420 hexagonal cells approximately 834 km^2 in area, generated in a lattice across the conterminous United States based on the Environmental Monitoring and Assessment Program (EMAP) North American hexagon coordinates (White et al., 1992). This hexagon area is manageable for making monitoring and management decisions in nationwide analyses (Potter et al., 2016). Hexagons containing fewer than four FIA plots were excluded from the analysis. The G_i* statistic sums the differences between the mean values in a local sample, determined in this case by a moving window of each hexagon with its six immediate neighbors and the global mean of all the forested hexagonal cells in the conterminous 48 States. G_i* is a standardized z-score with a mean of 0 and a standard deviation of 1, with values $>$ 1.96 representing significant spatial clustering of greater mean plot-level conservation scores ($p < 0.025$) and values < -1.96 representing significant spatial clustering of lower plot-level conservation scores ($p < 0.025$), because 95% of the observations under a normal distribution should be within approximately 2 standard deviations of the mean (Laffan, 2006).

Additionally, Pearson correlations among the plot-level importance-weighted conservation indices (RI_p, ED_p, and $REDI_p$) were calculated in SAS 9.4 (SAS Institute Inc., 2013).

2.5. Comparisons across protected area classifications

The plot-level conservation metrics were intersected with a map of the official U.S. national inventory of protected area status (Conservation Biology Institute, 2016) to test whether significant differences existed between the conservation value of protected and unprotected forests, and of forests with different degrees of protected status. This dataset encompassed 132,673 FIA plots across the conterminous 48 United States. The plots were intersected in ArcMap® 10.1 (ESRI, 2014) with a map of United States Gap Analysis Program (GAP) conservation status (Fig. 2). GAP classifies the status of United States protected areas into four categories (United States Geological Survey, 2013):

- Status 1: An area having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a natural state within which disturbance events are allowed to proceed without interference or are mimicked through management.
- Status 2: An area having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a primarily natural state, but which may receive uses or management practices that degrade the quality of existing natural communities, including suppression of natural disturbance.
- Status 3: An area having permanent protection from conversion of natural land cover for the majority of the area, but subject to extractive uses of either a broad, low intensity type or localized intense type. It also confers protection to federally listed endangered and threatened species throughout the area.
- Status 4: An area where there are no known public or private institutional mandates or legally recognized easements or deed restrictions held by the managing entity to prevent conversion of natural habitat types to anthropogenic habitat types. The area generally allows conversion to unnatural land cover throughout, or the management intent is unknown.

While the International Union for the Conservation of Nature's World Database on Protected Areas is the global standard for recording protected area status (Juffe-Bignoli et al., 2014), it leaves much U.S. forestland unclassified, including a large proportion of federally owned land in the western half of the country, where most of the land is in federal ownership. The GAP data, on the other hand, assigns protected area status for most such areas, including National Forest System and Bureau of Land Management general public land, although some areas, such as Native American reservations and land under the jurisdiction of the U.S. Department of Energy and U.S. Army Corps of Engineers, are assigned an "unknown" conservation status. GAP also provides a somewhat more streamlined classification, with only three protected area classifications (and one "unprotected" designation) compared to seven by IUCN (and no designation for the absence of protection). Table 1 provides a comparison between the IUCN and GAP conservation designation systems.

To test the null hypotheses that there was no significant difference in plot-level conservation-weighted importance values between protected and unprotected status of forest plots in the continental United States, and between plots of differing levels of protection, a set of exact two-sample Wilcoxon rank-sum tests (Conover, 1971) was conducted using the NPAR1WAY procedure in SAS 9.4 (SAS Institute Inc., 2013), with p-values generated by 10,000 Monte Carlo runs. The first of these compared protected (GAP Status 1, 2 and 3) to unprotected (GAP Status 4). The second compared "restricted use" designations not subjected to potential extractive uses (GAP Status 1 and 2) to the "multiple use" designation that can allow for extractive uses (GAP Status 3). FIA plots located within areas of "Unknown" conservation status were excluded from these analyses. Mean plot-level conservation-weighted importance values also were calculated for the four protected area statuses (and the "Unknown" status), with a multiple sample Kruskal-Wallis test in the NPAR1WAY procedure in SAS 9.4 used to test whether the groups were significantly different. Additionally, the first analysis described above was repeated separately for the 10% of the plots (excluding those with "Unknown" conservation status) with the highest RI_p, ED_p, and $REDI_p$ scores, respectively. This allowed for an assessment of the proportion of these plots with the greatest conservation value that were in either protected or unprotected forests.

To evaluate regional differences in the association between conservation value and protected status, the Wilcoxon rank-sum tests described above were repeated for the plots within each of 11 broad ecoregion divisions delineated to reflect large ecological climate zones (Cleland et al., 1997; Cleland et al., 2007). Similarly, Kruskal-Wallis multiple sample tests were conducted for each ecoregion division to assess significant differences among the protected area classes.

3. Results

3.1. Species-level conservation value assessments

Across the 352 North American tree species encompassed by the assessment, RI and ED were weakly and negatively correlated ($r = -0.169$, $p = 0.0014$) (Supplementary Fig. 1). REDI was positively correlated with both ($r = 0.351$ with RI and $r = 0.799$ with ED; $p < 0.0001$ for both).

RI values (Supplementary Table 1) ranged from 0 for great leadtree (*Leucaena pulverulenta*) and 6.29 for Arizona cypress (*Cupressus arizonica*), which are both species with large distributions that barely extend into the United States, to 100 for a set of very rare species that occur entirely within the borders of the U.S. (Virginia roundleaf birch [*Betula uber*], bristlecone fir [*Abies bracteata*], Torrey pine [*Pinus torreyana*], Monterey cypress [*Cupressus macrocarpa*], and Florida yew [*Taxus floridana*].) The mean for RI was 67.06, and the median was 75.98 (Table 2).

None of the three variables that constituted RI were highly correlated with each other ($r = 0.156$ for R_N and R_L; $r = 0.511$ for R_N and A; $r = -0.181$ for R_L and A; all $p < 0.05$), indicating that each of these variables quantifies a different facet of rarity. For R_N, tree species occurred on 1745.7 FIA plots on average, with a minimum of 0 (for 32 species too rare to be detected using a spatially unbiased sample) and a maximum of 34,601 (for red maple [*Acer rubrum*]) (Table 2). For R_L, the mean number of trees per plot was 4.11 across species, ranging from 0 to 22.06. The species, on average, covered approximately 61 million ha (A), ranging from about 6000 to 420 million ha, and had 75% of their distribution within the United States (E).

ED values ranged from 4.02 MY for a set of four closely related white oak species to 170.44 MY for giant sequoia (*Sequoiadendron giganteum*) and coast redwood (*Sequoia sempervirens*). The mean and the median for ED were 37.179 and 31.98, respectively.

Giant sequoia had the highest REDI score (156.95 MY), which was not surprising as it ranked highly for both RI and ED. Other species with high REDI scores included Florida yew (134.86), both Florida torreya (*Torreya taxifolia*) and California torreya (*Torreya californica*) (104.24 and 99.57, respectively), coast redwood (103.59), and bristlecone fir (94.25). Several of the species with the lowest scores are relatively common species outside the U.S. but with small ranges in the country, including great leadtree (0), netneaf oak (*Quercus rugosa*) (0.59),

Table 1
Comparison of the IUCN World Database on Protected Areas and the United States Gap Analysis Program (GAP) conservation designation systems.

IUCN category	GAP category	U.S. Protected Area Designation
Ia: Strict Nature Reserve	1	Federal Wilderness Area, Research Natural Area, State Nature Preserve/Reserve
Ib: Wilderness Area	2	Biosphere Reserve, Wilderness Study Area, State Wilderness Area
II: National Park	1	National Park General Public Land
	2	State Park (< 5000 acres)
III: Natural Monument or Feature	2	National Monument (> 5000 acres), Botanical Area/Reserve, National Natural/Historic Landmark (> 5000 acres), National Scenic Area (> 5000 acres)
IV: Habitat/Species Management Area	2	National Wildlife Refuge, Old Growth Habitat, Wildlife Management Area, State Bird Sanctuary
V: Protected Landscape/Seascape	1	National Preserve, Wild River
	2	National Monument (< 5000 acres), National Parkway, National Natural/Historic Landmark (< 5000 acres), National Recreation Area, National Scenic Area (< 5000 acres), National Trail, Scenic Viewshed, Scenic River, State Botanical Area, State Conservation Area/Park, State Park (> 5000 acres), State Natural Area, Municipal Forest
	3	National Conservation Area, Recreation River, Wetland Reserve Program Land, State Open Space
VI: Protected Area with Sustainable Use of Natural Resources	3	Federal Experimental Forest, State Forest, Municipal Watershed, Waterfowl Production Area
Unassigned	1	Nature Preserve, Research or Demonstration Area, Research Natural Area
	2	Ecological Reserve, Environmental Study Area, Late Successional Reserve, National Historic Trail, Special Biological Area, Special Management Area, Wildlife Protection Area, State Game or Wildlife Sanctuary, Municipal Park, Private Conservation Holder Lands
	3	National Forest General Public Land, Military Reservation, Bureau of Land Management General Public Land, Managed Hunting Area, Scenic Byway, State Scenic Area, State Education Forest, State Research Forest, Municipal Open Space, Municipal Recreation Area
	4	Private Unprotected Land
	Unknown	Native American Reservation, Army Corps of Engineers Land, Department of Energy land, Tennessee Valley Authority Land, State University Land

See https://d2k78bk4kdhbpr.cloudfront.net/media/content/files/PADUS_CBIEdition_V2_DesignationCrosswalk.pdf for a more detailed crosswalk between the designation systems.

Table 2
Mean, standard deviation (SD), minimum and maximum for the three indices, and for the four components of the Rarity Index, across the 352 North American tree species included in the assessment.

Indices/scores	Mean	SD	Min	Max
Rarity Index (*RI*)	67.06	25.60	0	100
National rarity of occurrence (R_N)	1745.7	3601.8	0	34,601.0
Local rarity of occurrence (R_L)	4.11	3.54	0	22.06
National area of distribution (*A*)	60,934,286.9	84,107,444.5	6015.4	419,846,828.4
Endemicity (*E*)	75.07	34.10	0.20	100
Evolutionary Distinctiveness (*ED*)	37.17	28.49	4.02	170.44
Rarity/ED Index (*REDI*)	23.69	21.49	0	156.95

Notes: R_N, number of Forest Inventory and Analysis (FIA) plots on which species occurs; R_L, mean number of trees across plots on which species occurs; *A*, area of species distribution in United States, in hectares; *E*, percent of each species' total range in United States.

Mexican white oak (*Q. polymorpha*) (0.97), Mexican blue oak (*Q. oblongifolia*) (1.45), and slender oak (*Q. graciliformis*) (1.93). The median REDI score was 18.29 and the mean was 23.69.

A small but statistically significant phylogenetic signal was detected for the Rarity Index ($K = 0.021$, $p = 0.001$), and for its components R_L ($K = 0.029$, $p = 0.001$) and *A* ($K = 0.021$, $p = 0.001$), but not for R_N ($K = 0.011$, $p = 0.687$) (Supplementary Figs. 2–4). These results indicate that members of some evolutionary groups have similar levels of rarity. These include members of the *Torreya*, *Cupressus*, *Magnolia*, *Castanea*, and *Aesculus* genera, which mostly contained species with high *RI* values, while the *Sideroxylon* and *Salix* genera and parts of the Betulaceae and Fabaceae families and the Myrtales and Sapindales orders contained mostly species with low *RI* values (Fig. 1). Values of *A* were generally high (smaller distributional area) across gymnosperms, and for species of Arecaceae, Ericales, and Sapindales outside of *Acer*, while values were generally low (larger distributional area) for *Acer*, *Celtis*, and several species of *Carya* (Supplementary Fig. 3). For R_L, local rarity was generally higher (lower within-plot density) for angiosperms than for gymnosperms, with values particularly high in Magnoliaceae, Ulmaceae, and Rosaceae, and in *Salix*, *Carya*, and *Aesculus* (Supplementary Fig. 4).

Across the 132,673 FIA plots included in the analysis, the plot-level importance-weighted rarity and ED values (RI_p and ED_p) were weakly and negatively correlated ($r = -0.196$, $p < 0.0001$).

The Getis-Ord analysis identified statistically significant geographic hotspots of plot-level RI_p in the southern and western regions of the United States, including much of California, the Great Basin (Nevada and Utah), the southwestern States of Arizona and New Mexico, central Texas, and most of Florida (Fig. 3A). The hotspots of the highest RI_p values were located in central and northern California, and nearby central Oregon and southwestern Idaho. Geographic coldspots of RI_p were located in the Great Lakes States and in the Northeast, as well as in portions of the northern Rocky Mountains in Montana, Idaho, Wyoming, and Colorado. Hotspots of moderately high ED_p values were identified along the Pacific Coast from northern California through Oregon and Washington, as well as in northern Minnesota; the central Atlantic region; southern Louisiana and southern Florida; and in the northern Rocky Mountains of Washington, Idaho, and Montana (Fig. 3B). Significant coldspots of moderately low ED_p values were found in central California; southeastern Montana, northeastern Wyoming, and western South Dakota; the lower Midwest; south-central Texas; and the Gulf Coast of Florida. Finally, significant hotspots of very high $REDI_p$ values were identified along the Pacific Coast of northern California and in southern Florida, while hotspots of moderately high values were detected in the Great Basin, in eastern Kansas and western Missouri, western Tennessee, southern Louisiana, and a region from Delaware and Maryland through northern Georgia (Fig. 3C). Cold spots of relatively low $REDI_p$ values, meanwhile, were detected in southeastern Arizona; the Rocky Mountain states from Montana through Colorado; Texas; southern Missouri; the Northeast; and the Great Lakes States.

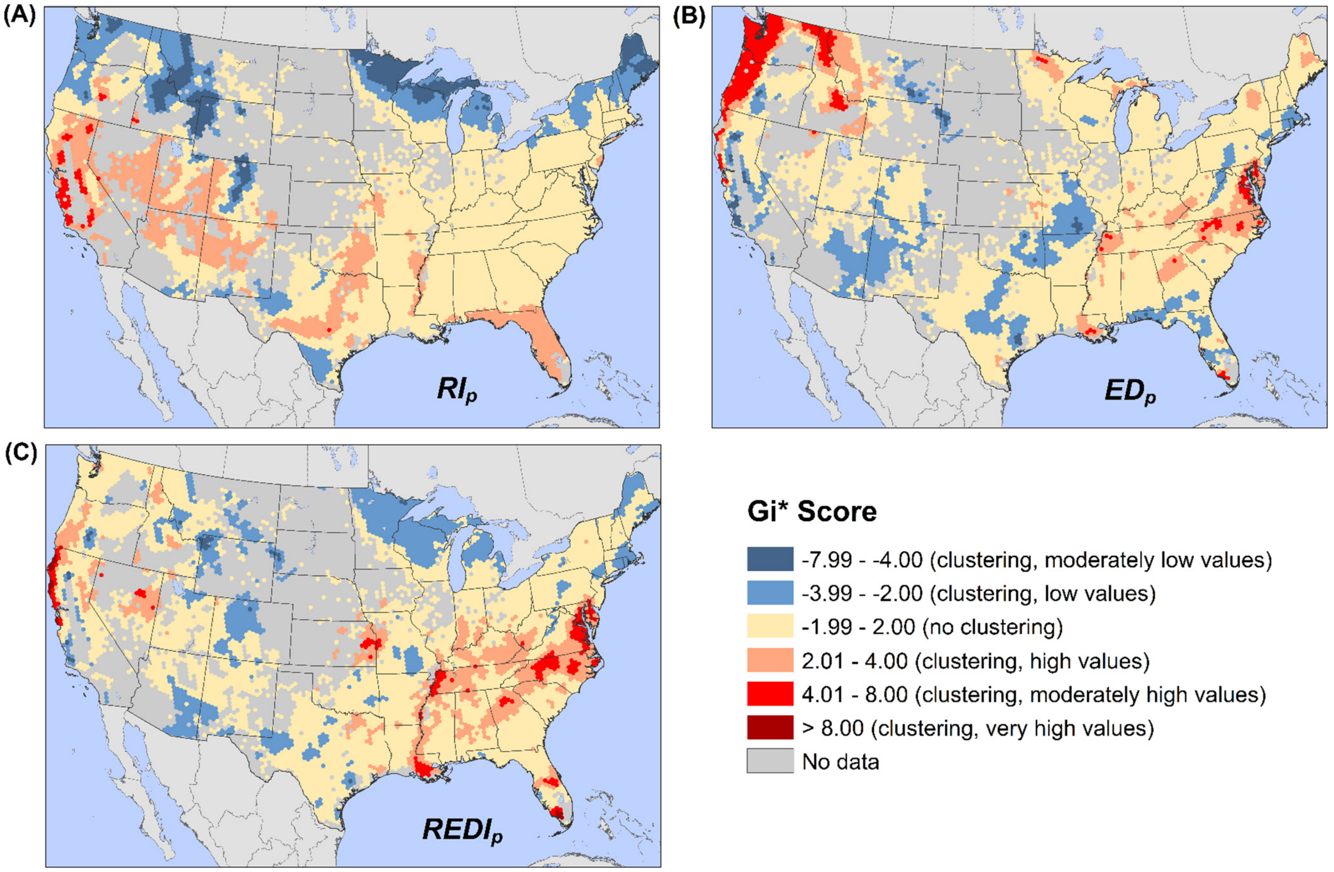

Fig. 3. Hotspots of forest tree rarity across the United States, from United States Department of Forest Service Forest Inventory and Analysis (FIA) data, using 6420 hexagons of approximately 834 km^2 in area. Values are Getis-Ord G_i* scores for mean plot-level importance values weighted by (A) Rarity Index (RI_p), (B) Evolutionary Distinctiveness (ED_p), and (C) Rarity and Evolutionary Distinctiveness Index ($REDI_p$). G_i* scores > 2 represent areas of significant clustering of high rarity values while scores less than −2 represent areas of significant clustering of low rarity values. See Fig. 2 for state labels.

3.2. Protected areas and rarity indices

About 36% of the FIA plots (n = 47,902) occurred on land with some degree of protection (GAP Status 1, 2 or 3), while about 60% were unprotected (GAP Status 4, n = 80,087). The protected status of about 4% was unknown (n = 4684). Mean plot-level conservation-weighted importance values (RI_p, ED_p, and $REDI_p$) were statistically different between plots on protected lands (GAP Status 1, 2 and 3) and those on unprotected private lands. Specifically, RI_p and $REDI_p$ were 9.58% and 9.47% higher, respectively, on unprotected plots (55.14 versus 50.32, and 11.91 versus 10.88; $p < 0.0001$ for both comparisons using two-sample Wilcoxon rank-sum tests). ED_p, however, was 5.39% higher on protected plots (19.15 versus 18.17, $p < 0.0001$).

Meanwhile, the means of two of the three conservation-weighted importance values were significantly higher on the 35,899 multiple use (Status 3) plots than on the 12,003 restricted use plots (Status 1 and 2). Specifically, RI_p was not significantly different (50.38 versus 50.12, $p = 0.073$), while ED_p and $REDI_p$ were significantly different (19.30 versus 18.71 [3.15%] and 10.89 versus 10.83 [0.55%], respectively; $p < 0.0001$ for both).

Differences among GAP Statuses for all conservation-weighted importance values were statistically significant at $p < 0.0001$, as determined by a multiple sample Kruskal-Wallis test. Among the four GAP statuses, the status with greatest protection (Status 1) had the lowest plot mean RI_p value (45.94), while unprotected areas (Status 4) had the highest mean plot RI_p value (55.14) (Table 3). Plots on land with unknown protected status, including mostly Native American tribal holdings along with lands administered by the U.S. Department of Energy and the U.S. Army Corps of Engineers, had an even higher mean RI_p (55.63). Alternatively, mean plot ED_p was highest in Status 1 forests (19.54), followed by multiple use forests (Status 3, 19.30) and lowest in Status 2 protected forests (17.97) and forests of unknown status (16.61). Mean plot $REDI_p$, incorporating both rarity and evolutionary distinctiveness, was highest in unprotected forests (11.91) and lowest in Status 1 protected forests (10.50) and in forests with unknown protected status (10.24).

Table 3
Mean Forest Inventory and Analysis (FIA) plot-level importance values, weighted by rescaled species Rarity Index (*RI*), Evolutionary Distinctiveness (*ED*), and Rarity-Evolutionary Distinctiveness Index (*REDI*) scores, across each of the four Gap Analysis Program (GAP) conservation designations, as well as for plots for which the conservation status is unknown. Differences among GAP Statuses for all conservation-weighted importance values were statistically significant at $p < 0.0001$ using a multiple sample Kruskal-Wallis test.

		RI_p		ED_p		$REDI_p$	
GAP status	FIA plots	Mean	SD	Mean	SD	Mean	SD
1	5617	45.94	20.71	19.54	9.99	10.50	7.05
2	6386	53.80	19.75	17.97	9.84	11.11	6.87
3	35,899	50.38	19.16	19.30	10.59	10.89	6.17
4	80,087	55.14	15.16	18.17	11.13	11.91	7.62
Unknown	4684	55.63	18.42	16.61	9.87	10.24	5.52

Additional analyses determined the degree to which protected areas (Status 1, 2 and 3) conserved plots with the 10% highest values for the three conservation-weighted indices. The results indicate that a majority of these plots are unprotected for all three indices: 53% for RI_p, 57% for ED_p, and 78% for $REDI_p$ (Table 4). The mean values for each

Table 4

Number and percent of Forest Inventory and Analysis (FIA) plots with the highest 10% of values for each of the conservation-weighted index values that are in protected and unprotected forests, and the mean and standard deviation of those index values; the means between protected and unprotected were significantly different according to Wilcoxon rank-sum tests.

	Protected				Unprotected				Difference
Index	n	Percent	Mean	SD	n	Percent	Mean	SD	*p*
RI_p	6007	46.94	79.55	3.68	6791	53.06	80.80	4.15	< 0.0001
ED_p	5449	42.58	38.40	5.63	7349	57.42	42.11	9.15	< 0.0001
$REDI_p$	2798	21.86	27.34	7.57	10,000	78.14	27.22	6.65	0.0001

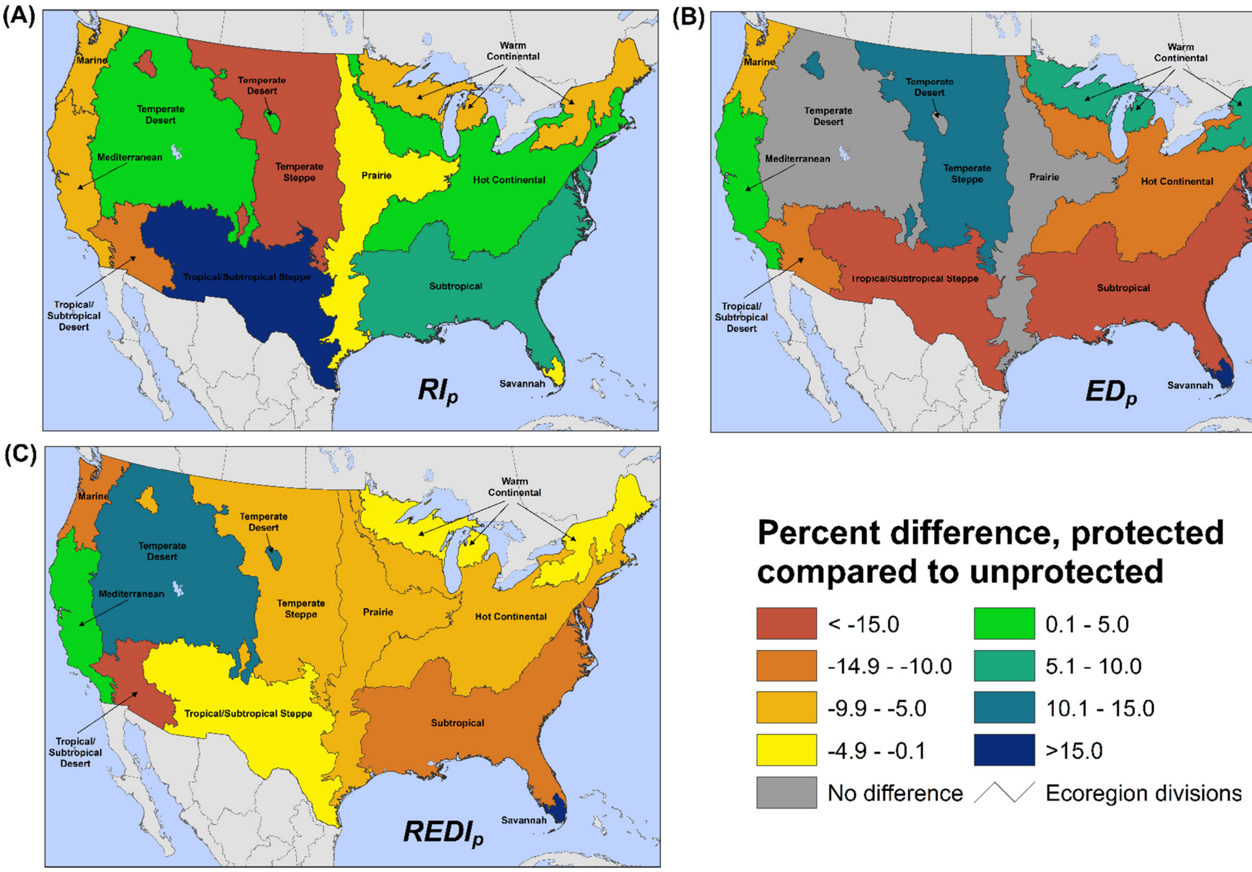

Fig. 4. Percent difference in Forest Inventory and Analysis (FIA) mean plot-level importance values weighted by (A) Rarity Index (RI_p), (B) Evolutionary Distinctiveness (ED_p), and (C) Rarity and Evolutionary Distinctiveness Index ($REDI_p$) between protected and unprotected areas within each of 11 ecoregion divisions in the conterminous United States. Significance differences were tested using Wilcoxon rank-sum tests. Conservation status was determined by the United States Gap Analysis Program (GAP) (Conservation Biology Institute, 2016).

were significantly higher on unprotected plots.

Regional variation was apparent in the mean plot-level differences between protected and unprotected forests for the conservation-weighted importance values (Fig. 4). RI_p was on average higher in protected forests in parts of the Eastern United States (the Hot Continental and Subtropical ecoregion divisions) and in the Interior West (Temperate Desert and Tropical/Subtropical Steppe), but was lower in protected forests elsewhere (Fig. 4A). ED_p was considerably higher in protected forests in California (Mediterranean ecoregion), the high plains (Temperate Steppe ecoregion), the Great Lakes and Northeastern region (Warm Continental), and southern Florida (Savannah ecoregion), but was considerably lower in forests throughout much of the East (Hot Continental and Subtropical ecoregions) and Southwest (the Tropical/Subtropical Desert and Tropical/Subtropical Steppe ecoregions) (Fig. 4B). Finally, $REDI_p$ was slightly higher in protected forests in parts of the West (the Mediterranean and Temperate Desert ecoregions) and in southern Florida, but was lower in protected forests throughout the rest of the country (Fig. 4C). In all but one division, the differences among GAP Statuses of the conservation-weighted importance values were statistically significant at $p < 0.05$. The single exception was the Prairie ecoregion, where $p = 0.3842$ for ED_p and 0.3289 for $REDI_p$.

4. Discussion

This conservation assessment prioritized 352 United States tree species by integrating an index of geographic rarity (RI), as a proxy of general species vulnerability, with evolutionary distinctiveness (ED), as an indicator of the likelihood that species possess unusual traits or provide rare ecosystem services. Because rarity encompasses multiple aspects that vary across scales (Rabinowitz, 1981), focusing on a single facet of rarity could result in conservation assessments that are misleading (Bland et al., 2015). Therefore, RI in this set of assessments incorporates national area of distribution (*A*), a broad-scale indicator of rarity; national rarity of occurrence (R_N), a medium-scale indicator of habitat specificity; and local rarity (R_L), a fine-scale indicator of species density. Each is associated with different extinction processes (Hartley and Kunin, 2003).

The RI and ED indices, and the combined Rarity-Evolutionary Distinctiveness Index (REDI), may be useful in determining which species to include in both in situ and ex situ conservation efforts. In general, the species with the highest overall REDI scores were gymnosperm species with small distributional areas contained entirely within the United States, such as giant sequoia, Florida yew, Florida torreya, coast redwood, and Santa Lucia fir, but angiosperm exceptions included Joshua tree, American holly (*Ilex opaca*), Osage-orange (*Maclura pomifera*), loblollybay (*Gordonia lasianthus*) and sourwood (*Oxydendrum arboreum*) (Supplementary Table 1). Similarly, there was a small but significant phylogenetic signal for RI, indicating that members of some evolutionary groups – such as *Cupressus*, *Magnolia*, *Castanea*, and *Aesculus* – have similarly high levels of rarity (Fig. 1).

It was possible to apply the results of the species rarity and ED assessment in a biogeographic context by combining them with species occurrence data from each of > 130,000 standardized and spatially unbiased plots across the conterminous 48 states. Specifically, species-level RI, ED and REDI values were used to weight plot-level importance values. The resulting plot-level measures of conservation value were employed to identify statistically significant geographic hotspots and cold spots of rarity and ED, and to determine whether plot-level rarity and ED values are significantly higher in areas under conservation protection or in areas that are not.

Geographic rarity has long been a focus of species conservation attention, including in prioritization efforts (e.g., Farnsworth et al., 2006; Gauthier et al., 2010; Jimenez-Alfaro et al., 2010). More recently, conservation assessments have begun to incorporate the evolutionary distinctiveness of species as a factor informing prioritization decision-making (Larkin et al., 2016) and evaluations of conservation effectiveness (Jetz et al., 2014; Veron et al., 2017). Such geographical rarity and ED information can be applied together in a spatial context to identify priority conservation areas with relatively high vulnerability and evolutionary irreplaceability, respectively (sensu Margules and Pressey, 2000).

4.1. Geographic patterns of rarity and evolutionary distinctiveness

The Getis-Ord analysis identified locations where tree species with higher- or lower-than-expected values of rarity and ED have accumulated, information that can be useful in understanding and monitoring broad-scale patterns of conservation value. In this assessment, geographic hotspots of RI_p generally were limited to southern and far western parts of the United States. Some of these areas correspond with areas of high tree endemism identified by Jenkins et al. (2015), including much of Florida and California (Fig. 3A). Coldspots of rarity, meanwhile, included areas near the borders of Canada and Mexico, where many of the tree species have relatively small portions of their distributions in the United States, and in the northern and central Rocky Mountains, where forests consist mainly of common species with ranges that extend north past the border. (It is worth noting that marginal populations of species may require conservation attention given their potential for genetic differentiation (Eckert et al., 2008) and higher susceptibility to environmental change (Hampe and Petit, 2005).) Hotspots of ED_p, meanwhile, are more widely scattered across the country, and are the result of clustering of high ED along the Pacific Coast of California, Oregon, and Washington; in the northern Rocky Mountain region; and in scattered locations across the East (Fig. 3B). Following the interpretation of Mace et al. (2003), these can be considered “museums” of life, where evolutionary diversity persists, while at least some of the coldspots of ED_p can be thought of as “cradles of diversity,” where diversity currently is being generated. These include the hardwood-species-rich areas of the southern Midwest and Florida, and the conifer-rich area of California ringing the Central Valley. This assessment prioritizes areas where ED persists over where it is being generated, but it is possible to make a case for conserving areas that serve as nurseries for species radiations. Finally, the geographic hotspots of $REDI_p$ (Fig. 3C) are locations where both species vulnerability and evolutionary distinctiveness are high, and thus are places where biodiversity is most likely to be lost with the fewest possibilities for replacement, and thus where protection is the most urgently needed (sensu Margules and Pressey, 2000). Coldspots of $REDI_p$ require less intervention to maintain the biodiversity present in these locations, beyond ongoing monitoring of species rarity trends. Hotspots and coldspots of rarity and ED, however, represent one factor among many that can be considered when identifying areas for conservation priority across broad scales. Other factors incorporated in the selection of conservation reserve sites, for example, include environmental gradients and geographic context (Kamei and Nakagoshi, 2006), habitat diversity (Miller et al., 1987), and the optimization of different facets of biodiversity within a reserve network (Prado et al., 2010; Rodrigues and Gaston, 2002).

4.2. Protected area effectiveness

The results of this study also offer insights into the conservation effectiveness of forest protected areas, which is important to evaluate in the context of ongoing and developing threats to tree species (Potter et al., 2017b). Among other conservation objectives, forest preserves should be comprehensive in that they include all forest ecosystems, and should be representative in that they encompass all the biodiversity within an ecological region (Kanowski, 2000). The results of the comparison between protected and non-protected areas detected significant differences in mean plot-level conservation-weighted importance values ($RI_{p,}$ ED_p, and $REDI_p$) between the two. Rarity (RI_p) and the combined index ($REDI_p$) were higher in unprotected forests, while ED (ED_p) was higher in protected forests. The mostly highly protected areas (GAP Status 1), in fact, had by far the lowest mean RI_p, while the highest values were for unprotected forests (GAP Status 4) and those for which protected status was unknown (Table 3). Additionally, when considering only the plots with the highest 10% of values for each index, the majority occurred in unprotected areas (Table 4). These results underscore the tendency for protected areas, including in the United States, to encompass a biased sample of biodiversity that focuses on remote locations that are unsuitable for commercial activities (Margules and Pressey, 2000), places that are unlikely to face land conversion pressures even in the absence of protection because they have low productivity or minimal economic interest (Joppa and Pfaff, 2009). While Jenkins et al. (2015) found that the geographic configuration of protected areas in the United States to be nearly opposite patterns of endemism, the results of the current analysis are more equivocal. For example, rarity was higher in unprotected forests nationally, but was higher in protected areas across much of the East (Fig. 4A), despite the fact that the proportion of plots in protected areas was relatively small (18.5% in the Hot Continental and 12.1% in the Subtropical) compared to the West (82.2% in Temperate Desert and 64.0% in Mediterranean). On the other hand, mean ED_p was considerably lower in protected forests across most of the East than in unprotected forests. The opposite pattern was the case in two ecoregions in the West, the Mediterranean and the Temperate Steppe. In these areas, rarity appears to be negatively related with ED on many plots; in other words, plots with high ED consisted mainly of relatively common species, while those with high rarity consisted mainly of species with low ED. These inverse patterns between rarity and ED result at least partially from the fact that small plant families have fewer rare species than expected, while large families have more (Lozano and Schwartz, 2005). At the same time, larger families tend to encompass more recent speciation events (including the 58 relatively recently diverged species from Fagaceae in this study), and therefore less ED.

A particularly noteworthy finding of this assessment was that plots in multiple-use protected forests (Status 3) had significantly higher ED_p and $REDI_p$ mean values than restricted-use forests (Status 1 and 2). These restricted-use reserves include designated wildernesses, national parks, national wildlife refuges, research natural areas, and some national monuments and state parks (Table 1). An important objective for these areas is to effectively conserve the full range of biodiversity values, with the Convention on Biological Diversity's Aichi Biodiversity Target 11 calling specifically for ecologically representative coverage by protected areas (Juffe-Bignoli et al., 2014). Meanwhile, the multiple-use protected areas in the United States such as National Forest and Bureau of Land Management general lands (Status 3), which had higher conservation-weighted importance values, are not included in the IUCN definition of protected areas. The results of this conservation effectiveness comparison, therefore, underscore the fact that both designed preserves and off-reserve conservation actions play important roles in securing biodiversity (Rayner et al., 2014).

Most in situ conservation of forest tree genetic resources, in fact, occurs on lands outside of strict protection in public, private and traditional ownerships, including those used primarily for wood production (FAO, 2014b). Whenever possible, therefore, the conservation of rare and high-ED forest tree species should be integrated into the management and regulation of these forests, particularly when they are under public ownership and control. Specifically, managers at the site-level should apply silvicultural and other management actions that ensure biodiversity and evolutionary processes are maintained in forest populations (Ratnam et al., 2014; Schaberg et al., 2008). At broader scales, managers should incorporate principles of landscape ecology and adaptive management, such as maintaining structural complexity and floristic diversity within and across forest stands, using a variety of management strategies implemented at different scales, maintaining or restoring connectivity between protected areas, and managing for heterogeneity across forest landscapes (Kanowski and Boshier, 1997).

4.3. Conclusions

Forest conservation efforts, including the establishment and management of protected areas, should preserve the composition, structure, function and evolutionary potential of forest biodiversity (Dudley, 2008). To be effective, regional networks of protected areas must be representative of the biodiversity present in the region (Gaston et al., 2008; Kanowski, 2000). This includes safeguarding both evolutionary distinctiveness and the multiple facets of rarity that vary with scale (Rabinowitz, 1981). The assessment described in this paper incorporates rarity and ED in a prioritization of tree species at a national scale. It then applies the resulting information to identify locations with high conservation values associated with rarity and ED, and evaluates the degree to which existing protected areas are effective in conserving species of high conservation priority. The necessity of this analysis is apparent given the long list of threats to forest biodiversity, including the global movement of dangerous insects and pathogens, the loss of forest cover, changing climate conditions, catastrophic fires, and the unsustainable harvesting of trees (FAO, 2014b).

The results of the assessment were equivocal, indicating that protected forest areas effectively conserve ED across the United States, but not rarity. Areas with the highest level of protection (GAP Status 1) had the highest mean plot ED_p values, but the lowest mean plot RI_p values (Table 3). Conversely, unprotected areas (GAP Status 4) and areas of unknown conservation status had the highest RI_p values and among the lowest ED_p values. Unprotected areas had the highest overall $REDI_p$ values. The effectiveness of protected areas to conserve rarity and ED, meanwhile, varied across the United States, with regional variation in which conservation-weighted important values were higher in protected forests. Decision-makers therefore should acknowledge this heterogeneity and apply conservation strategies at appropriate management scales.

Considering the number and extent of threats to forest tree species, as well as the potential inadequate enforcement of conservation protections in reserve areas resulting from the lack of oversight and failure to enforce protected area regulations (FAO, 2014b), it also will be important to evaluate whether protected areas are sufficient for future biodiversity conservation needs (Potter et al., 2017b). This includes the protection of the irreplaceable functional roles and services of forest trees (Mouillot et al., 2013) as well as tree rarity and ED. Such an assessment would move beyond understanding the representativeness of forest biodiversity under protection, and would analyze the degree to which it is buffered from external threats, as measured by the retention or loss of biodiversity over time (Gaston et al., 2008). To the extent possible, such an analysis also should test the effectiveness and impacts of various management activities on the rarity, ED and functional diversity of forest trees in multiple-use protected areas.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.05.007.

Acknowledgments

The author thanks the organizers of this special issue for their invitation to write this paper, and to the guest editor and three reviewers for their insightful and helpful comments. He also appreciates helpful advice from Kurt Riitters and Songlin Fei, data compilation assistance from Julie Canavin, and the efforts of many Forest Inventory and Analysis field crew members to collect the data used in this study. This research was supported through Cost Share Agreements 15-CS-11330110-067, 16-CS-11330110-038 and 17-CS-11330110-025 between the USDA Forest Service and North Carolina State University.

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