US protected lands mismatch biodiversity priorities

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Edited* by Edward O. Wilson, Harvard University, Cambridge, MA, and approved March 17, 2015 (received for review September 23, 2014)

Because habitat loss is the main cause of extinction, where and how much society chooses to protect is vital for saving species. The United States is well positioned economically and politically to pursue habitat conservation should it be a societal goal. We assessed the US protected area portfolio with respect to biodiversity in the country. New synthesis maps for terrestrial vertebrates, freshwater fish, and trees permit comparison with protected areas to identify priorities for future conservation investment. Although the total area protected is substantial, its geographic configuration is nearly the opposite of patterns of endemism within the country. Most protected lands are in the West, whereas the vulnerable species are largely in the Southeast. Private land protections are significant, but they are not concentrated where the priorities are. To adequately protect the nation's unique biodiversity, we recommend specific areas deserving additional protection, some of them including public lands, but many others requiring private investment.

conservation priorities | protected areas | endemism | range size | extinction

Protected areas are the most widespread and effective means to conserve natural ecosystems. Given that habitat loss is the primary threat to species survival, which places society chooses to protect will largely determine how many and which species survive. The original intent of many protected areas in the United States was to protect landscapes, not biodiversity. Nevertheless, protected areas are still the backbone of conservation in the country—as they are globally.

We describe geographic patterns of biodiversity and the distribution of protected areas and land ownership in the United States. We then combine them to map priorities for future protection. Our focus is the continental United States minus Alaska, recognizing that Alaska is biodiversity poor and a substantial fraction of it is already within protected areas. We also exclude Hawaii and US territories because, although rich in endemic species, they are comparatively data poor.

We can assess coverage of protected areas by how well they include different elements of biodiversity, be they ecosystems (1), biophysical landforms (2–4), or individual species (5–8). We focus on species, because their extinction is irreversible (9, 10). Previous studies of the US protected area system focused mainly on federally listed endangered species (11–15); we consider all species within taxa for which data are sufficient.

Knowing precisely where individual species occur limits inferences. We compiled species' range maps for taxa where all species in the taxon are relatively well-documented within the United States, recognizing the limits of such data (10, 16–18). These are, however, the most comprehensive and readily applicable data for guiding decisions. We mapped diversity by overlaying maps for various subsets of species in each taxon (*Methods*).

Geographic patterns of total species richness differ substantially among taxa (Fig. 1). Mammal richness is highest in the west, birds along the coasts, and reptiles broadly across the warmer south. Amphibians, freshwater fish, and trees are most diverse in the humid east and, especially, the warm and humid Southeast. These patterns are interesting, worthy of further study, but do not direct conservation. Widely distributed species dominate overall patterns of species richness (19), but they are generally not the species in need of conservation efforts.

In identifying conservation priorities, one must consider both existing protected areas and the intrinsic vulnerability of species. Vulnerable species tend to be in two groups (10): those with small geographic ranges, which is often correlated with local rarity, and large-bodied species that are sparsely distributed across large ranges. The latter species, which are relatively few but include predators like panthers and wolves, were largely extirpated from the east and still face persecution across large extents of the west.

Most imperiled species are of the first group: small range size is the best predictor of extinction risk and, thus, the first metric for conservation priority (20–22). We focus on small-ranged species defined in several ways. First, we consider endemics—those with their entire range in the United States (*Methods*). Amphibians (70%) and freshwater fish (68%) show the highest levels of endemism, followed by reptiles (30%), trees (29%), mammals (28%), and birds (<3%). Patterns of endemism for all taxa are consistently centered in the Southeast, although the west also has significant mammal endemism (Fig. 1).

Next, we consider "small-ranged species," those having ranges smaller than the median size, and do so from two perspectives. There are species whose ranges are small by global standards and those that are small relative to species within the United States. For globally small-ranged species, most birds and mammals are in the west (Fig. 2). This pattern is in contrast with their endemism patterns, for many globally small-ranged birds and mammals have ranges extending into Mexico or Canada. Amphibian ranges are so small (Table S1) and isolated that no location has more than two species with overlapping ranges, although 61 small-ranged species occur in the country. A general characteristic of regions with small-ranged amphibians is complex topography. For instance, 18

Significance

The United States has one of the oldest and most sophisticated systems of protected areas in the world. Given the large amount of information on the country's biodiversity, and the potential resources available, one might expect it to do well in protecting biodiversity. We find that it does not. The United States protected areas do not adequately cover the country's unique species. To improve the coverage, we map priorities for multiple taxa and recommend specific areas for immediate conservation attention. These areas contain a mix of public and private land, meaning that major progress in conservation will require actions in both the public and private sectors, and will succeed only if done in the correct areas.

Author contributions: C.N.J., K.S.V.H., S.L.P., and J.O.S. designed research; C.N.J. performed research; C.N.J. analyzed data; and C.N.J., K.S.V.H., S.L.P., and J.O.S. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1418034112/-/DCSupplemental.

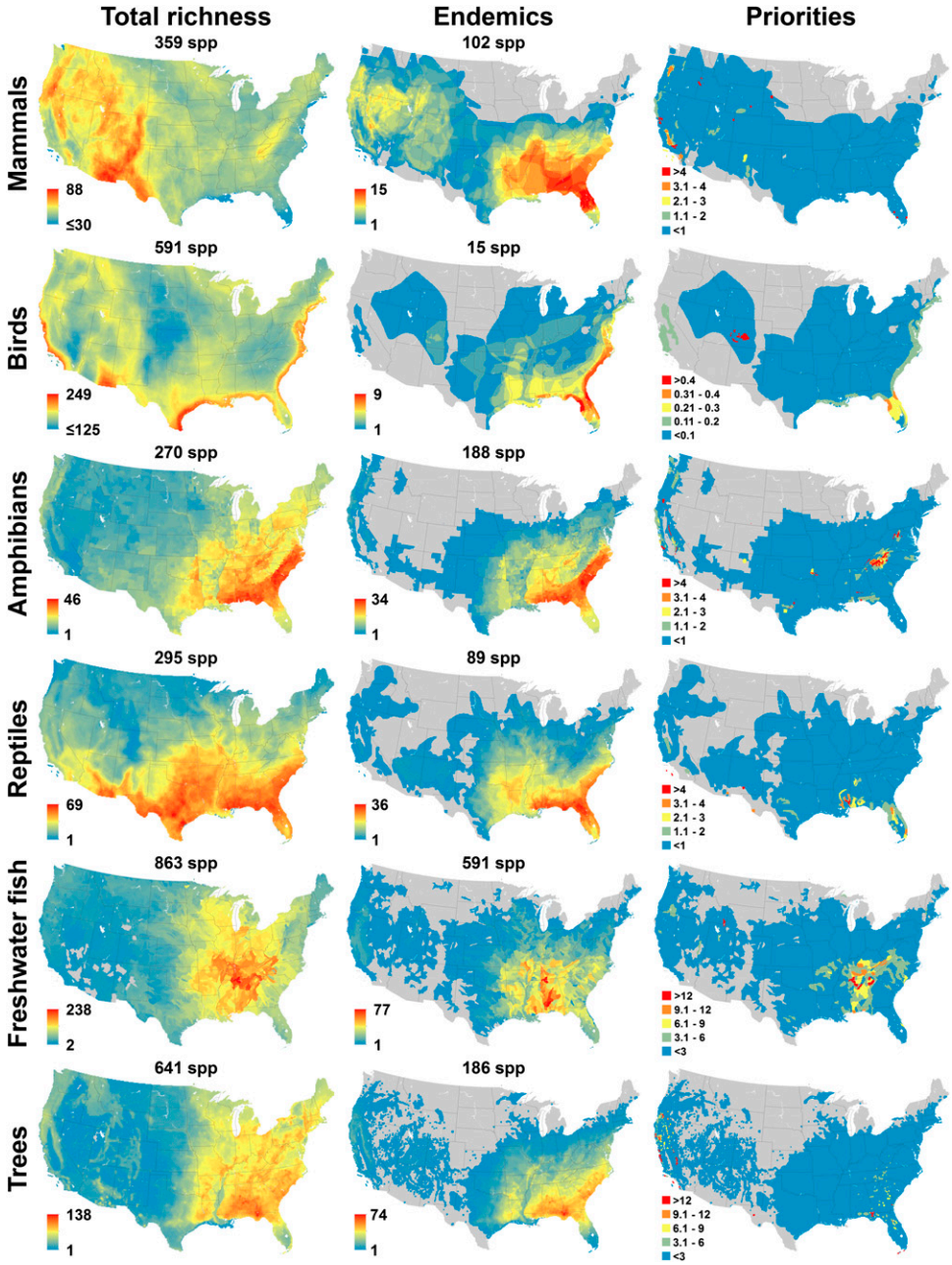

Fig. 1. Biodiversity of the lower continental United States and priority areas for individual taxa. Total richness is the number of all species within the taxonomic group. Endemics are species whose entire range is within the lower 48 states. Priorities map the sum of individual species' priority scores across the taxon.

small-ranged amphibians, all of them Plethodontid salamanders, live within the Appalachian Mountains, although their individual ranges rarely overlap. This result matches findings of earlier global-scale studies (23, 24).

Similar patterns emerge for species having ranges small relative to species in the United States (Fig. 2). Small-ranged mammals concentrate mostly in the west. Small-ranged birds concentrate in the west and the coasts, although their generally large ranges mean all areas have at least one "small-ranged" bird. The Southeast, particularly the southern Appalachians, has many small-ranged amphibians, mostly salamanders. Similar analyses were not possible for reptiles, freshwater fish, or trees because no globally comprehensive databases are available. Threatened species show no consistent geographic patterns across taxa, with few places having more than two IUCN threatened species of any particular taxon (Fig. 2).

Are available biodiversity data sufficient to make informed choices about priorities? We will always need to prioritize based on some subset of species or other proxy for overall biodiversity, but some next steps to expand our knowledge are clear. We recommend wider ranging assessments of reptiles and freshwater fish, which would enable a more precise evaluation of their endemism. A global assessment for reptiles is underway through the International Union for Conservation of Nature (IUCN), but a similarly comprehensive effort for freshwater fish seems more distant. Maps for trees need revision to reflect recent knowledge on species' distributions and taxonomy.

Assessments of other taxonomic groups would enable more comprehensive planning for the nation's biodiversity. Just as the taxa we analyze do not always coincide in their biodiversity patterns, taxa for which we lack range data may have their own

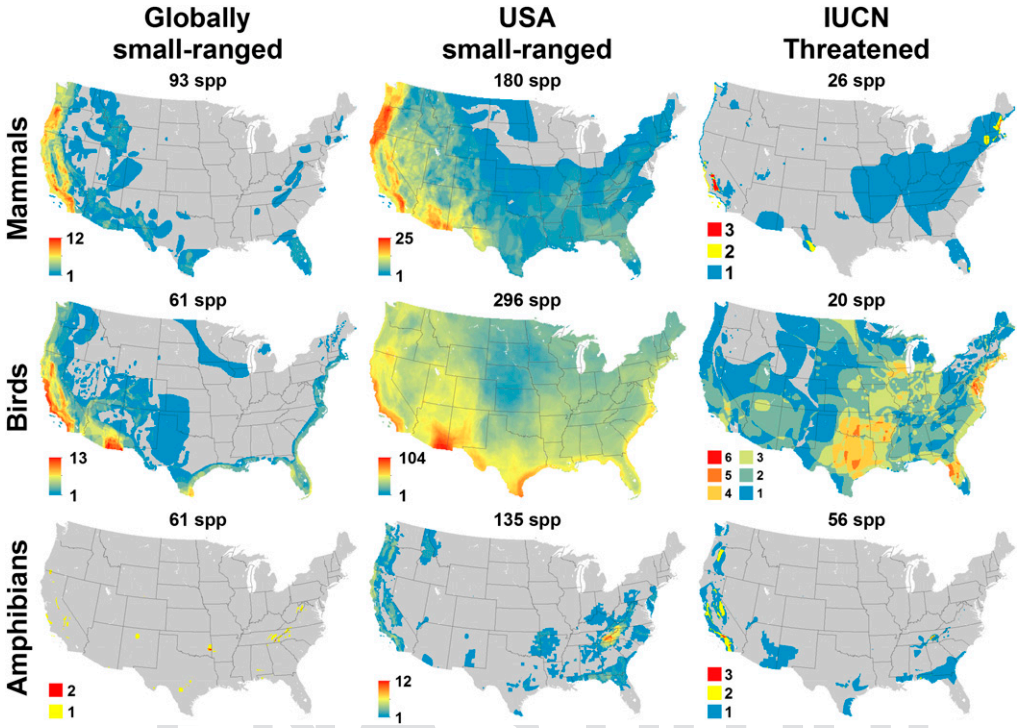

Fig. 2. Small-ranged and threatened species. Globally small-ranged are those species with ranges smaller than the global median for that taxon. USA small-ranged are those species with ranges smaller than the median for the species in the lower 48 states. IUCN Threatened are species considered vulnerable, endangered, or critically endangered on the IUCN Red List.

novel patterns. Other plant taxa would be particularly informative because diversity patterns for trees likely differ from those of plants that predominate in grasslands and other nonforest ecosystems. For invertebrates, which are almost certainly more diverse than vertebrates or plants, butterflies might be the best candidate for a nationwide database. Butterflies are diverse, charismatic, and data rich compared with other invertebrates.

Another area for possible improvement is the range maps themselves. Such maps have an inherent tendency for commission errors, including areas that species once occupied but currently do not, or areas that once had habitat but have since lost it (25). For shorter-term planning, it would certainly be useful to document better what part of a species range has habitat and whether it is occupied (26). Importantly, however, species may reoccupy currently vacant areas, and habitats can potentially recover, at least in the long term. For long-term conservation, basing decisions solely on currently occupied habitat would discount the possibility of habitat recovery or of species reoccupying currently unoccupied areas.

In addition to individual species, there is the possibility of using other measures of biodiversity or geophysical proxies. For example, using maps of ecosystems (1, 27, 28), or geophysical features such as elevation and soils (3), are other approaches for evaluating the representativeness of a protected area system.

How well does the United States protect biodiversity? Only 7.8% of the lower 48 states is within an IUCN categorized protected area (Fig. 3*A*), below the global average of 10.3% (29). Approximately 6% is in stricter IUCN categories of I to IV, about average for the globe (29). The United States employs a broadly comparable system of management categories through the Gap Analysis Program (GAP) (30). The best-protected areas—GAP Status 1 and 2—show a similar rate of 7.1% (Fig. S1 and *SI Results*).

These percentages mask a strong geographic bias. Most protected areas are in the west, which tends to be less suitable for agriculture and development and where a large fraction of the land is in federal ownership (Fig. 3*B*). Much of the publicly owned land (i.e., federal, state, and local), however, has no assigned IUCN category and/or is GAP status 3, indicating that it is to be maintained as a particular land cover but is subject to extractive use (e.g., logging, mining, grazing). Some of these public lands may have limited protection with respect to conservation, such as by the National Forest Management Act or the Endangered Species Act if they contain a federally protected species. For some individual species, these legal protections may be significant, though we do not consider them further here. Nevertheless, most of the non-IUCN ranked public lands are also in the west, matching the pattern for IUCN-ranked areas.

Most land in the center and east of the country is unprotected and privately owned. A major instrument for conservation on private land is easements. While a complete national inventory of easements is still underway (31), the partial data suggest that much of the land thus far protected is not ideally positioned for biodiversity conservation. More than 22.6% of the documented easement area is in Maine and Montana, states that together cover 6% of the total area of the lower 48 states, but have almost no endemism or small-ranged species. Florida and California, states with substantial biodiversity, reassuringly are third and fourth in easement area with more than 6% of the total each, in 1.9% and 5.3% of the total area, respectively. However, endemic-rich states in the Southeast (Tennessee, Kentucky, North Carolina, South Carolina, Mississippi, Alabama, Georgia), which make up 10.7% of the total land area of the lower 48 states, collectively contain only 7.8% of the easement area. In other words, these biodiverse states that are mostly private land, and which should be a focus of easement efforts, have less area protected than if easements were randomly distributed across the country. It appears that private land protection efforts, similar to public protected areas, are not prioritizing the most endemic-rich areas of the country, or at least are having less success in those areas.

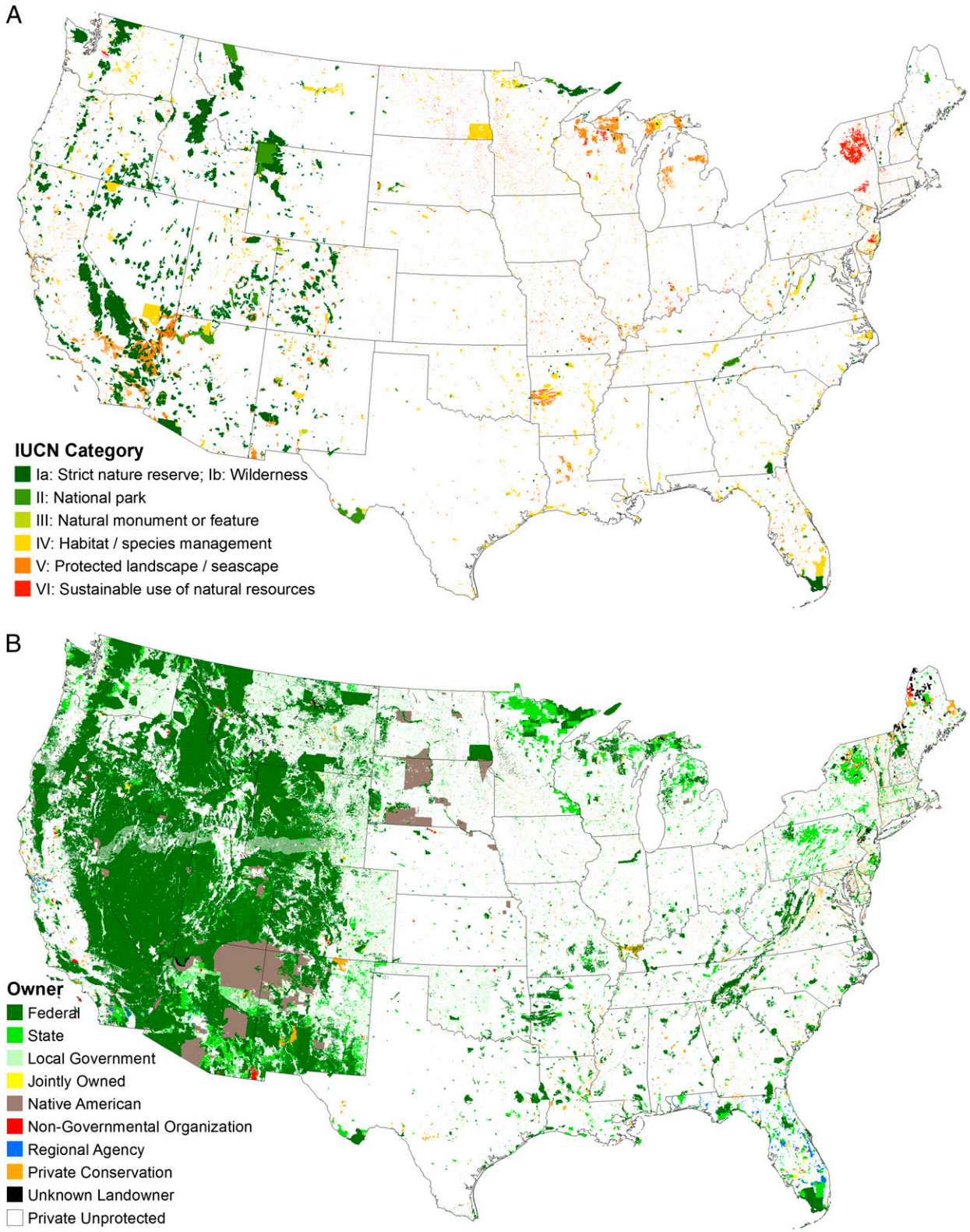

Fig. 3. Protection status and ownership of lands in the lower 48 states. (*A*) Existing protected areas colored by IUCN category (41). (*B*) Ownership status of public, private, and Native American lands.

Where might the United States efficiently expand protection for biodiversity? To prioritize lands for future conservation, we focused on the >1,200 endemic species, as their survival depends almost entirely on actions within the country. For each species, we calculated a priority score equal to the proportion of the species' range that is unprotected (i.e., not in IUCN I to VI protected areas) divided by the area of the species' range. This score increases as range size decreases, in accordance with the

well-established relationship between range area and extinction risk (20–22). Conversely, if a large proportion of the species' range is within protected areas, the score accordingly decreases. Priority maps sum scores across all endemic species in a taxonomic group (Fig. 1) and across all taxonomic groups (Fig. 4).

Priorities for individual taxa vary substantially, although areas in the Southeast and California tend to have higher priority (Fig. 1). These priorities reflect both the concentration of endemics in these regions and the low rate of protection in the Southeast. Importantly, high-priority areas for individual taxa largely do not overlap. For example, although amphibians and reptiles have similar patterns for endemism, their highest priority areas are markedly different, although both are in the Southeast (Fig. 1).

Summing the priority scores across all taxa, the highest-priority areas are mostly in the Southeast, California, and Texas (Fig. 4). These areas cover a relatively small portion of the country, but are inordinately important for biodiversity. They are largely unprotected, although there are exceptions such as Great Smoky Mountains National Park and the Sequoia, Kings Canyon, Yosemite complex in California. Some priority areas likely have already lost habitat. Range maps largely do not reflect contemporary habitat losses. As a result, local conservation actions will need further guidance by using refined biodiversity maps (32–35). Nevertheless, our analysis indicates that remaining habitat in these areas, and potential for restoring habitat, is a top priority for biodiversity conservation.

To improve the coverage of biodiversity, we recommend nine foci, labeled in Fig. 4 and described below. Some priorities remain in public land although with insufficient protection to earn an IUCN ranking. A prime example is the Blue Ridge Mountains along the Tennessee, North Carolina, and Virginia border (labeled 1 in Fig. 4). Much of this region has substantial biodiversity value, but is inadequately protected under its current classification as National Forest. Raising the protection level of these lands, emphasizing ecosystem protection and low-impact recreation over extractive uses, would be a major conservation gain. More difficult may be the priority areas that are mostly private land, where current protection is likely even more limited or nonexistent, and conservation options may be more limited and costly.

Substantial progress in protecting the nation's biodiversity will require improving conservation on both public and private land.

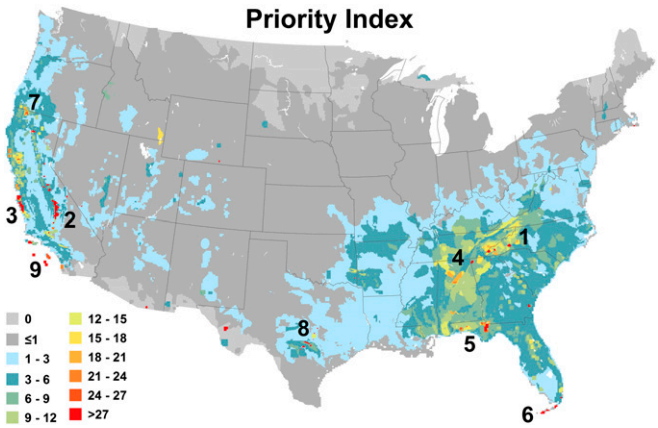

Fig. 4. Summed priority scores across all taxa and recommended priority areas to expand conservation: 1, Middle to southern Blue Ridge Mountains; 2, Sierra Nevada Mountains, particularly the southern section; 3, California Coast Ranges; 4, Tennessee, Alabama, and northern Georgia watersheds; 5, Florida panhandle; 6, Florida Keys; 7, Klamath Mountains, primarily along the border of Oregon and California; 8) South-Central Texas around Austin and San Antonio; 9, Channel Islands of California.

On private lands, local and state land trusts are essential, possibly through land purchases, conservation easements, and similar instruments. To save biodiversity, conservation actors must focus greater attention to biodiversity priorities, through analyses such as ours. Failure to do so could mean the extinction of the country's unique species.

Recommended Priority Areas (See Locations in Fig. 4)

1) *Blue Ridge Mountains*: Particularly the middle to southern sections, including the Cherokee, Nantahala, Pisgah, and Jefferson National Forests. This region is a major priority for amphibians, mainly because of salamanders, and for fish and trees. Much of the area is federal land.
2) *Sierra Nevada Mountains*: Particularly the southern section. This region is a priority mainly because of amphibians and trees. Much of the area is federal land.
3) *California Coast Ranges*: This region is a priority mainly because of trees, amphibians, and mammals. Substantial portions are federal land.
4) *Tennessee, Alabama, northern Georgia watersheds*: This region is a priority mainly because of its exceptional fish diversity, for which it is globally significant. There is also substantial reptile and amphibian diversity in some areas. Most of the region is privately owned.
5) *Florida panhandle*: This region is a priority mainly because of trees, fish, and reptiles. Almost none of the region is within IUCN ranked protected areas. Most of the region is privately owned, but with some federal and state lands.
6) *Florida Keys*: A priority mostly because of trees. A moderate amount of the Keys is within IUCN ranked protected areas and other public lands.
7) *Klamath Mountains*: Primarily along the border of Oregon and California. This priority is mainly because of trees, and somewhat for amphibians and fish. Much of the area is federal land.
8) *South-Central Texas around Austin and San Antonio*: This area represents a cluster of sites that are priorities mainly because of amphibians, but also fish and reptiles. The region is nearly all privately owned.
9) *Channel Islands of California*: The Channel Islands are priorities mainly because of trees, reptiles, and mammals. Significant portions of the islands are within IUCN ranked protected areas, or are federal land.

Results are available in GIS format at BiodiversityMapping.org.

Methods

We mapped diversity by overlaying range maps for terrestrial vertebrates, freshwater fish, and trees, the taxa for which spatial data were sufficient. Range maps for birds were from BirdLife International (36), for amphibians and mammals from IUCN (37), for reptiles and freshwater fish from NatureServe (38, 39), and for trees from the US Geological Survey (40). Some species in the original tree dataset are presently considered subspecies. We merged those into the parent species. Original tree data are available online at: esp.cr.usgs.gov/data/little/.

For all species, we excluded extinct and nonnative species when indicated in the data and parts of species' ranges considered transitory/migratory or outside the native range. For birds, ranges included breeding and nonbreeding range. We excluded seabirds. We also removed the Bachman's Warbler (*Vermivora bachmanii*) and Ivory-billed Woodpecker (*Campephilus principalis*), because they are generally regarded to be extinct.

In selecting species endemic to the study area, we used a 20-km buffer around the Natural Earth (www.naturalearthdata.com) definition of land, including islands. This buffer is to account for inconsistencies between mapped land boundaries and the delimited polygon ranges for terrestrial species. Thus, our definition of species endemic to the study area is somewhat liberal. For birds, we based endemism on the combined breeding and nonbreeding range because our goal is to identify species whose future

wholly depends on actions in the United States. There are additional species that are restricted to the study area based on only their breeding (10 species) or nonbreeding (8 species) range. For freshwater fish, we removed some species as endemics based on other sources that indicate their distributions ranged outside the study area (*Strongylura marina*, *Trinectes maculatus*, *Dormitator maculatus*, *Ariopsis felis*, *Acipenser oxyrinchus*, *Lampetra ayresii*, *Spirinchus thaleichthys*, *Thaleichthys pacificus*). For trees, we also checked Kew Botanical Gardens, Tropicos, Global Biodiversity Information Facility, and other online sources for evidence that a species' native range extended outside the United States. We revised databases for taxonomic revisions where feasible.

Data on protected areas were from the PAD-US database (30). We used ArcGIS 10 for maps and analyses. Maps use the Albers Equal Area Conic projection.

ACKNOWLEDGMENTS. We thank Anupam Anand for collating tree-species data and Robert Dunn and Nick Haddad for critical discussions about this study. C.N.J. was supported by the Brazilian agency Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior (CAPES) through Ciência Sem Fronteiras Program A025_2013.

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Supporting Information

Jenkins et al. 10.1073/pnas.1418034112

SI Results

GAP status descriptions: Only GAP 1 and 2 correspond to a protected area as defined by IUCN. There is no direct crosswalk between the IUCN I-VI categories and GAP 1 and 2. Descriptions below of all GAP statuses are from gapanalysis.usgs.gov/blog/iucn-definitions.

GAP 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 (of natural type, frequency, intensity, and legacy) are allowed to proceed without interference or are mimicked through management.

GAP 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.

GAP Status 3: Area having permanent protection from conversion of natural land cover for the majority of area. Subject to extractive uses of either broad, low-intensity type (e.g., logging) or localized intense type (e.g., mining). Confers protection to federally listed endangered and threatened species throughout the area.

GAP Status 4: No known public/private institutional mandates/legally recognized easements.

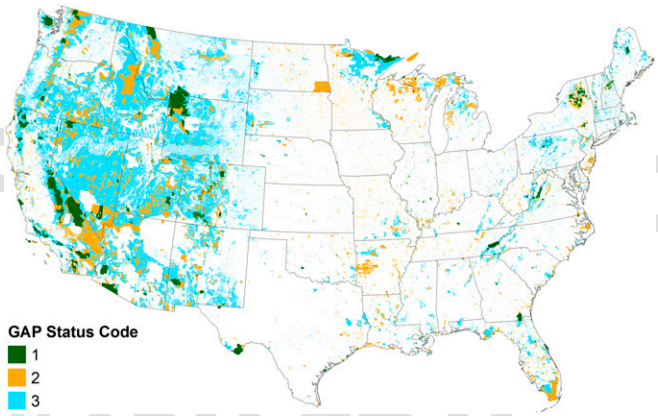

Fig. S1. Existing protected areas, public lands, and Native American lands shown by GAP status (1).

1. US Geological Survey, Gap Analysis Program (2012) Protected Areas Database of the United States (PADUS), Version 1.3 Combined Feature Class.

Table S1. Summary statistics for species in the study area

Taxonomic group	No. of species	Median range size for US species, km^2	Median range size for group globally, km^2	Globally small-ranged species	Threatened species (IUCN)
Mammals	359	914,636	195,679	93	26
Birds	591	4,900,903	567,542	61	20
Amphibians	270	92,762	4,686	61	56
Reptiles	295	—	—	—	—
Freshwater fish	863	—	—	—	—
Trees	641	—	—	—	—

Range size reflects the entire global range for a species, not only within the study area. Globally small-ranged species are those with ranges smaller than the global median of that group. Global range size data were not available for reptiles, freshwater fish, and trees. Threatened species are those listed as vulnerable, endangered, or critically endangered on the IUCN Red List.

Priority Index