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R. Travis Belote

Kevin Barnett

Matthew S. Dietz

Laura Burkle

Clinton Jenkins

See next page for additional authors

Authors

R. Travis Belote, Kevin Barnett, Matthew S. Dietz, Laura Burkle, Clinton Jenkins, Lindsay Dreiss, Jocelyn L. Aycrigg, and Gregory H. Aplet

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R. Travis Belote [a,*], Kevin Barnett [a], Matthew S. Dietz [b], Laura Burkle [c], Clinton N. Jenkins [d], Lindsay Dreiss [e], Jocelyn L. Aycrigg [f], Gregory H. Aplet [g]

[a] The Wilderness Society, Research Department, 503 W. Mendenhall Ave, Bozeman, MT 59715, United States of America
[b] The Wilderness Society, Research Department, Oakland, CA 94612, United States of America
[c] Montana State University, Department of Ecology, Bozeman, MT 59717, United States of America
[d] Florida International University, Department of Earth and Environment & Kimberly Green Latin American and Caribbean Center, Miami, FL 33199, United States of America
[e] Defenders of Wildlife, Center for Conservation Innovation, Washington, DC 20036, United States of America
[f] University of Idaho, Department of Fish and Wildlife Sciences, Moscow, ID 83844, United States of America
[g] The Wilderness Society, Research Department, Denver, CO 80202, United States of America

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ABSTRACT

International and national initiatives aim to conserve at least 30% of lands and waters by 2030. To safeguard biodiversity, conservation actions must be distributed in places that represent ecosystem and species diversity. Various methods of prioritizing sites for conservation have been used in local and global assessments. However, the performance and consequences of alternative methods are usually unknown. Such comparisons are needed to confidently implement national and international conservation initiatives. Here, we compared four widely-used methods of prioritizing sites in the contiguous United States for conserving species of mammals, birds, amphibians, and reptiles. Specifically, we calculated and mapped species richness, rarity-weighted richness, and two complementarity-based prioritizations (additive benefit function [ABF] and core area zonation [CAZ] in the software Zonation). We compared maps derived from these alternatives with respect to spatial locations and overlap, patch size distributions of the top-30% priorities, and existing ownership and protected-area status. We used species-accumulation curves across ranked priorities to evaluate performance of methods and compared results at 30% total area. Mapped locations and patch sizes of the highest priorities varied by taxonomic class and method of prioritization. Complementarity-based methods (ABF and CAZ) more efficiently represented species than methods based on richness or rarity-weighted richness, especially for taxa with higher beta diversity (amphibians). ABF and CAZ methods also resulted in greater conservation opportunity for the top 30% of priorities compared to maps of richness. Area-based conservation targets, such as the "30 by 30" initiative, must distribute limited resources in ways that safeguard all species. Our results show that spatial locations and configuration, performance, and conservation opportunity vary among prioritization methods and taxonomic classes.

1. Introduction

Life on Earth is experiencing a sixth mass extinction (Ceballos et al., 2015). Nearly one-third of terrestrial vertebrates in the contiguous United States (CONUS) are considered vulnerable (Dietz et al., 2020). To minimize the extinction crisis, we must eliminate the causes of species imperilment (Wilcove et al., 1998). Global and national campaigns such as "Half Earth" and "30 by 30" (an initiative to conserve at least 30% of global land and marine area by the year 2030) represent calls to protect more land to prevent loss of species (Dinerstein et al., 2019; Jung et al., 2021; Noss et al., 2012). In January 2021, U.S. President Joseph R. Biden issued an executive order requesting recommendations for "conserving at least 30 percent of our lands and waters by 2030." This raises the obvious question: which half, or which 30%?

For these area-based conservation efforts to successfully prevent extinction, protected areas and conservation actions must be located to

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* Corresponding author.
E-mail address: travis_belote@tws.org (R.T. Belote).

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best represent the full complement of species and the habitats upon which they depend (Venter et al., 2014). To date, however, most protected areas have not been strategically located to represent biodiversity (Jenkins et al., 2015). Many protected areas were established to safeguard scenic, geologic, or other special features in places with minimal economic and political conflict (Pressey, 1994; Venter et al., 2018). Most protected areas in the US, for instance, are located where climates, soils, and topographic settings are poorly suited for agriculture, infrastructure, and human settlement (Aycrigg et al., 2013; Belote, 2018; Huston, 2005).

Scientists have used a variety of methods to prioritize land to best represent species, including identifying areas rich in total number of species or number of vulnerable species (Dietz et al., 2020; Jenkins et al., 2013; Myers et al., 2000), calculating rarity-weighted richness (weighting species by their range sizes before summing occurrence; Albuquerque and Beier, 2015; Stein et al., 2000) or similar biodiversity indices (Jenkins et al., 2015), or using optimization algorithms intended to efficiently distribute sites among species (Csuti et al., 1997; Moilanen et al., 2014; Possingham et al., 2000). The consequences of choosing among alternative prioritization methods are not always clear. As policy makers seek to meet area-based conservation targets—such as 30% area by 2030—more work is needed to compare the performance of different approaches in prioritizing sites for conserving biodiversity (Albuquerque and Beier, 2015; Csuti et al., 1997).

The utility of different biodiversity prioritizations may be best understood in the context of measures of biodiversity across scales: alpha (α), beta (β), and gamma (γ) diversity. Alpha diversity is a measure of local diversity (i.e., the number of species occurring at a single site). Gamma diversity is a measure of regional diversity (i.e., the number of species occurring across all sites in a given region). Beta diversity is a measure of the difference in species composition among sites. While alpha and gamma diversity are measured by the number of species at different scales, beta diversity has been quantified in many ways (Anderson et al., 2011). The simplest estimates of beta diversity can be calculated as either the ratio or the difference between gamma diversity and mean alpha diversity (i.e., $\gamma/\overline{\alpha}$ or $\gamma - \overline{\alpha}$; Whittaker, 1975).

These scale-dependent measures of species diversity are important to consider when prioritizing areas to represent biodiversity in a network of sites. Consider a situation where every species occurs in every site (mean alpha diversity = gamma diversity). One site would represent all species, and proportional targets for each species could be achieved by protecting that same proportion of land area. Alternatively, if every site were composed of completely different species (i.e., 100% turnover among every pair of sites, or maximum beta diversity) then all sites would be needed to represent all species. Of course, patterns of species diversity and composition are more complex than either of these extreme scenarios. Protecting biodiversity requires consideration of alpha diversity to evaluate which species occur in which sites, gamma diversity to know whether all species are represented, and beta diversity to understand how to prioritize among sites.

Priority maps of richness alone represent alpha diversity. Maps of alpha diversity are useful for understanding where ranges or suitable habitats of the most species overlap and for evaluating coarse patterns of the relationship between protected areas and biodiversity (Jenkins et al., 2015; McKerrow et al., 2018). Optimization algorithms usually account for beta diversity through the principle of site complementarity (Pollock et al., 2020). Site complementarity in conservation planning refers to how well each additional site adds conservation features (in our case, species) to an established pool of sites. Two sites with high beta diversity between them (i.e., large differences in species composition) would be characterized by high complementarity. Each site complements the other to represent many species. While biodiversity prioritizations based on richness alone have been criticized for not accounting for complementarity among sites (Brown et al., 2015), weighting species by the inverse of their range sizes has been shown to approximate the efficient representation of species provided by optimization (Albuquerque and Beier, 2015; Csuti et al., 1997). Rarity-weighted richness maps, therefore, may also offer a simple and efficient means of prioritizing sites to represent biodiversity (Jenkins et al., 2015).

Calls to protect as much as half of the terrestrial area on Earth provide an aspirational target to sustain biodiversity into the future (Wilson, 2016). To date, research has focused on evaluating how to represent ecoregions and species with these targets in mind (Dinerstein et al., 2017; Pouzols et al., 2014). However, alternative methods of biodiversity prioritization may direct us to different lands and therefore different recommendations for protected-area establishment. Given differences in alpha and beta diversity, maps of conservation priorities focusing on hotspots of diversity, rarity-weighted richness, or site complementarity may vary. To our knowledge no research has compared the biodiversity outcomes of protecting 30% of land using different prioritization methods. Understanding the consequences of alternative methods is critical as policy makers prioritize lands and waters for conservation to support area-based targets.

Additionally, there may be tradeoffs among biodiversity prioritization methods, including ease of interpretation by policy makers, efficiency in representing species, geographic distributions of priorities, and opportunities for conserving habitat. The ability to formally protect habitats of species in traditional conservation reserves (e.g., designated wilderness) may be limited by ownership rights or management objectives. Federal lands administered by the U.S. government with multiple resource objectives (e.g., timber production, mining) represent opportunities to establish protected areas through new policy or land designations. However, conservation activities in addition to designating protected areas may be required to safeguard habitat for species, including conservation easements, financial incentives (direct payments or tax benefits), or other effective area-based conservation measures (OECMs; IUCN-WCPA Task Force on OECMs, 2019).

Here we compare alternative biodiversity prioritizations for addressing terrestrial vertebrate conservation in CONUS using maps of suitable habitat for species and subspecies of mammals, birds, amphibians, and reptiles. Our research was guided by five primary questions. (Q1) How do gamma, beta, and mean alpha diversity vary among taxonomic classes (i.e., mammals, birds, amphibians, and reptiles)? (Q2) How do maps of biodiversity prioritization based on richness (alpha diversity of sites), rarity-weighted richness, and complementarity-based methods differ in location and arrangement of priorities? (Q3) How well do different biodiversity prioritization methods represent the full complement of species (i.e., gamma diversity) in the top 30% of high-priority lands? (Q4) How much area would need to be conserved to represent 95% of all species under different prioritizations and different levels of individual species representation? (Q5) How do the top 30% of priority areas differ in their distribution with respect to existing protected areas, federal lands, and private lands?

2. Materials and methods

We obtained gridded 30-m × 30-m resolution maps of suitable habitat for 1697 species and subspecies (hereafter "species") of mammals, birds, amphibians, and reptiles for CONUS through the US Geological Survey's Gap Analysis Program (U.S. Geological Survey Gap Analysis Program, 2018). We focus on these species because methods of producing suitable habitat were consistent across species for the entire area. We recognize that analysis of additional taxa will be needed to safeguard a more comprehensive set of species. Suitable habitat for each species was estimated by selecting areas within range maps where a species is likely to occur based on biophysical conditions (see McKerrow et al., 2018 for more details on methods for mapping suitable habitat). For all analyses, we evaluated patterns for all species pooled, as well as for mammals, birds, amphibians, and reptiles separately. We combined the winter, summer, and year-round habitat maps for birds. The data include suitable habitat for 1719 species, but we clipped data to contiguous land area (i.e., removed islands), which reduced the number of species in our dataset. We coarsened the resolution to 4950 m × 4950 m (roughly 5 km) using the AGGREGATE tool in ArcMap v 10.7 because of data-processing limitations. Each pixel is assigned a "1" for suitable or a "0" for unsuitable habitat. A simplified diagram of our methods is in Supplemental Fig. 1.

2.1. Q1: alpha, beta, and gamma diversity among taxa

We calculated gamma diversity, mean alpha diversity, and beta diversity for all species pooled, as well as mammals, birds, amphibians, and reptiles separately. While there are many ways of calculating beta diversity (Anderson et al., 2011), we chose to calculate it as (gamma diversity / mean alpha diversity) − 1 (Whittaker, 1975). This estimate of beta diversity represents a simple ratio corresponding to our conception of how composition among sites varies in relation to the total number of species. Subtracting 1 from this ratio results in beta diversity equaling 0 if all species are found in every site.

2.2. Q2: maps of alternative biodiversity prioritizations

Using our coarsened habitat maps, we calculated four different indices of biodiversity prioritization: species richness, rarity-weighted richness (RWR), and two optimization algorithms conducted in Zonation version 4.0 (Moilanen, 2007; Moilanen et al., 2014). Richness was calculated by summing the binary suitable habitat maps of all species (i.e., producing a map of estimated alpha diversity). RWR was calculated by summing the inverse of total suitable habitat area (Albuquerque and Beier, 2015); species with smaller suitable habitat area received a higher weighting than those with larger suitable habitat area. Zonation complementarity-based priorities are produced by iteratively removing grid cells based on two alternative rules, the additive benefit function (ABF) and core-area zonation (CAZ). ABF more heavily weights species richness whereas CAZ more heavily weights rare species, but both algorithms assign priorities to grid cell locations that best represent species composition (i.e., maximizing gamma diversity by prioritizing sites with high complementarity). Within Zonation software, we used default settings of additional parameters including using a warp factor of 200 and kept the boundary length penalty at 0. Moilanen (2007) describes details of the Zonation ABF and CAZ algorithms.

We assessed areas of agreement among prioritization methods in the context of the "30% by 2030" area-based target by overlaying the top-ranked 30% of pixels. We first reclassified the priority maps to bin the top 30% priorities into one class. We then overlaid these top 30%-priority maps to create new maps showing where one, two, three, and all four methods placed a pixel into the top 30% of priorities. We also calculated the proportion of total area in CONUS within these overlapping 30% priorities.

To assess landscape patterns of priorities, we identified patches of high-priority areas by grouping adjacent pixels within the top 30% for each method and taxonomic class. Specifically, we used the REGION GROUP tool in ArcGIS 10.7 to group adjacent pixels of the top 30% priorities. We based this grouping on four-neighboring pixel rule (using eight-neighboring pixels yielded similar results) and described adjacent pixel groups as "patches" of high priority. We then calculated the number of patches, as well as the average, median, and maximum size of patches, for the top-30%-priority pixels for each method and taxonomic class.

2.3. Q3: species-accumulation curves and performance of methods at 30% total area

After mapping priorities based on richness, RWR, ABF, and CAZ, we rank-ordered the pixel locations based on priority and plotted species-accumulation curves using the *specaccum* function in the R package *vegan* (Oksanen et al., 2019). In other words, we calculated how many total species would be accumulated as sites are added according to their priority, be it based on richness, RWR, ABF, or CAZ. Species-accumulation curves allowed us to compare how well different methods could represent species at different amounts of total area.

We first calculated and plotted species-accumulation curves based on species presence in pixels. We then calculated and plotted species-accumulation curves based on two different thresholds of proportion of species habitat representation across pixels (10% or 30% of each species' suitable habitat area). Our species-accumulation curves were created by counting the number of species in the highest priority pixel, then the number of unique species in the next highest priority pixel, and so on. Based on presence, species were counted if at least one pixel of suitable habitat was co-located with a pixel that was accumulated along the rank of priorities. Based on the 10% and 30% proportional thresholds, we only counted a species after either 10% or 30% of its suitable habitat was included in the accumulation of pixels. Representing species based on presence only would likely not protect the habitat area needed for a species to persist. Because individual species' area-targets are typically not developed, we used 10% and 30% suitable habitat area as two representation thresholds for our primary analysis. Proportional habitat targets have been mostly arbitrary, but other assessments have used proportional targets that vary with range size or extent with a minimal target of 10% of a species habitat (Rodrigues et al., 2004). In addition to using presence, 10%, and 30% suitable habitat as thresholds of representation, we also created "heatmap matrix" figures to summarize how species could be accumulated across priorities using a range of representation thresholds in 5% bins (Supplemental Fig. 2).

In response to "30 by 30" initiatives, we summarized our data based on species represented at 30% total area of CONUS. Specifically, we calculated the number and proportion of total species represented based on presence, 10%, or 30% thresholds at 30% of the total area of CONUS for all species-accumulation curves. However, species-accumulation curves display the number and proportion of species represented across the full range of area (from 0 to 100% total area) allowing us to compare the performance of prioritization methods for other area-based targets (e.g., 50% for assessing the "Half Earth" campaign).

We evaluated how well individual species' suitable habitat was represented at 30% total area among methods by comparing histograms of suitable-habitat representation (i.e., the percentage of each species' suitable habitat that would be represented within the top 30% priorities for each method). We also explored how representation of species at 30% total area varied by the size of species' habitat area. To do this, we produced scatterplots of the representation of each species against their total habitat area among different prioritization methods.

For each prioritization method, we also assessed patterns of species of conservation concern based on the classification of Dietz et al. (2020). While we did not create new prioritizations using species of conservation concern, we evaluated how well species of conservation concern would be represented as a post hoc assessment. We reasoned that the goal of "30 by 30" and other area-based targets is to conserve all species, but we were interested in how well prioritizations across all species would represent the subset of species known to be of conservation concern.

2.4. Q4: total area needed to represent 95% of species

Using the species-accumulation curves, we calculated the area needed to represent 95% of all species. Rather than focusing on the predetermined area-based target as above (i.e., 30% total area), we asked how much area is required to represent most species. Specifically, we calculated the percent area of CONUS required to represent 95% of all species pooled and mammals, birds, amphibians, and reptiles, separately, using the four prioritization methods and the three representation thresholds of species as above. Ninety-five percent of species was used as a convenient proportion of species to compare methods, but our accumulation curves display the full range of area and species represented.

2.5. Q5: distribution of priorities within existing protected areas and land ownership

Finally, we assessed the protected status of the top 30% of priority lands for each prioritization method using the USGS Gap Analysis Project's (USGS-GAP) Protected Areas Database version 1.4 (U.S. Geological Survey Gap Analysis Program, 2016). Specifically, we evaluated what proportion of the top 30% priority land was within protected areas (i.e., lands classified as GAP 1 or 2), unprotected federal lands (GAP 3 lands managed for multiple-use by the US federal government), and other lands with unknown conservation mandates (typically privately held lands). GAP 1- and 2-status lands are classified as highly protected because the management objectives include protection of biodiversity, mandates to maintain natural land cover, and prohibitions of most human exploitation of resources (U.S. Geological Survey Gap Analysis Program, 2016), though some GAP 2-status lands allow for state-regulated hunting. Unprotected federal lands (i.e., federal lands not classified as GAP 1 or 2) permit commercial development of timber and mineral resources, but also represent opportunities for efficiently safeguarding species based on existing legal authority and policy processes for elevating protected status (e.g., through national monument, wilderness, or national wildlife refuge designations).

While we focus here on how biodiversity priorities are distributed among protected areas as a post hoc assessment, we also conducted analyses where protected areas were included in the prioritization calculations. Specifically, we assessed maps and species-accumulation curves of richness weighted by the proportion of suitable habitat within existing protected areas, rarity- and representation-weighted richness (sensu Jenkins et al., 2015), and ABF and CAZ algorithms that optimized priorities after factoring in locations of protected areas. ABF and CAZ priority values with and without protected areas were highly correlated (Supplemental Fig. 3), therefore, we focused on evaluating protected areas as a post hoc assessment (see Supplemental Figs. 4–6 and Supplemental Tables 1–2 for the results of our analysis that included protected areas in the calculations of priorities).

3. Results

3.1. Q1: alpha, beta, and gamma diversity among taxa

Mean alpha diversity across all pixels (i.e., 24.5-km^2 pixels) and taxonomic groups was 248 species, with beta diversity equaling 5.8 (Table 1). Birds exhibited the highest gamma and mean alpha diversity but the lowest beta diversity, while amphibians exhibited the lowest gamma and mean alpha diversity but the highest beta diversity. Beta diversity for species of conservation concern was higher than for all species together.

Table 1
Gamma diversity (total number of species), mean alpha diversity (average number of species overlapping each 4950-m^2 pixel), and beta diversity ((gamma / alpha) − 1)) for all species combined, and mammals, birds, amphibians, and reptiles, separately. High beta diversity represents larger differences in species composition among pixels.

	Gamma	Alpha (mean)	Beta
All species	1697	248	5.8
Mammals	447	52	7.6
Birds	641	153	3.2
Amphibians	283	15	17.9
Reptiles	326	27	11.1
All species of concern	519	12	42.3
Mammals of concern	160	7	21.9
Birds of concern	123	4	29.8
Amphibians of concern	125	1	124.0
Reptiles of concern	111	1	110.0

3.2. Q2: maps of alternative biodiversity prioritizations

Spatial patterns of priorities varied by prioritization method and taxonomic class (Figs. 1 and 2). Consistent with global latitudinal gradients in species diversity, the southern US dominates priority locations based on richness. Maps of rarity-weighted-richness priorities were similar to maps of richness but with relatively higher values along the West Coast, in the southern Appalachian Mountains, and the Ozark region. Patterns of priorities also varied by taxonomic class. Priorities for mammals were concentrated in the West, with some variability among methods. Priorities for birds were concentrated in the Rocky Mountain West and the Southeast, with patterns also varying by method. Amphibian priorities for richness were highest in the East, but the other priority methods elevated the importance of the Southwest, the Northern Rockies, and the West Coast. Reptile priorities were concentrated in the South, with RWR, ABF, and CAZ also distributing priorities up the West Coast.

Half of the total area of CONUS was in the top 30% of priorities for at least one method based on the analysis of all species combined (Figs. 2 and 3, Supplemental Fig. 7), and the top 30% of all four priorities overlapped in 12% of CONUS. Similar patterns held for each of the taxonomic groups (Supplemental Fig. 7). In pairwise comparisons, the ABF and CAZ top-30% priority areas agreed on 78% of the area identified as the top 30% for all species (Fig. 2). Similarly, the RWR top priorities included 78% of the pixels identified as the top 30% by ABF (but only agreed on 70% of the pixels selected by CAZ). Richness produced the lowest agreement with the other three methods (68% agreement with RWR, 65% with ABF, and 51% with CAZ). While the area of overlapping top-30% priorities among methods was similar for taxonomic classes, the geographic distribution of overlap varied significantly, with mammal priorities concentrated in the West, amphibians in Appalachia and the Southeast, and reptiles in the South (Fig. 3).

The top-30%-priority pixels were arranged in several large and many small patches which varied by method and taxonomic class (Fig. 4; Supplemental Fig. 8). The top-30% area identified using the CAZ method resulted in fewer patches with smaller maximum-sized patches, but larger average- and medium-sized patches (Figs. 2 and 4). The top-30% priorities based on amphibian richness tended to result in fewer patches with the largest patch among taxa, though the median value of patch size for amphibian-richness priorities was only 24.5 km^2 (the size of one pixel). There tended to be more patches of smaller size for the top-30% priorities for birds than other taxa. The top-30% priorities for richness of all species resulted in the largest single patch at almost 1.9 million km^2 (representing over 81% of the total area of top-30% priorities), followed by RWR at 1.5 million km^2, ABF at 1.2 million km^2, and CAZ at 848,000 km^2.

3.3. Q3: species-accumulation curves and performance of methods at 30% total area

Prioritizing pixels based on richness almost always represented fewer species compared to the other prioritization methods, at least across the initial half of priorities (Fig. 5, Table 2). For most taxonomic classes and thresholds using all prioritizations, the methods converged after half the area of CONUS was included, though richness priorities tended to still capture fewer species (Fig. 5).

Zonation ABF and CAZ algorithms almost always outperformed other prioritization methods at representing species in the top-30% priorities of CONUS (Fig. 5, Tables 2 and 3). Differences in performance of methods varied by target threshold of representation of each species and taxonomic class. The top-30% priority pixels of CONUS could at least nominally (i.e., based on presence) represent 99% of species based on richness and RWR and 100% of species based on the Zonation algorithms.

Differences between prioritization methods varied more when using representation thresholds of 10% or 30% of species' habitat area within

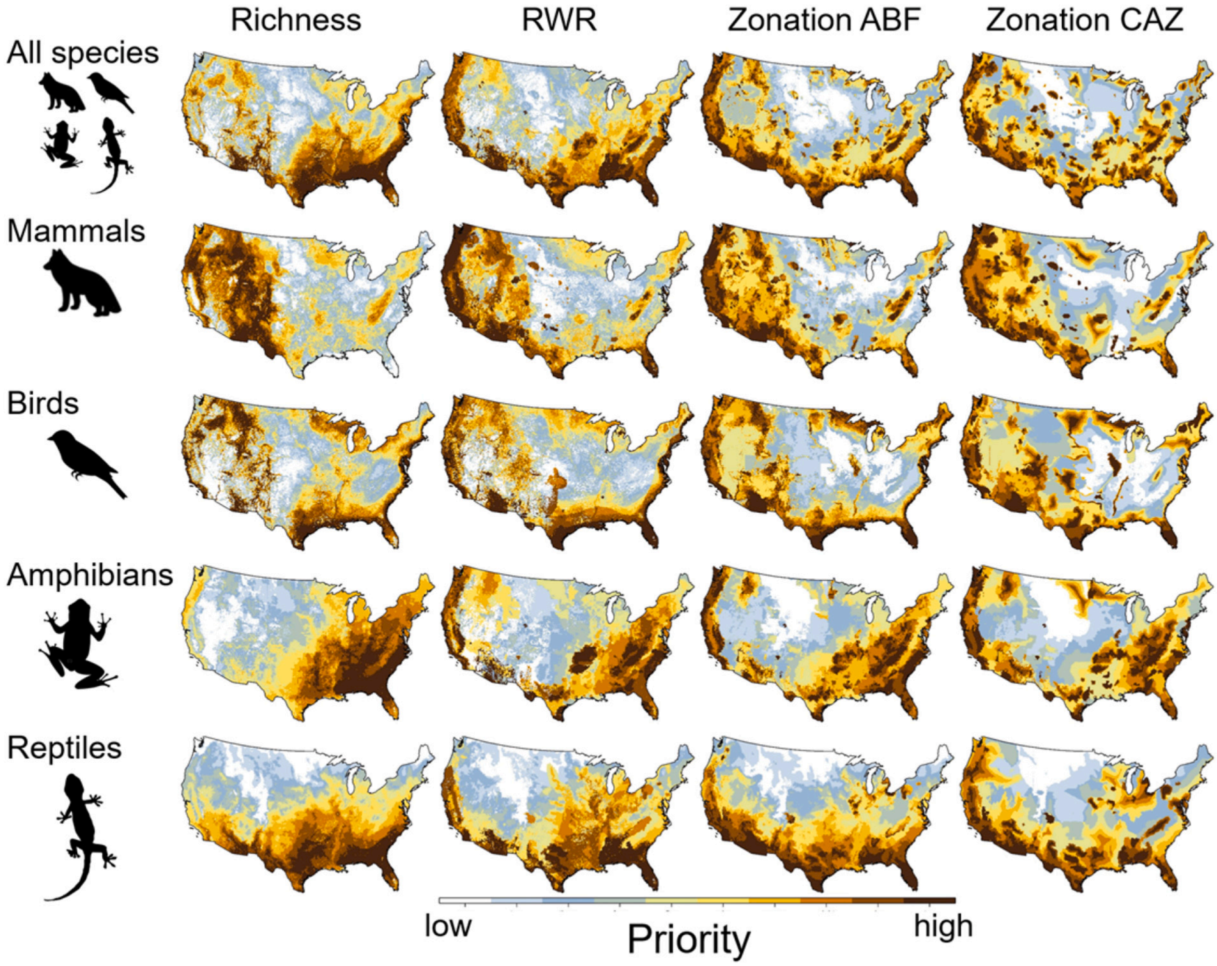

Fig. 1. Four alternative methods for prioritizing lands for biodiversity conservation (richness, rarity-weighted richness [RWR], and Zonation's additive benefit function [ABF] and core area zonation [CAZ]) for all species combined (top row), and mammals (second row), birds (third row), amphibians (fourth row), and reptiles (bottom row), separately. Color bins represent deciles for each map.

the top 30% total area of CONUS. When 10% of each species' suitable habitat was required, richness prioritization included 92%, RWR included 93%, ABF included 98%, and CAZ included 99% of species (Fig. 5 and Table 2). Achieving 30% of each species' suitable habitat, richness prioritization captured 68%, RWR included 76%, ABF included 78%, and CAZ included 77% of species. We observed similar comparisons of performance across taxa with some notable exceptions. Specifically, at a 30% target threshold for each species, richness performed better at representing bird species than other methods (Table 2).

Species of conservation concern tended to be better represented based on the 30% proportional habitat threshold compared to all species (Table 2 and Supplemental Fig. 9). RWR represented nearly as many species of conservation concern as ABF and CAZ algorithms. Richness was poorer at representing species, with the exception of birds—where richness did nearly as well as ABF and CAZ.

The distribution of species' representation at 30% of the total area of CONUS varied among prioritization methods (histograms in Fig. 6). RWR, ABF, and CAZ prioritization resulted in around 30% of species being very well represented (i.e., >95% of suitable habitat shown as the right-hand red bar in representation histograms of Fig. 6). RWR left more species poorly represented (<5% of species' habitat) compared to ABF and CAZ priorities (left hand grey bar in histograms of Fig. 6). Not surprisingly, species with large areas of suitable habitat tended to have lower proportions of their habitat represented across prioritizations (scatter plots of Fig. 6).

3.4. Q4: total area needed to represent 95% of species

The area needed to represent 95% of species varied by prioritization method, target threshold of proportional representation of species, and taxonomic class (Fig. 5 and Table 3). Zonation ABF and CAZ always performed better than richness or RWR. Using presence only, 95% of all species can be represented in <1% of the area of CONUS using either ABF or CAZ, whereas 18% of CONUS is needed using richness and 6% area is needed using RWR. The target of representing at least 10% of each species' suitable habitat takes 21% of CONUS to capture 95% of species using ABF compared to 17% area using CAZ, 36% using rarity-weighted richness, and 35% using richness prioritizations. The target of representing at least 30% of each species' suitable habitat takes 43% of CONUS to capture 95% of species using CAZ compared to 45% using ABF, 54% using rarity-weighted richness, and 57% using richness prioritizations. Similar patterns occur across taxa, again, with notable exceptions in birds that indicated richness prioritization required less area than the alternatives when focusing on the target of representing 30% of species' habitat area.

Less area was required to represent 95% of species of conservation concern using ABF or CAZ prioritizations compared to the area needed to represent all species (Table 3 and Supplemental Figure 9). For example, 31% of the total area under CAZ could represent 95% of all species of conservation concern at 30% proportional habitat area threshold. The area needed to represent 95% of species at 30% habitat area threshold varied by taxonomic class with amphibians requiring less

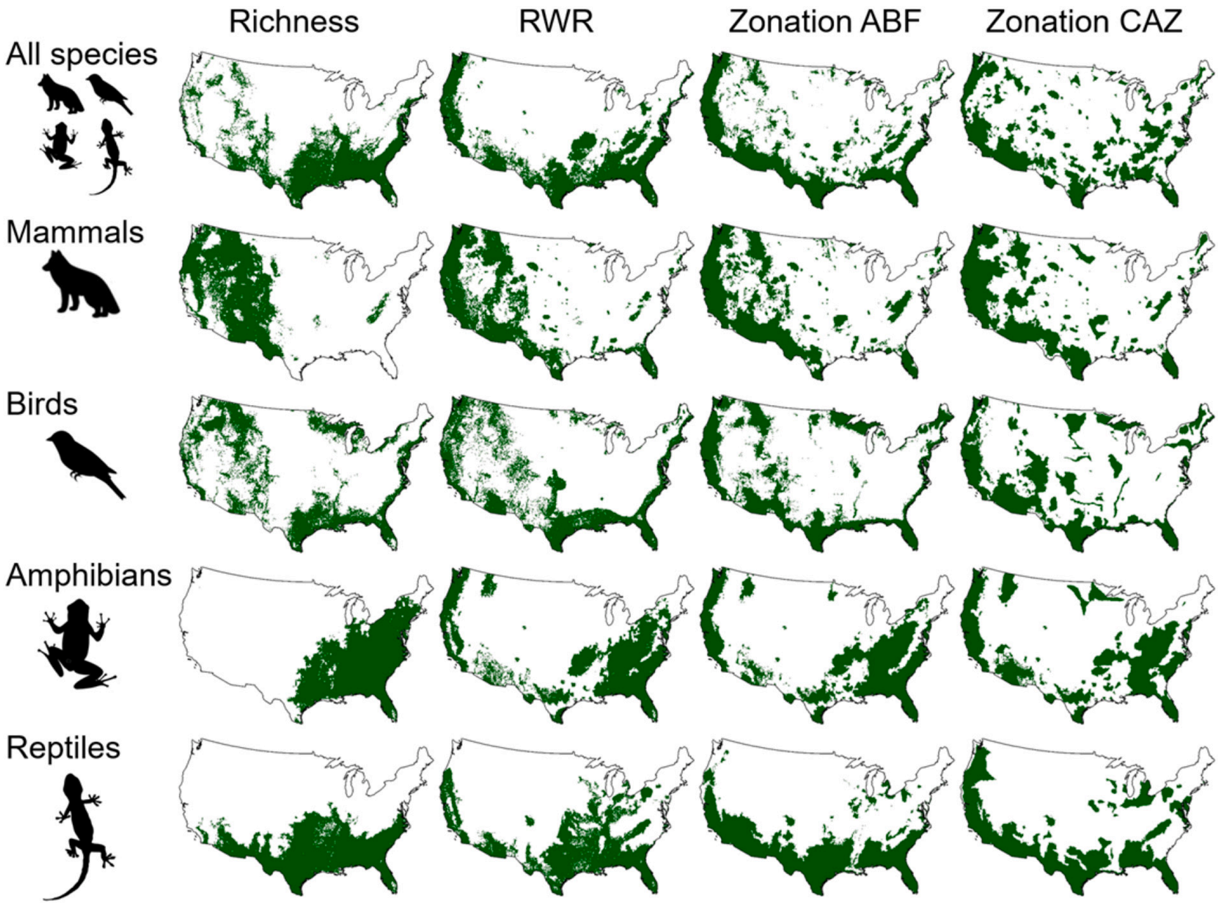

Fig. 2. The top-30%-priority areas based on four methods of biodiversity prioritization (Richness = species richness, RWR = rarity-weighted richness; Zonation ABF = additive benefit function; Zonation CAZ = core area zonation) for all species combined (top row), and mammals (second row), birds (third row), amphibians (fourth row), and reptiles (bottom row), separately. Which 30% to prioritize conservation depends on method and taxonomic class.

area (as little as 12%) and birds requiring the most area (a minimum 35% area would be needed).

3.5. *Q5: distribution of priorities within existing protected areas and land ownership*

The amount of area within protected, unprotected federal, and unprotected non-federal land varied among prioritization methods for the top 30% of priority land (Table 4). The top 30% of ABF and CAZ priorities were already better protected compared to richness and RWR priorities; 12% of the top 30% of both ABF and CAZ priorities were in GAP 1 or 2 areas, whereas only 6% and 8% were in GAP 1 or 2 lands for richness and RWR priorities, respectively. More of the top 30% of ABF and CAZ priorities were also within unprotected federal lands (21% and 22% for ABF and CAZ, respectively) compared to richness (13% in unprotected federal) and RWR (15% unprotected federal) priorities.

4. Discussion

Our results show that at least 10% of suitable habitat area for 99% of all terrestrial vertebrate species could be represented within 30% of CONUS. However, alternative methods for prioritizing pixels to safeguard biodiversity produced different maps that varied in how well they represent species. Results also varied by taxonomic class, which is partially explained by patterns of beta diversity. Optimization algorithms that consider complementarity were most efficient at representing biodiversity and produced fewer and generally larger priority patches with greater public-land conservation opportunities. We discuss these differences and their implications for conservation and the “30 by 30” initiative below.

4.1. *Differences among prioritization methods*

The locations of the top 30% of pixels for biodiversity conservation depend on the prioritization method. Priorities based on richness of all species tend to be concentrated in the Southeast, where overall species richness is highest. This pattern is consistent with the widely-observed increase in species diversity with decreasing latitudes (Schrodt et al., 2019). RWR and ABF, which heavily weight pixels with range-limited species that occur in species-rich locations, concentrated priorities along the coasts and southern border. CAZ, which prioritizes pixels where individual species are found in few other locations, identified more widely distributed priorities. CAZ prioritizes pixels that include endemic species in otherwise species-poor areas—resulting in high priorities assigned to locations that are “overlooked” by other methods. For example, the occurrence of the endemic Black Hills red-backed vole (*Myodes gapperi brevicaudus*) in the relatively species-poor Black Hills of South Dakota places the region into a high priority using CAZ.

The two Zonation methods (ABF and CAZ) were more efficient than other methods at representing species in minimal area, though at a 30% habitat threshold, RWR does as well for all species, taxonomic classes, and species of conservation concern (Table 3). The number of species represented at the 30% habitat threshold on 30% of the CONUS is comparable for RWR, ABF, and CAZ algorithms (over 75% for all species and over 90% for species of conservation concern; Table 2). Except for birds, richness underperforms by comparison.

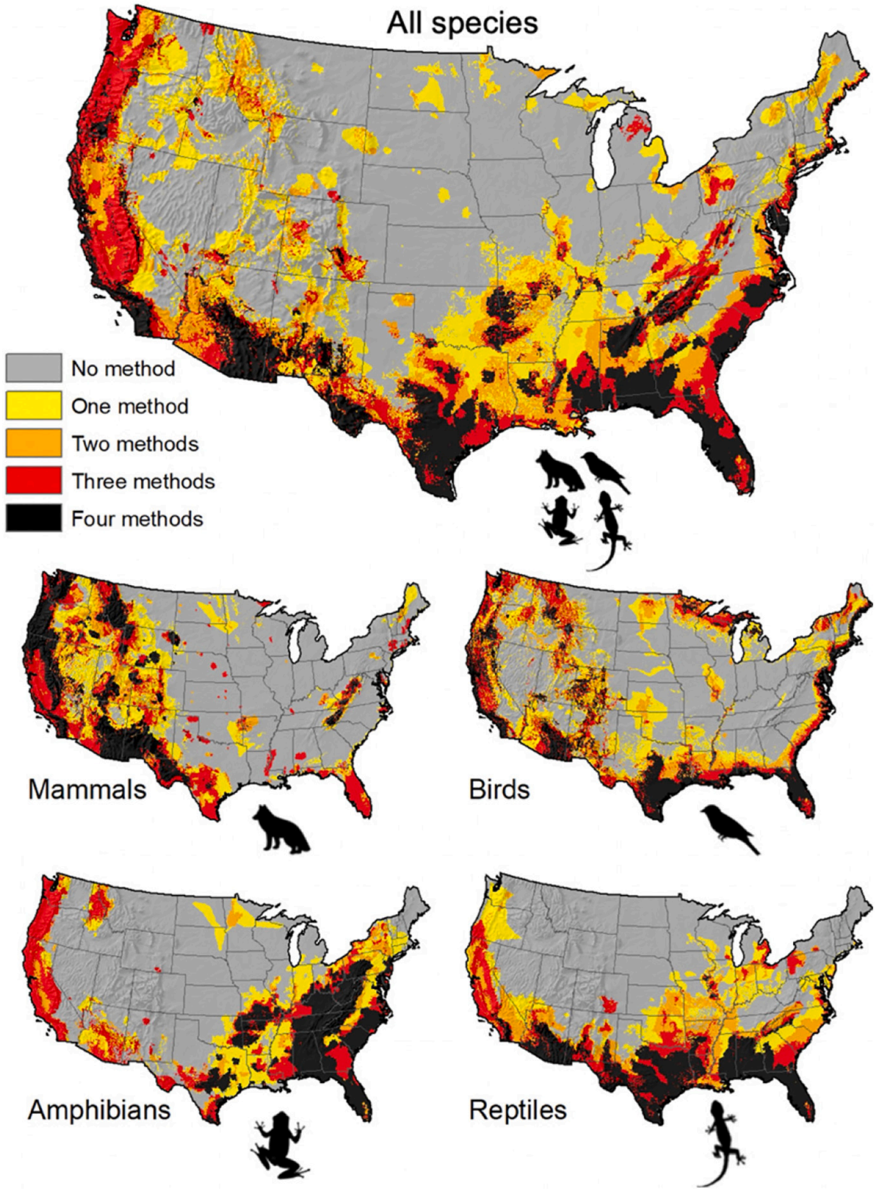

Fig. 3. Overlapping top-30% priorities among the four methods of prioritization for all species (top) and four taxonomic classes. Grey represents areas where no method placed the pixel in the top-30% highest priority. Black represents areas where all four methods placed a pixel in the top-30% highest priorities. Proportions of total area within overlapping classes are shown in Supplemental Fig. 7.

The four prioritization methods resulted in different patch size distributions, though all were highly skewed, with a few large patches and many small patches (Fig. 4, Supplemental Fig. 8). In the majority of cases the 30%-richest pixels were arranged in one very large patch. Except for CAZ (and, in one case, ABF), all methods resulted in the top 30% of priorities being represented as thousands of single pixels (~25 km^2). CAZ produced by far the smallest number of patches with the most even distribution of patch sizes. Spatial patterns of CAZ are likely the result of the iterative removal algorithm that tends to result in connected priorities (Moilanen, 2007). Patterns of aggregated priorities like those produced by CAZ could benefit conservation plans aimed at maintaining large-scale ecological processes. Small areas may be sufficient to protect habitats of some species (Boyd et al., 2008). However small disconnected patches of priorities could result in uncoordinated conservation actions which may not sustain ecological processes and viable species populations—both of which require large, contiguous blocks of conserved land. Additional work is needed to evaluate spatial patterns of conservation priorities and the area needed to sustain species (Boyd et al., 2008). The right size and arrangement of conservation reserves has been long debated (sensu Simberloff and Abele, 1982), and our work suggests that different prioritization methods result in different patch size distributions of adjacent high-priority pixels.

4.2. *Differences among taxa*

Maps of priorities varied by taxa, with mammals concentrated in the West, amphibians in the Southeast, reptiles across the South, and birds more widely distributed (Fig. 2). Similarly, taxa differed in the distribution of patch sizes identified by the prioritization methods, with birds generally prioritized in a higher number of smaller patches than other taxa for all methods except CAZ. All methods identified a largest-priority patch for reptiles in excess of 1.5 million km^2.

Across the prioritization methods, species of conservation concern were better represented than all species. Species of concern tend to have smaller suitable habitat areas than other species (Dietz et al., 2020), which could explain this result. Range size (or, in our case, area of

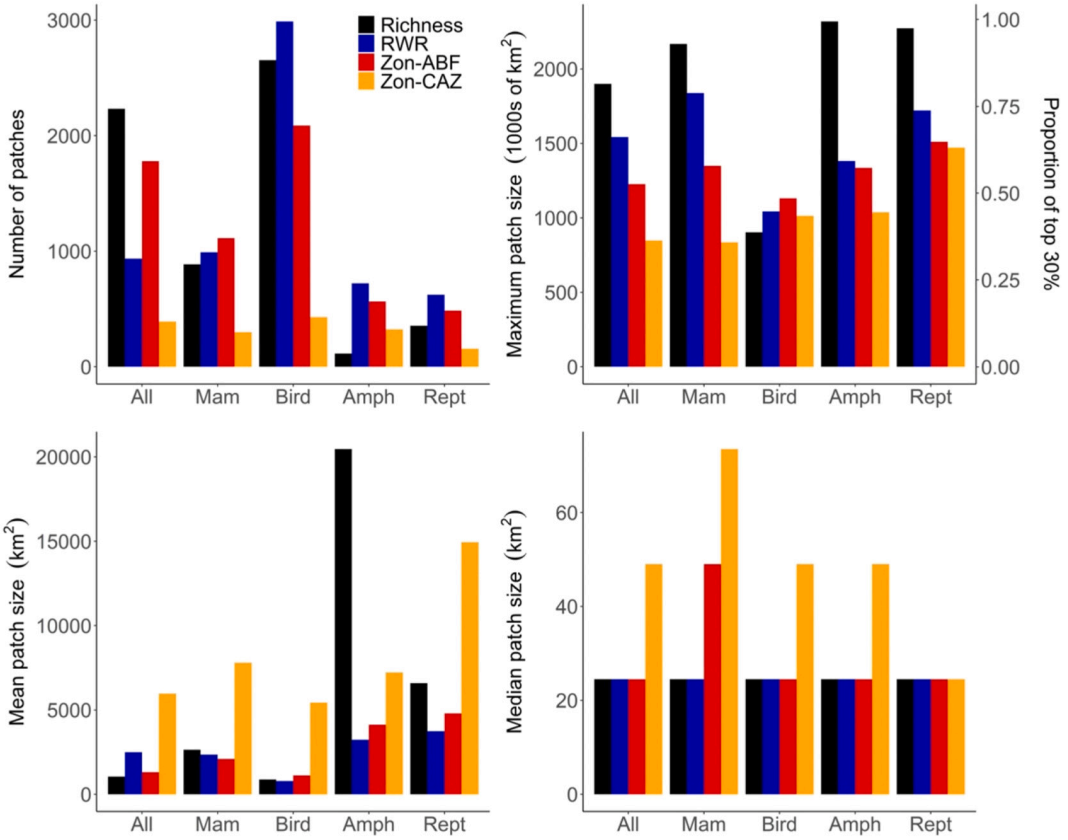

Fig. 4. Characteristics of patches of the top-30% priority of lands from four methods of biodiversity prioritization (Richness = species richness, RWR = rarity-weighted richness, Zon-ABF = Zonation additive benefit function, Zon-CAZ = Zonation core area zonation) and four taxonomic classes (All = all species combined, Mam = mammals; Bird = birds; Amph = amphibians; Rept = reptiles). Patch metrics of the top-30% priorities included number of patches (upper left), maximum patch size (upper right), mean patch size (lower left), and median patch size (lower right). Maps of top-30%-priority areas are in Fig. 2. The top-30% of Zon-CAZ priorities were typically distributed in fewer larger patches, and the top-30% priorities based on other methods were dominated by one large patch with many small patches the size of one pixel.

suitable habitat) has been considered a proxy for extinction risk (Jenkins et al., 2015) and often used in other biodiversity prioritizations (Dietz et al., 2020). Species with smaller ranges tended to be better represented across all prioritization methods (Fig. 6). In fact, range-limited species often occur in areas with high species richness and pixels with range-limited species receive high priority from the ABF and CAZ optimization algorithms.

4.3. *Interactions between prioritization methods and taxa: implications of beta diversity*

Complementarity-based methods that distribute priority pixels to maximize beta diversity (i.e., ABF and CAZ algorithms) were nearly always most efficient at representing species. Complementarity of sites is a widely acknowledged requirement for efficiently representing species in conservation reserve design (Sarkar, 2012). For taxa with lower beta diversity (e.g., birds), richness alone may serve as an adequate prioritization method. In fact, prioritizing pixels based on richness (i.e., alpha diversity) alone was the best method at representing bird species at 30% habitat thresholds. However, when beta diversity is high (e.g., amphibians), richness performs poorly as a prioritization method. If species composition among sites varies significantly (i.e., high beta diversity), methods such as CAZ are better at capturing biodiversity more efficiently. In other words, accounting for site complementarity in conservation planning is most critical when beta diversity is high.

Driven by a desire to understand the causes of differences in species composition among sites, a growing number of ecological studies have documented patterns of beta diversity (Anderson et al., 2011). While site complementarity depends on beta diversity (i.e., differences in species composition) to select sites, few investigations have directly linked beta diversity to site complementarity (Pollock et al., 2020). We recommend that ecologists interested in biogeographic patterns of species composition and conservation scientists interested in protecting biodiversity develop a shared research agenda (Pollock et al., 2020). Understanding how and why species composition varies along environmental gradients would allow conservation scientists to design actions aimed at sustaining biodiversity among sites and through time, especially with rapid environmental change. Identifying a network of sites for conservation based on site complementarity and beta diversity in light of environmental gradients can incorporate movement and dispersal of species among protected areas and ensure biodiversity conservation despite environmental changes (Lawler et al., 2020). Other research could investigate whether representing environmental diversity (Carroll et al., 2017) among a system of conservation priorities would also represent well species diversity.

4.4. *Implications for prioritization*

Identification of priority sites for inclusion in any effort to protect 30% of species' habitat by 2030 will depend both on the methods used and the species included. Our results indicate that RWR, ABF, and CAZ are able to represent >75% of all species and >90% of species of conservation concern at the 30% habitat threshold on 30% of CONUS. Individual taxonomic classes can be represented at even higher levels. The performance of these methods at 30% total area supports the findings of Albuquerque and Beier (2015). They showed that rarity-weighted

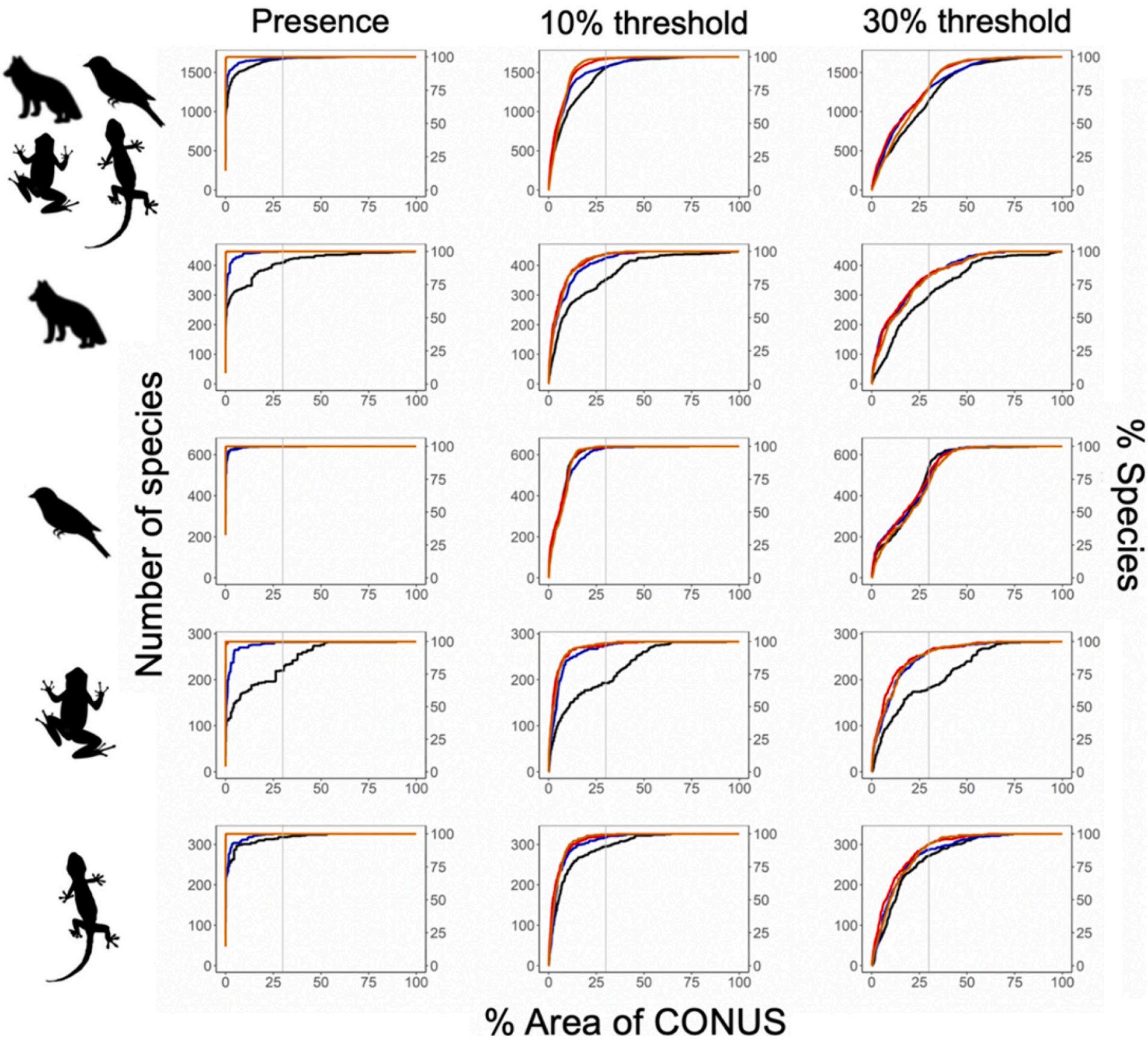

Fig. 5. Species-accumulation curves for four methods of biodiversity prioritization based on three thresholds of proportional habitat (presence, 10% habitat, or 30% habitat). The four prioritization methods include species richness (black line), rarity-weighted richness (RWR, blue line), and Zonation's additive benefit function (ABF, red line) and core area zonation (CAZ, orange line) for all species combined (top row), and mammals (second row), birds (third row), amphibians (fourth row), and reptiles (fifth row), separately. The vertical line represents 30% of the total area of CONUS. Accumulation curves for species of conservation concern are shown in Supplemental Fig. 9. In general, species accumulate with area more slowly using richness as the prioritization method compared to the other methods.

Table 2
Percent of species represented at 30% of the total area of the contiguous US based on four biodiversity-prioritization methods: species richness, rarity-weighted richness (RWR), and Zonation's additive benefit function (Zon ABF) and core area zonation (CAZ). Species were represented based on presence and two thresholds of species habitat representation (10% and 30%). Zonation algorithms often represented the most species. As the threshold of representation for species' habitat area increased from presence to 30%, fewer species were represented.

	Presence				10% threshold				30% threshold			
	Richness	RWR	Zon ABF	Zon CAZ	Richness	RWR	Zon ABF	Zon CAZ	Richness	RWR	Zon ABF	Zon CAZ
All species	99	99	100	100	92	93	98	99	68	76	78	77
Mammals	92	100	100	100	79	95	98	98	66	81	82	81
Birds	100	100	100	100	99	99	100	100	85	76	78	71
Amphibians	78	100	100	100	68	97	98	99	65	93	93	92
Reptiles	98	100	100	100	90	97	99	100	83	88	92	92
All species of concern	97	98	100	100	88	95	99	100	72	91	93	94
Mammals of concern	81	100	100	100	72	98	100	100	59	93	93	93
Birds of concern	100	100	100	100	97	98	98	100	91	89	93	93
Amphibians of concern	64	100	100	100	58	100	100	100	57	99	100	100
Reptiles of concern	97	100	100	100	90	96	99	100	85	95	97	98

Table 3

Percent area of the contiguous US needed to represent 95% of all species and mammals, birds, amphibians, and reptiles, separately, based on four biodiversity prioritization methods: species richness, rarity-weighted richness (RWR), and Zonation's additive benefit function (Zon ABF) and core area zonation (Zon CAZ). Species were represented based on presence and two thresholds of species habitat representation (10% and 30%). Zonation algorithms were often most efficient (required less area) at representing 95% of species. As the threshold of representation for species' habitat area increased from presence to 30%, more area was required to represent 95% of species.

	Presence				10% threshold				30% threshold			
	Richness	RWR	Zon ABF	Zon CAZ	Richness	RWR	Zon ABF	Zon CAZ	Richness	RWR	Zon ABF	Zon CAZ
All species	18	6	<1	<1	35	36	21	17	57	54	45	43
Mammals	38	5	<1	<1	47	30	23	22	59	49	51	51
Birds	2	1	<1	<1	16	21	15	14	37	38	40	41
Amphibians	46	7	<1	<1	53	26	15	13	62	34	32	36
Reptiles	18	8	<1	<1	41	24	17	15	50	46	36	34
All species of concern	27	12	<1	<1	47	29	13	11	68	42	33	31
Mammals of concern	62	5	<1	<1	64	21	13	14	92	39	34	34
Birds of concern	5	6	<1	<1	18	21	16	11	38	36	37	35
Amphibians of concern	50	7	<1	<1	56	12	5	5	62	17	12	13
Reptiles of concern	28	11	<1	<1	40	25	8	7	43	28	22	21

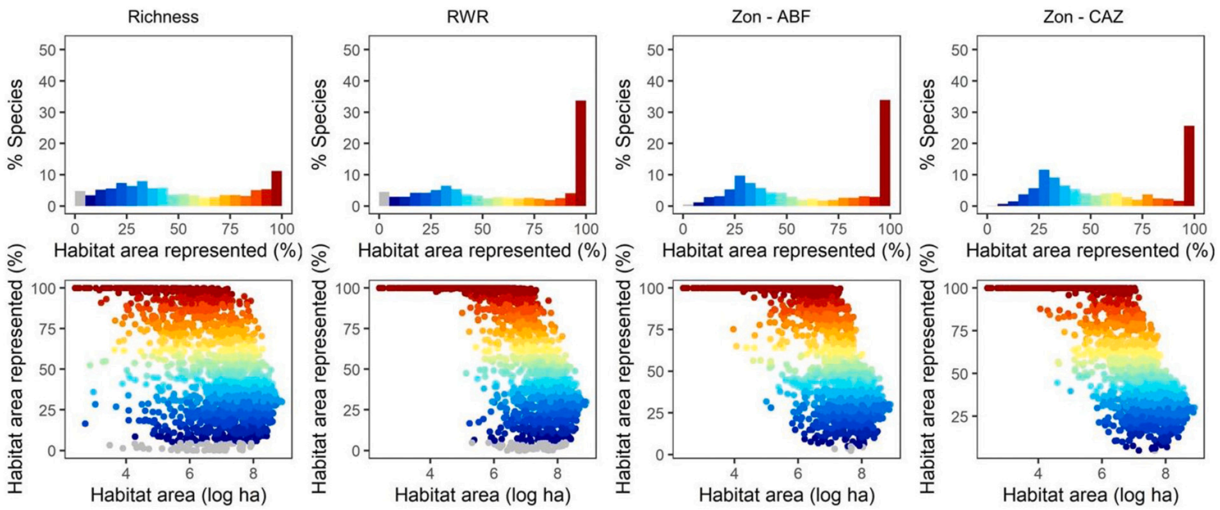

Fig. 6. (Top row) Histograms of the percent of suitable habitat for species represented at 30% CONUS using different prioritization methods including richness, rarity-weighted richness (RWR), Zonation additive benefit function (Zon - ABF), and Zonation core area zonation (Zon - CAZ). (Bottom row) Scatterplots show how representation of species varies with their total habitat area. Species with smaller suitable habitat area tended to be better represented at 30% of CONUS compared to species with larger suitable habitat area.

Table 4

Top 30% of land among four alternative biodiversity-prioritization methods (richness, rarity-weighted richness [RWR], and Zonation's additive benefit function [Zon ABF] and core area zonation [Zon CAZ]) vary with respect to unprotected non-federal lands, unprotected federal land, and existing protected areas. Values represent the proportion (%) of the top-30% priority land that occurs within each ownership and protected class (e.g., 81% of the 30%-most-species-rich areas are in unprotected non-federal land). Alternative prioritization methods are grouped by ownership. For all species and most taxonomic classes, the top 30% of Zonation priorities were more protected and represented greater conservation opportunities than species richness or RWR. Most of the top-30% priorities of all methods were located on unprotected non-federal land.

	Unprotected non-federal				Unprotected federal				Protected			
	Richness	RWR	Zon ABF	Zon CAZ	Richness	RWR	Zon ABF	Zon CAZ	Richness	RWR	Zon ABF	Zon CAZ
All species	81	77	67	67	13	15	21	22	6	8	12	12
Mammals	46	53	55	57	41	32	31	30	13	15	14	13
Birds	73	72	68	67	19	18	21	21	9	10	11	12
Amphibians	90	77	78	73	6	15	14	18	4	8	8	9
Reptiles	86	84	76	75	9	10	15	16	5	5	9	9

richness tends to perform as well, or nearly as well, as CAZ at representing species across several study sites and various taxa. Not surprisingly, focusing conservation only on regions with high alpha diversity would fail to protect all species, a finding similar to those of a global analysis of marine mammals (Astudillo-Scalia and Albuquerque, 2020). The proportion and configuration of habitat required to maintain viable populations is unknown for most species. But as more knowledge is gained about the viability of species populations, future work could vary the proportional targets for each species to prioritize efforts.

Our research includes only terrestrial vertebrates. Other recent biodiversity priorities also included fish and trees (Jenkins et al., 2015) and pollinators (NatureServe's map of biodiversity importance). Across the taxonomic classes, we assessed whether priorities were correlated (Supplemental Fig. 10). Only richness of amphibians and reptiles were positively correlated; richness of amphibians and mammals was negatively correlated. This suggests that one taxonomic group may not serve as a proxy for other groups using richness. However, correlations between priorities of taxonomic classes within ABF and CAZ algorithms tended to be positive because Zonation algorithms distribute priorities to maximize complementarity, which results in more similar geographic patterns (compare ABF and CAZ outputs for taxa in Figs. 1 and 2). While incidental opportunities may exist to represent species based on proxy or surrogate taxa (sensu Leal et al., 2020), we urge caution in making this assumption broadly. As habitat maps of more species and taxonomic groups are developed (e.g., invertebrates, herbaceous plants, fungi), researchers should continue to develop more taxa-inclusive prioritizations.

Further, our assessment involved analysis only of suitable habitat of species. Others have suggested that efforts to prioritize protected-area expansion should consider additional factors, such as ecosystem diversity, geophysical diversity, habitat connectivity, carbon sequestration, climate-change refugia, and cost (Carroll and Ray, 2021; Jung et al., 2021; Chauvenet et al., 2020; Dinerstein et al., 2019; Roberts, O'Leary, & Hawkins, 2020). Analyses show that inclusion of these additional factors into prioritization schemes results in different maps of priorities (Carroll and Ray, 2021; Lawler et al., 2020; Simmons et al., 2021). Moreover, prioritizations conducted at different spatial scales may result in different priorities (Pouzols et al., 2014).

In addition to the challenges presented by different targets and different scales, researchers will need to consider challenges posed by the complexity of the prioritization methods themselves. While ABF and CAZ algorithms performed better than the rank orders of richness or RWR, they are not always easily understood by policy makers and the public. In contrast, maps of richness (alpha diversity) are easily understood and communicated as priorities for conservation action. Richness maps clearly identify the number of species likely to inhabit any given area. RWR, ABF, and CAZ maps lack this information. Even though maps of richness did not efficiently represent biodiversity priorities, they are widely used in regional conservation assessments to identify priorities, especially when biodiversity is considered a co-benefit to other conservation values (see, e.g., Buotte et al., 2020; McKinley et al., 2019. Species-rich areas are often considered “the biggest bang for the buck,” but our results do not support this conclusion (see also Astudillo-Scalia and Albuquerque, 2020).

4.5. *Implications for conservation*

Conservation prioritization requires identifying actions to achieve specific objectives (Game et al., 2013). Designating protected areas, establishing conservation easements, restoring ecosystems, managing invasive species, and funding species-specific conservation will be needed to sustain biodiversity. We identified places for efficiently implementing these activities. Interestingly, the method that most efficiently represents biodiversity (i.e., CAZ) also distributed more of the top 30% of lands in existing protected areas and unprotected federal land (Table 4). In other words, the most efficient prioritization method also provided the best opportunities to implement actions on protected lands and unprotected public lands. Still, most ($\geq$55%) of the top 30% of every prioritization method occurs outside of public land.

When feasible on unprotected public lands, we recommend establishing new protected areas or conservation reserves that prohibit harmful activities such as resource extraction, road building, and unsustainable recreation that negatively impact species. Outside of public lands, conservation easements could secure habitat from development. Other activities that address the primary threats to species will be needed across all lands (Wilcove et al., 1998). For instance, even within established protected areas, species will need to be monitored for threats associated with invasive pathogens and ongoing changes in climate.

Protected areas are an important strategy for conserving biodiversity, and identifying where to establish or expand them is a valuable exercise. However, safeguarding species will require that new protected areas be viewed as part of an inclusive set of regional and landscape conservation plans. Such planning must be appropriately sized to provide for the conservation of species' populations and ecological processes that maintain them (Belote et al., 2021). The methods we evaluated resulted in a set of patches either too large to practically guide protected area designation or likely too small to sustain viable populations of most species. Our results can be a useful guide to the location of future conservation activities and may help conservation planners understand the consequences of alternative methods among different taxa, but they also highlight the challenges in locating the optimal 30% to be protected by 2030.

We suggest our maps and others like them inform regional and landscape conservation planning. Within priority regions and landscapes, an inclusive set of stakeholders should develop and implement comprehensive conservation strategies that integrate protected areas, ecological restoration, and sustainable land use to address the objectives of the “30 by 30” initiative. More research could be conducted on the overlap between conservation priorities and diverse human communities. The spatial dispersion of priority maps we observed from CAZ could also better reflect human diversity in terms of race and socioeconomic conditions (sensu Belote et al., 2021), which may provide opportunities for creating diverse and inclusive conservation campaigns. Conservation actions implemented to sustain biodiversity should be designed and implemented in a way that engages and empowers – not alienate and disenfranchise – people who live in priority places.

5. Conclusions

One of the primary goals of campaigns to protect or conserve 30% of land and water by 2030 (with the ultimate goal of protecting “half Earth”) is to sustain biodiversity (Dinerstein et al., 2019; Jung et al., 2021; Visconti et al., 2019). On which 30% of lands should we focus conservation attention? This will depend on what taxa are included and what prioritization method is used. Our intent was not to produce *the* map representing the best 30% of sites to protect, but instead to demonstrate the variation in maps between different prioritization methods. Representing all species (i.e., gamma diversity) requires distributing priorities to capture diversity among sites (i.e., beta diversity), which is done using the complementarity-based prioritization methods. Ultimately, conservation actions implemented to safeguard all species will require eliminating the causes of species decline, and implementing diverse conservation actions across ownerships, not simply designating “30 by 30.” Designating protected areas will remain necessary, but not sufficient, to the conservation of biodiversity.

CRediT authorship contribution statement

R. Travis Belote: Conceptualization, Data curation, Formal analysis, Software, Visualization, Writing – original draft. **Kevin Barnett:** Conceptualization, Software, Writing – review & editing. **Matthew S. Dietz:** Conceptualization, Writing – review & editing. **Laura Burkle:** Conceptualization, Writing – review & editing. **Clinton N. Jenkins:** Conceptualization, Writing – review & editing. **Lindsay Dreiss:** Conceptualization, Writing – review & editing. **Jocelyn L. Aycrigg:** Conceptualization, Writing – review & editing. **Gregory H. Aplet:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109378.

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