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An assessment of vulnerable wildlife, their habitats, and protected areas in the contiguous United States

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ABSTRACT

Although they are the foundations of most efforts to conserve biodiversity, protected areas in the United States have, historically, not always been located in the most important areas to accomplish this goal. We investigated the overlap between suitable habitat for wildlife species of conservation concern and the location of public and private highly protected areas to assess the degree to which current highly protected areas are providing fine-scale habitat for wildlife species of conservation concern, to explore the relationship between the size of total suitable habitat of a species and its vulnerability to extinction, and to identify the species that are poorly represented in highly protected areas and determine where their habitats overlap—i.e., where future protected areas may best be located. We found that nearly one third of terrestrial wildlife species in the contiguous U.S. are vulnerable to extinction and that even though there is a relationship between total suitable habitat area and vulnerability, we find that synthetic indices of endemism and rarity-weighted richness are not necessarily good indicators of whether a species will be of conservation concern. Of all 537 wildlife species of conservation concern, only 62 (11%) are well represented in highly protected areas. To increase representation of habitats of wildlife species of conservation concern, scientists and managers should look to preserve lands where there is the greatest overlap among habitats for species of concern that are currently poorly represented in the reserve system, with special focus on species with small ranges on public lands.

1. Introduction

Protected areas are the foundations of most regional, national, and global efforts to sustain natural ecological processes and conserve biodiversity (Bertzky et al., 2012). Studies show that, worldwide, biodiversity is substantially higher inside than outside well-managed terrestrial reserves (Gray et al., 2016) because protected areas reduce the loss and degradation of natural habitats (Bruner et al., 2001; Naughton-Treves et al., 2005) and slow the rate of extinction of threatened species that occur therein (Butchart et al., 2012). For these reasons, the Convention on Biological Diversity (CBD) has set a goal to conserve at least 17% of terrestrial areas worldwide by 2020—the Aichi Target 11 (Woodley et al., 2012). Similarly, The Global Deal for Nature, a science-driven plan to save the diversity and abundance of life on Earth, has set a goal to conserve at least 30% of the Earth's surface by 2030 as a milestone toward the ultimate goal of half of the planet protected by 2050 (Dinerstein et al., 2019).

The proportion of the Earth's land area that purportedly must be protected to achieve conservation goals is often extrapolated from regional studies (e.g., Pressey et al., 2003) and clearly cannot be tested experimentally at a global scale. Many scientists agree, however, that ambitious targets can be useful (e.g., Wilson, 2016) as long as protected areas adhere to the principles of conservation biology (e.g., Noss and Cooperrider, 1994; Margules and Pressey, 2000; Dinerstein et al., 2019): 1) they represent the full range of native ecosystem types and successional stages; 2) they are sufficiently large and well distributed to maintain viable populations of all native species; 3) they are sufficiently connected to allow movement of species between reserves; and 4) they are left sufficiently untrammeled so that large-scale natural processes—such as fires, floods, and disease outbreaks—are allowed to occur. When considering biodiversity, the precise *proportion* of land protected may, in fact, matter less than the *spatial distribution* of protected areas (Dinerstein et al., 2019).

Yet, historically, protected areas on public lands in the United States

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have often been established through a combination of political expediency, attempts to avoid resource-use conflicts, and a public desire for primitive recreation, solitude, and outstanding natural scenery—-with only a relatively recent appreciation for the contribution of protected areas to sustaining plant and animal populations, with notable exceptions for charismatic fauna (e.g., Porcupine caribou [*Rangifer tarandus granti* Allen]) and iconic flora (e.g., giant sequoia [*Sequoiadendron giganteum* Buchholz]) (Cordell et al., 2005). National Wildlife Refuges are another notable exception, although they were often established for the "production" of migratory waterfowl and did not have a strong and singular wildlife conservation mission until the passage of the National Wildlife Refuge System Improvement Act in 1997 (Public Law 105–57). As a result, public protected areas may not have always been located in the most important areas for conservation of biodiversity. Private land protected areas are varied in their goals, incorporating everything from farmland preservation to protecting open space around cities to preserving habitat for endangered species. Some non-governmental conservation organizations (e.g., The Nature Conservancy) have a biodiversity-conservation mission, but often focus on rare or threatened plant species. We predict, therefore, that our current protected-area system—both public and private—is not capturing habitats for wildlife species of conservation concern nearly as well as it could be, considering its relatively large size.

Currently, only 15% of the Earth's terrestrial realm and 13% of the United States' land area (7.1% of the contiguous US) are highly protected (Bertzky et al., 2012), and the likelihood of achieving the aforementioned targets by 2020 or 2030 is diminishing. There is hope, however, that deliberate, species-targeted conservation planning will mitigate the shortfall in area with better representation of habitats for species of conservation concern. But how should scientists or managers go about representing habitats for vulnerable species in highly protected areas?

Previous research has investigated how well *ecosystems*—which can serve as rough proxies for species' habitats—are represented in highly protected areas in the United States (Aycrigg et al., 2013; Dietz et al., 2015). Ecosystem representation, however, may be necessary but not sufficient for species' protection—especially if ecosystems are examined at a too-broad level of classification. For example, Venter et al. (2014) modeled several scenarios where current and new protected areas worldwide would cover 20% of Earth's surface. A scenario with the sole purpose of adequately protecting threatened bird, mammal, and amphibian species could protect habitat for all 4118 threatened (defined as IUCN Red List Critically Endangered, Endangered, or Vulnerable) species (100%). In contrast, only 867 threatened species (21%) could be protected in a scenario that ensured only that each of the Earth's 821 terrestrial ecoregions—a *broad* measure of ecosystem type—received at least 17% protection per the CBD's 2020 target. Scientists have recently pointed out that although ecoregional representation within protected areas increased substantially from 1954 to 2013, species representation within protected areas increased much less because ecoregions may be too coarse of a filter to capture the habitat needs of endemic, narrow-ranged, or specialist species (Visconti et al., 2019). Although achieving ecosystem representation at a finer level of classification (e.g., Dietz et al., 2015) than the ecoregions in the example above may serve to capture a greater proportion of species of conservation concern, these assessments still may serve only as imprecise proxies for protecting species; species-level assessments may, therefore, also be necessary.

In fact, many scientists have addressed the need for protected areas to capture species-level biodiversity at various scales (Pressey, 1994; Margules and Pressey, 2000; Gaston et al., 2008; Aycrigg et al., 2016; Pimm et al., 2018; Venter et al., 2018). Recent studies have investigated the general mismatch between current protected areas and biodiversity hotspots (McKerrow et al., 2018) or between protected areas and places rich in range-limited and endemic species (Jenkins et al., 2015). While these evaluations of conservation priorities that are based on measures of total species richness, range limitations, or endemism are useful (Belote et al., 2017a, 2017b), they focused on indices of biodiversity, as opposed to conducting a direct assessment of habitat needs for species of conservation concern. Many previous biodiversity prioritization assessments rely on the assumption that range size is associated with species vulnerability to extinction (Albuquerque and Beier, 2015; Jenkins et al., 2015). Yet many species that are not of conservation concern may in fact have smaller areas of suitable habitat than species of conservation concern, and vice versa.

Here, we investigate the overlap between suitable habitat for wildlife species of conservation concern and the location of highly protected areas in the contiguous U.S., with three goals in mind: to assess the degree to which current highly protected areas are providing fine-scale habitat for wildlife species of conservation concern, to explore the relationship between the size of total suitable habitat of a species and its vulnerability to extinction, and to identify the species that are currently poorly represented in highly protected areas and determine where their habitats overlap—an indication of where future protected areas would be most efficiently located to conserve species.

This assessment is valuable for several reasons. First, we are focusing on species of conservation concern, rather than measuring the complete community of species (i.e., total richness), irrespective of conservation status, in a given area. Second, our definition of species of conservation concern does not rely on proxies of vulnerability derived from limited range size, but rather includes only those species that are actually listed as vulnerable by law (Endangered Species Act [ESA]) or widely accepted standards (IUCN Red List and NatureServe). This method complements previous research that determined conservation priorities based on synthetic biodiversity indices, such as that used by Jenkins et al., 2015, which calculated priority scores for each of a group of endemic plant and animal species equal to the proportion of the species' range that is unprotected, divided by the area of a species' range, and summed across all taxa. Moreover, because we are including multiple assessments of vulnerability—as opposed to evaluating just one, such as ESA listing—we are effectively creating a new and more inclusive classification of vulnerability. Third, concentrating on species of conservation concern rather than weighted-richness indices of all species allows us to explore the relationship between *individual* species' ranges and the locations of protected areas, so that we can make specific recommendations for species' management and recovery. Such an approach allows us to move beyond the much-needed "exposés" of the mismatch between locations of protected areas and patterns of biodiversity and to instead focus attention directly on conservation priorities for protecting habitats of species of conservation concern (Simberloff, 1998).

In this paper we answer the following questions:

1) What proportion of wildlife species in the contiguous United States are species of conservation concern? How much does that proportion vary by taxonomic class?
2) How does the total area of suitable habitat vary among individual wildlife species, by taxonomic class, and by conservation status?
3) How well do protected areas in the contiguous United States represent the habitats of wildlife species? What percent of wildlife species' habitats are in highly protected areas? How does that level of protection vary by class, conservation status, and area of suitable habitat?
4) How is the richness of species of conservation concern (SCC) distributed spatially across the contiguous United States?
    a. How are SCC that are currently poorly represented in highly protected areas distributed?
    b. How are SCC that are poorly represented and with small habitat areas distributed?
    c. How are SCC that are poorly represented and with small habitat areas and large opportunity for conservation distributed?

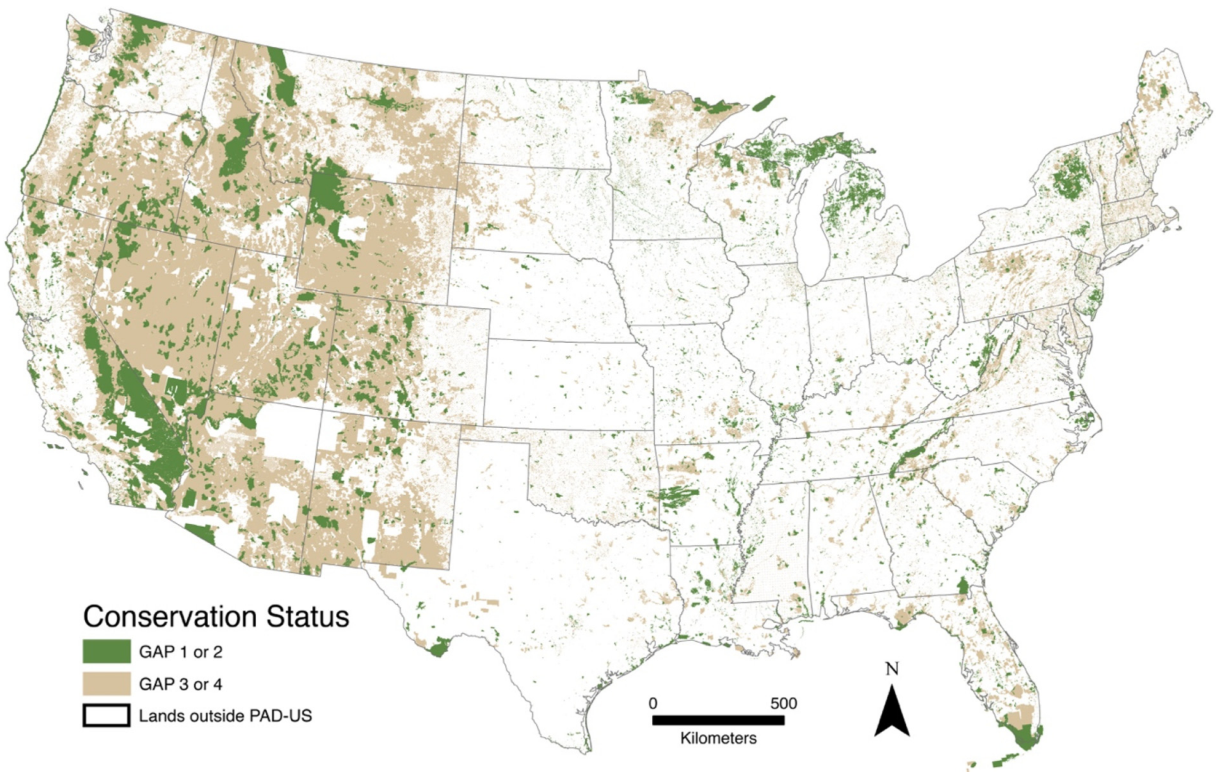

Fig. 1. The current protected-area system. The 48 contiguous United States with "highly protected areas" (GAP 1 or 2 status) in green and lands with "conservation opportunity" (GAP 3 or 4 status) in brown. White areas are lands not in the protected area database (PAD-US). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

Vertebrate species are the only animal taxa for which we have complete fine-scale habitat data across the contiguous United States. Fine-scale habitat data have recently become available for all terrestrial vertebrates across the contiguous United States, which is not the case for other animal or plant taxa. Invertebrate data, for example, are typically incomplete at a national scale, and spatial resolution of herbaceous vegetation data in the U.S. is usually available only at the county level (e.g., US Department of Agriculture PLANTS Database). In addition, because ecosystem representation analyses have already focused attention on woody vegetation dominance-types (e.g., the National Vegetation Classification System), we did not examine trees or shrubs. Because we are interested here in the current and possible future contribution of the *terrestrial* protected area system in protecting species of conservation concern, we focused on terrestrial vertebrate species of the contiguous United States—or what are commonly referred to as "wildlife." We also do not consider cetaceans, as they are outside the scope of this study, or fish, as there is a more tenuous relationship between land protection and fish habitat than there is for habitat of terrestrial vertebrates (due to human-caused disturbances, such as dams, outside of protected-area boundaries).

We used the most recent version of the highest-resolution mapped data available (30 m × 30 m) for wildlife habitats in the contiguous United States: U.S. Geological Survey GAP Analysis Program species habitat maps (Gergely et al., 2019). These data, published July 2018, represent the first complete compilation of terrestrial vertebrate models for the contiguous U.S. (fine-scale wildlife habitat data are incomplete for Alaska and Hawai'i), based on 2001 ground conditions (McKerrow et al., 2018). These models include all 1590 mammal, bird, amphibian, and reptile species found in the contiguous U.S. during summer, winter, or year-round and 129 subspecies of terrestrial vertebrates that the Gap Analysis Project team determined had ranges that were spatially distinct and had unique habitat relationships that warranted a separate subspecies model (Gergely et al., 2019). These GAP habitat maps are derived from a deductive habitat suitability model—the Wildlife Habitat Relations Model—which uses remotely-sensed spatial information on habitat variables within a species' range (based on known occurrence points) to predict spatial occupancy of a species (see complete methodology in Gergely et al., 2019). Therefore, we defined "total suitable habitat area" for each species by calculating the sum of every 30 m × 30 m pixel from these models.

We defined "species of conservation concern" (SCC) as any terrestrial vertebrate species that meets one or more of the following criteria: 1) listed as threatened, endangered, or a candidate species under the U.S. Endangered Species Act (USFWS, 2018); 2) classified by the International Union for Conservation of Nature (IUCN) as extinct in the wild (EW), critically endangered (CR), endangered (EN), or vulnerable (VU) (IUCN, 2019); or 3) classified by NatureServe either globally (G-rank), as an infraspecific-taxon (T-rank), or nationally (N-Rank) as possibly extinct (GH, TH, or NH), critically imperiled (G1, T1, or N1), imperiled (G2, T2, or N2), or vulnerable (G3, T3, or N3) (NatureServe, 2019). In this study we chose to be precautious and therefore inclusive.

To gauge the level of conservation protection, we used the Protected Areas Database of the United States (PAD-US) version 2.0 (USGS, 2018) published on September 30, 2018, which is a geodatabase of the national inventory of terrestrial and marine protected areas that are dedicated to the preservation of biodiversity and to other natural, recreational, and cultural uses, managed for these purposes through legal or other effective means. The geodatabase includes geographic boundaries, land ownership, land management, management designation, parcel name, area, and protection category. It is the most recent, comprehensive, and complete dataset for protected areas available in the U.S.

PAD-US classifies all lands into four categories with the following definitions: GAP 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 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 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 (for example, logging, off-highway vehicle recreation) or localized intense type (for example, mining); GAP 4—an area with 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.

In this paper, we defined "highly protected areas" as those lands classified as GAP status 1 or 2 (Fig. 1), which includes Wilderness Areas, National Parks, Bureau of Land Management Areas of Critical Environmental Concern, private nature reserves, and many other designations that are usually thought of as relatively strict conservation areas. It does not include general public lands without these designations, such as non-designated National Forest lands, which are open to logging, mining, oil and gas drilling, ski resort development, and other extractive uses. The PAD-US does not include many Native American reservations at any level of protection, even though parts of these jurisdictions (which can be quite large in the West) are managed for conservation. We defined "conservation opportunity" as those lands classified as GAP status 3 or 4 (Fig. 1), because they are often in the public estate (federal, state, or county management) and can be protected by law or policy and do not require purchase or conservation easements.

The PAD-US includes many overlapping mapped administrative boundaries each with its own GAP status. Therefore, for our analysis, we prioritized the spatial data layers in the PAD-US (v. 2.0) by "flattening" the data so that the highest protection status (e.g., GAP 1) would take precedence over a lower protection status (e.g., GAP 3). This conferred to any given area the highest of overlapping GAP-status designations. The flattened PAD-US dataset was then converted into a 30 m × 30 m raster dataset aligned to the GAP species habitat datasets.

To determine the proportion of wildlife species in the contiguous United States that are species of conservation concern and show the variation by taxonomic class (question 1), we calculated the proportion of all terrestrial vertebrates (Gergely et al., 2019) that are "species of conservation concern" as defined above for all species and by taxonomic class.

To quantify the variation in total area of suitable habitat by species, taxonomic class, and conservation status (question 2), we calculated summary statistics on suitable habitat area for each wildlife species. We then plotted the habitat area of each species, with kernel density distributions (i.e., a smoothed histogram) and box plots, to compare distributions by taxonomic class and by conservation status.

To evaluate how well highly protected areas represent the habitats of wildlife species, and show the variation in protection class, conservation status, and area of suitable habitat (question 3), we calculated the proportion of suitable habitat area occurring within GAP 1 or 2 protected areas for each of 1719 species (including 129 subspecies). We then investigated how these proportions of habitat protected varied by taxonomic class and conservation status. We displayed the results in 15 histograms representing all wildlife species, species of conservation concern, and species not of conservation concern for all species and by taxonomic class: mammals, birds, amphibians, and reptiles. We also used scatterplots to display how the proportion of habitat protected in GAP 1 or 2 areas varied with total suitable habitat area by taxonomic class and conservation status. In these scatterplots, we also represented conservation opportunity (total area in GAP 3 or 4) by the size of each plotted species point.

For the purposes of discussion, we set two arbitrary thresholds of levels-of-protection. We consider species with at least 50% of their suitable habitat in highly protected areas to be "well represented" in highly protected areas, species with at least 20% of their suitable habitat in highly protected areas "moderately represented," and species with < 20% of their suitable habitat in highly protected areas "poorly represented." These thresholds are convenient and consistent measures across species; they are not based on population ecology of individual species.

To analyze how the richness of species of conservation concern (SCC) is distributed spatially across the contiguous United States, including SCC that are poorly represented, have small (< 10,000 km^2 total) habitat areas, and large opportunities for conservation (question 4), we converted the 30 m × 30 m pixels of suitable habitat data into 1 km × 1 km pixels to significantly decrease processing time. This conversion was executed using the nearest neighbor method. We then overlaid each species occurrence of a) all SCC (n = 537); b) all SCC that are poorly represented in highly protected areas (< 20% in GAP 1 or 2 areas) (n = 363); c) all SCC that are poorly represented and have small (< 10,000 km^2 total) suitable habitat areas (n = 204); and d) all SCC that are poorly represented, have small suitable habitat areas, and have large opportunity for conservation (> 20% in GAP 3 or 4 areas) (n = 91). We mapped species richness for each of these 4 categories to identify areas where individual or multiple species of conservation concern co-occur.

3. Results

3.1. Question 1—Species of conservation concern

There are 1719 wildlife species and sub-specific taxa that we analyzed in the contiguous United States. Of these, nearly one-third (> 31%) are species of conservation concern—ranging from just under 20% of all birds to over 44% of all amphibians (Table 1).

3.2. Question 2—Suitable habitat by species, taxon, and conservation status

The total area of suitable habitat for each wildlife species varies greatly, from as small as 2.0 km^2 for the blanco blind salamander of Texas (*Eurycea robusta* Longley) to as large as 7,880,920.0 km^2 for the big brown bat (*Eptesicus fuscus* Beauvois).

In the contiguous U.S., the median suitable habitat area of all wildlife species is 80,602 km^2 (65,089 km^2 for mammals; 205,819 km^2 for birds; 11,143 km^2 for amphibians; and 68,816 km^2 for reptiles). The median suitable habitat area of all species *not* of conservation concern (202,495 km^2) was over 48 times larger than the median suitable

Table 1

Proportion of wildlife species that are vulnerable. Numbers (n) of wildlife species in the contiguous United States by taxonomic class and by species of conservation concern (SCC). The "class total/all total" column shows the proportion of species in each class compared to the total of all 1719 wildlife species. The "SCC/class total" column shows the proportion of species in each class that is considered a species of conservation concern. The "SCC/all total" column shows the proportion of species of conservation concern, in total and by class, compared to the total number of all wildlife species.

	n total	class total/ all total	n SCC	SCC/class total	SCC/all total
All terrestrial vertebrates	1719		537		31.24%
Mammals	459	26.70%	171	37.25%	9.95%
Birds	649	37.75%	129	19.88%	7.50%
Amphibians	284	16.52%	125	44.01%	7.27%
Reptiles	327	19.02%	112	34.25%	6.52%

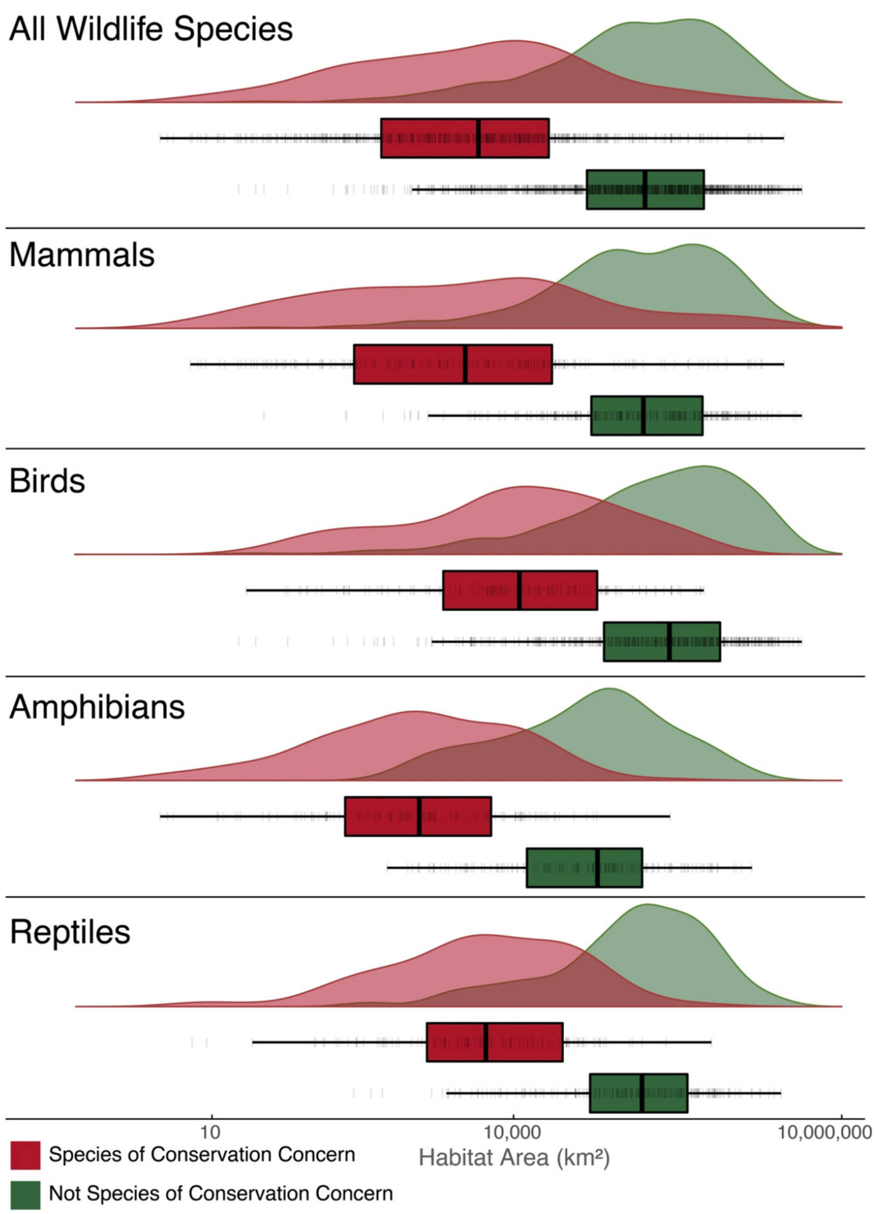

Fig. 2. Habitat limitations as a predictor of conservation concern. Kernel density distributions (smoothed histograms) of total suitable habitat areas for wildlife species of conservation concern (red) and not of conservation concern (green). Each tick mark is an individual species' total suitable habitat area across the contiguous U.S. Boxplots and whiskers show—for all wildlife and for each taxonomic class—the median suitable habitat area, the first and third quartiles of the distribution, and the 5th and 95th percentiles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

habitat area of species of conservation concern (4147 km^2) (Fig. 2). This general pattern repeats for all four classes of wildlife. Suitable habitat area for mammals not of conservation concern was nearly 64 times larger than that of species of concern (195,094 km^2 compared to 3051 km^2). Suitable habitat area for birds not of conservation concern was over 33 times larger than that of species of concern (358,106 km^2 compared to 10,796 km^2). Suitable habitat area for amphibians not of conservation concern was over 64 times larger than that of species of concern (66,783 km^2 compared to 1042 km^2). Suitable habitat area for reptiles not of conservation concern was over 38 times larger than that of species of concern (188,774 km^2 compared to 4938 km^2).

3.3. Question 3—Wildlife habitats within protected areas

The proportion of suitable habitat that is "highly protected" in GAP 1 or 2 areas (green areas in Fig. 1) also varies widely among species, including 11 species with none of their suitable habitat in highly protected areas and four species with 100% of their suitable habitat in highly protected areas (Shenandoah salamander [*Plethodon shenandoah* Highton and Worthington, 1967], Shenandoah mountain salamander [*Plethodon virginia* Highton, 1999], Palmer's chipmunk [*Neotamias palmeri* Merriam, 1897], and brown noddy [*Anous stolidus* Linnaeus, 1758].

Nearly half of species—irrespective of taxonomic class or conservation status—have under 10% of their total suitable habitat area highly protected (Fig. 3). Of the 1719 wildlife species in the contiguous U.S., only 88 species (just over 5%) are well represented ($\geq$50% of their habitat) in highly protected areas, and 337 species (just under 20%) are at least moderately represented ($\geq$20% of their habitat) in highly protected areas (blue bars in top panel of Fig. 3).

More importantly, for all 537 species of conservation concern, only 62 species (just over 11%) are well represented in highly protected areas, and only 174 species (just over 32%) are at least moderately represented in highly protected areas (red bars in top panel of Fig. 3). Species of conservation concern tend to be better represented in highly protected areas than those not of conservation concern. For all 1182 species not of conservation concern, only 26 species (just over 2%) are well represented in highly protected areas, and only 163 species (nearly 14%) are at least moderately represented in highly protected areas (green bars in top panel of Fig. 3).

For species of conservation concern, representation in highly protected areas varies slightly among taxonomic class, but general patterns

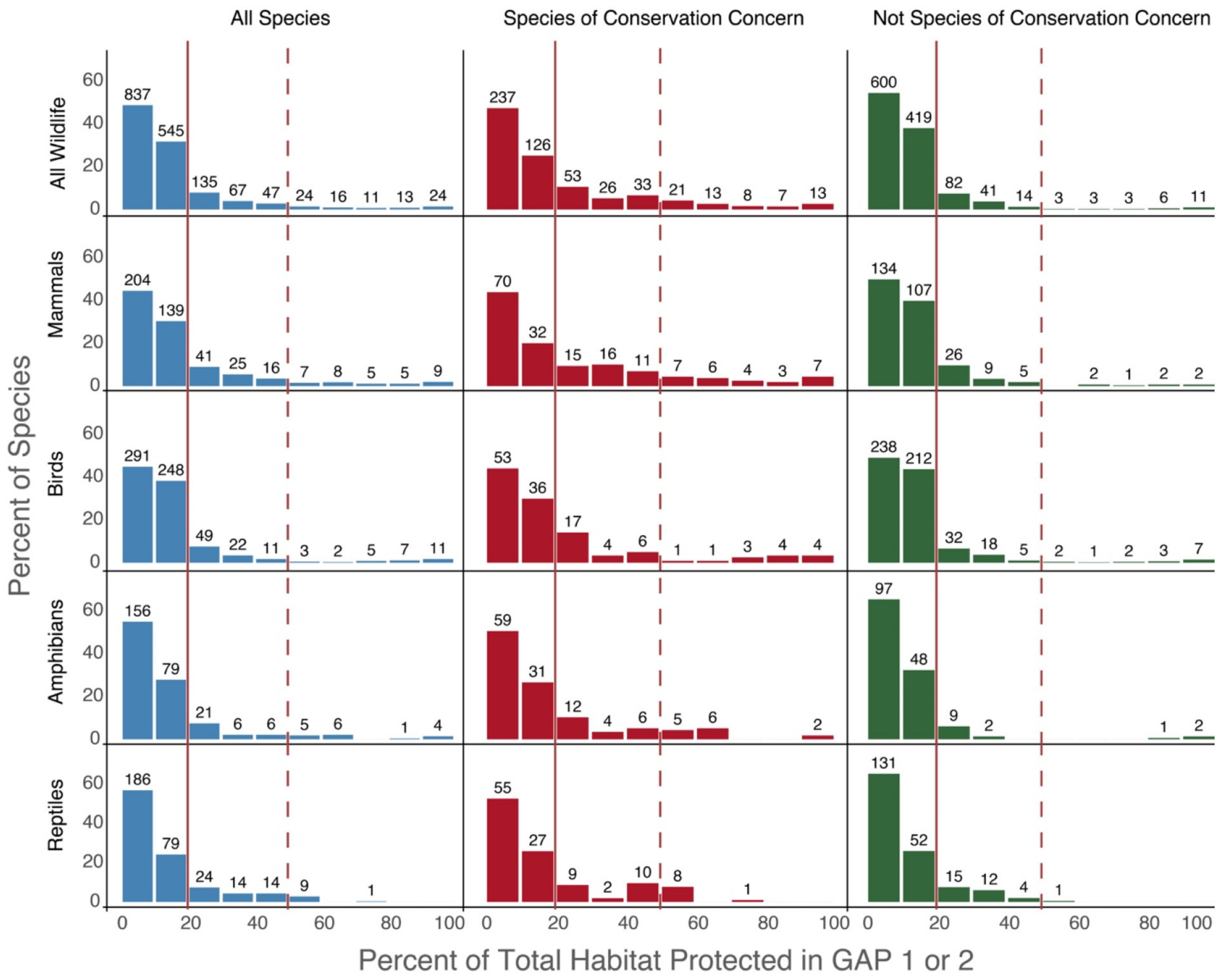

Fig. 3. How well the current protected-area system is capturing habitat for wildlife species of conservation concern. Distributions of wildlife species—by class and conservation status—according to the proportion of their total suitable habitat that is protected in GAP 1 or 2 areas in the contiguous United States. Species to the right of the dashed line are "well represented" in highly protected areas (50% or more). Species to the right of the solid line are at least "moderately represented" in highly protected areas (20% or more). Species to the left of the solid line are "poorly represented" in highly protected areas (< 20%). Numbers above the bars indicate total number of species in that decile bin.

were similar (red bars in lower four panels of Fig. 3). For mammals, just under 16% are well represented and just over 40% are at least moderately represented in highly protected areas. For birds, just over 10% are well represented and 31% are at least moderately represented in highly protected areas. For amphibians, slightly over 10% are well represented and 28% are at least moderately represented in highly protected areas. For reptiles, 8% are well represented and nearly 27% are at least moderately represented in highly protected areas.

We also investigated conservation opportunity as represented by the proportion of total suitable habitat occurring in GAP 3 or 4 areas (brown areas in Fig. 1) in the contiguous US. For species of conservation concern, the median value of suitable habitat occurring in GAP 3 or 4 areas was 18% (ranging from 0 to 98%). For mammals of conservation concern, the median value of suitable habitat occurring in GAP 3 or 4 areas was nearly 23% (ranging from 0 to 95%). For birds of conservation concern, the median value of suitable habitat occurring in GAP 3 or 4 areas was over 13% (ranging from 0 to 73%). For amphibians of conservation concern, the median value of suitable habitat occurring in GAP 3 or 4 areas was 16% (ranging from 0 to over 98%). For reptiles of conservation concern, the median value of suitable habitat occurring in GAP 3 or 4 areas was nearly 20% (ranging from < 1 to nearly 92%).

Fig. 4 plots total suitable habitat (x-axis), representation in highly protected areas (y-axis), and conservation opportunities (size of each species circle) on the same plane. This revealed which species of conservation concern (red circles) with small habitat areas that are poorly represented in highly protected areas have a high degree of conservation opportunity (Fig. 4). For example, there are 91 species of conservation concern that are poorly represented in highly protected areas but with at least 20% of their suitable habitat in GAP 3 or 4 areas (i.e., conservation opportunities). Of these 91 species, 26 are mammals, 12 are birds, 24 are amphibians, and 29 are reptiles.

3.4. Question 4—SCC habitat distribution in the contiguous United States

Total richness of wildlife species of conservation concern (Fig. 5) was highest along the west coast, along the southern border, and in several areas of the Ozark and Cumberland Plateau and Appalachian regions. Patterns of poorly represented species of conservation concern were similar to all species of conservation concern. However, range-limited and poorly protected species of conservation concern were concentrated in southern Arizona, south Texas, and Florida. Other areas hosting at least one such species are scattered throughout the contiguous United States. Locations of range-limited and poorly protected species with moderate conservation opportunity were more limited and concentrated in southern Arizona and Florida.

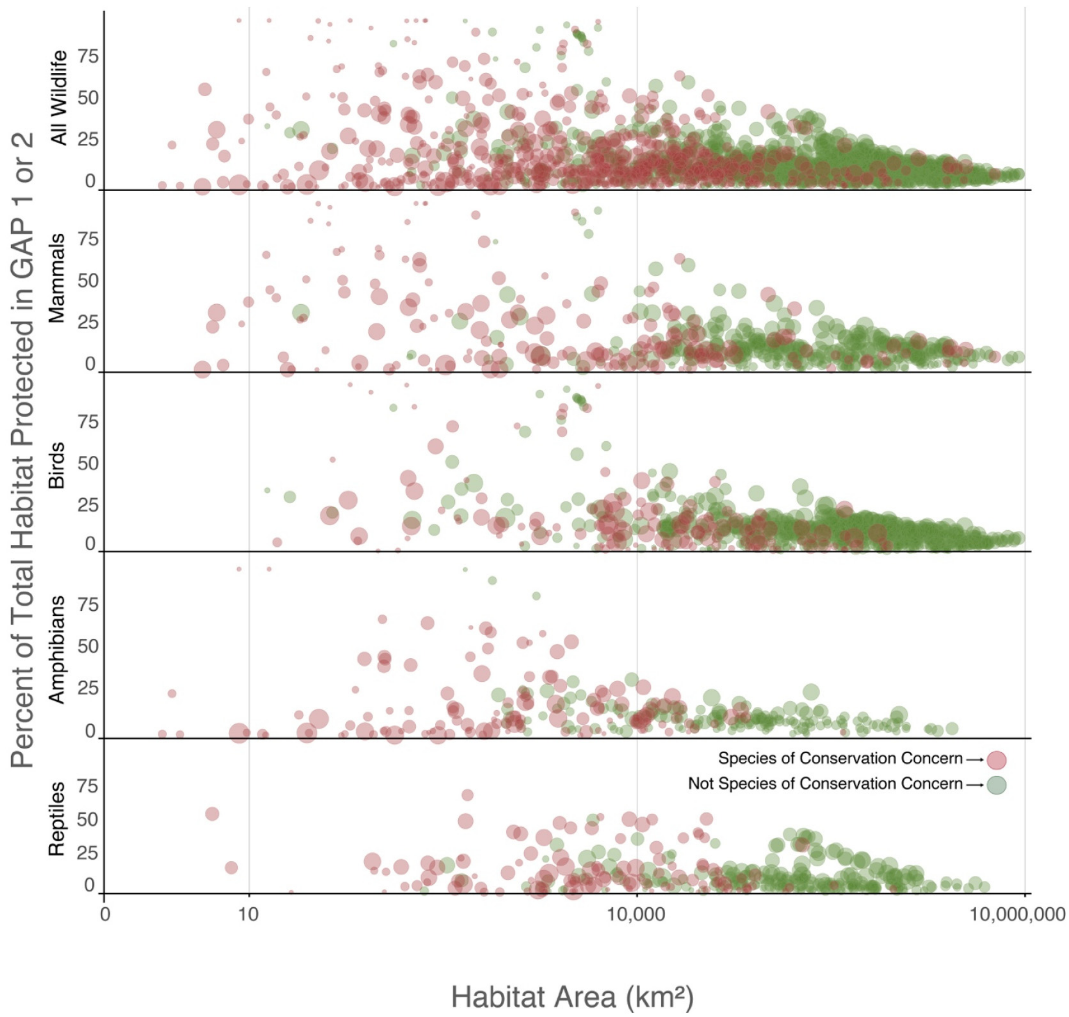

Fig. 4. Species that are poorly represented in the protected-area system and have greater opportunities for conservation. The relationship between total suitable habitat area (x-axis), the proportion of total habitat highly protected in GAP 1 or 2 areas (y-axis), and the proportion of total habitat as "conservation opportunity" in GAP 3 or 4 areas (size of the circles), by conservation status (red or green) and taxonomic class for each species of wildlife in the contiguous United States. Each circle represents one species (or select subspecies) of wildlife. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Clearly there is a biodiversity crisis in the United States, where nearly one third of all wildlife species are considered at least vulnerable to extinction. The threat extends across all taxonomic classes, but it is especially dire for amphibians. This vulnerability may be due to the insufficient overlap between protected areas and suitable habitat for species of conservation concern. Granted, some of these species are at the northern or southern extent of their ranges, and their suitable habitat may be large and/or well protected in Mexico or Canada. Still, even if those species are present and healthy in other countries, the habitats in the U.S. that should house them (but do not) could suffer from a loss of ecological function that those species would have provided locally. Conversely, many species of birds that are vulnerable in the U.S. may have even greater threats to their habitats in their wintering or breeding territories outside of the U.S. Future research could explore the concept of "regional responsibility" in which conservation effort could be allocated to different nations depending on the proportion of the distribution of a species that occurs there (Schmeller et al., 2008).

Our results provide insights into potential conservation priorities based on the degree to which the habitats of individual species of conservation concern are represented in highly protected areas. In recent decades, sophisticated conservation methods and algorithms have been developed to identify priorities for better protecting biodiversity in regional, national, and global systems of conservation reserves (e.g., Zonation, e.g., Moilanen et al., 2014, Pouzols et al., 2014). These tools have provided important insights into locations, for example, high in rarity-weighted richness that may warrant greater protection, but their outputs often conceal important patterns of individual species' habitats, range sizes, degree of protection, and opportunities for conservation. By focusing on patterns among individual species (and overlap of their suitable habitats), we are able to more fully evaluate where species occur, the sizes of their habitat areas, which species are in need of greater land protection, and what areas might be most important to protect for the greatest number of species that are vulnerable.

We are being conservative in identifying "species of conservation concern" as those that satisfy at least one of three measures of vulnerability: listing by ESA, IUCN, and NatureServe. There is good reason to be conservative. IUCN operates on a global scale of vulnerability and does not list species that are threatened only locally. As a result, only 82 species of wildlife are considered at least "vulnerable" by the IUCN in our complete tally of 537 species of conservation concern. The Endangered Species Act has always been, despite its mandate, influenced by politics, and many species that warrant inclusion on the ESA

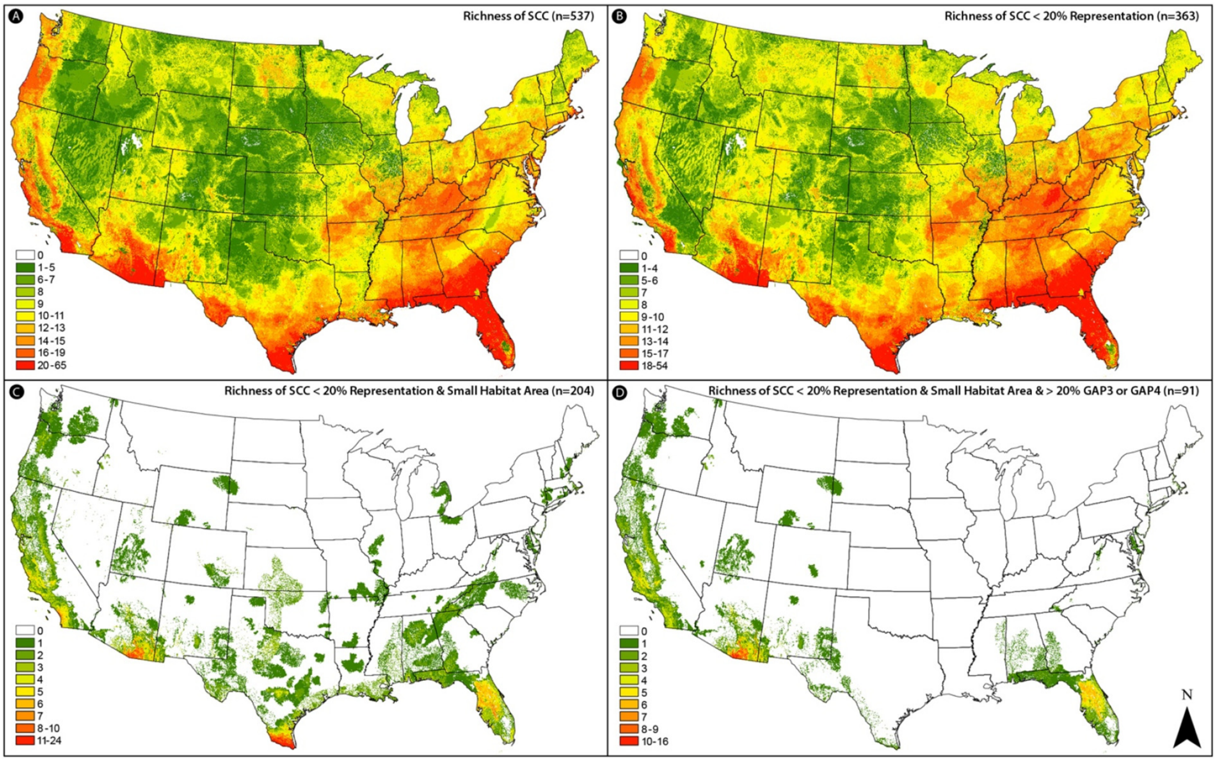

Fig. 5. Where habitats for wildlife species of concern are located. "Heat maps" of total richness of a) all wildlife species of conservation concern; b) all species in "a" that are poorly represented in highly protected areas; c) all species in "b" that have a small total suitable habitat area; and d) all species in "c" that have a large opportunity for conservation. The largest number in the legend of each map indicates the largest overlap in species number in a single square-kilometer location.

list are precluded for reasons of insufficient funding or conflicts with resource-development interests (Ando, 1999). Thus, only 113 of the 537 wildlife species of conservation concern in this analysis are listed by the ESA as threatened, endangered, or candidate species. The NatureServe national (N) ranking is the most inclusive of the measures we use. In fact, 504 of the 537 species of conservation concern are at least vulnerable according to the NatureServe N rank.

We are also being conservative in how we define "highly protected" areas. Although GAP 1 and 2 lands are often considered to be the only GAP categories with sufficient safeguards to be considered "protected" (e.g., by the IUCN: Dudley et al., 2013; Jenkins et al., 2015) some people may argue that GAP 3 lands, being in the public estate and "having permanent protection from conversion of natural land cover for the majority of the area (USGS, 2018)," should be considered "protected"—at least at some lower level of protected-area classification. Because of these two reasons, we do focus on the importance of GAP 3 lands for the conservation opportunity that they provide. In this analysis, however, we cannot confidently state that any given patch of suitable habitat in a GAP 3 area will, in fact, be protected in that "majority" area that remains in natural land cover. GAP 3 areas may *on average* have a relatively high level of protection, but any given area of GAP 3 lands may, at least in theory, be heavily impacted or converted to unnatural land cover. Therefore, we do not consider patches of suitable habitat in GAP 3 lands as protected.

In contrast, by using habitat suitability models as opposed to actual occupied habitat, we may be painting a rosier conservation picture than exists on the ground. Suitable habitat is likely to exceed occupied habitat for many species and, as a result, species reintroductions and intense habitat management may need to occur. We recognize this limitation, but given that we are limited by inconsistent occurrence data for all terrestrial vertebrates over the entire U.S., deductive habitat suitability modeling is the most pragmatic approach (Rondinini et al., 2011). Regardless, prioritizing areas of suitable habitat, be they occupied or not, is a valuable conservation goal—particularly when considering restoration priorities. It should be noted as well that changing climate conditions are likely to affect both the extent of suitable habitat available for some species as well as species' ability to reach these areas (Belote et al., 2017b).

Conservation planning can be accomplished at many levels of resolution—from global to national to biome to ecosystem to habitat. High resolution data have been shown to be important for biodiversity conservation. We have investigated protected-area contributions to species' habitat, the finest resolution of data available, but even at this level, all habitat requirements may not be met (e.g., vernal pools, caves, standing-dead trees). One must be sure to consider specialist species' needs in looking to conserve species of conservation concern, and even though this study is at 30 m resolution, it will not capture all necessary components of habitat, so the finest scale investigations at a local level must still be done on the ground. In addition, we are not accounting for genetic variation that may be lost if protected areas of a species' habitat are spatially adjacent and missing major geographic areas of a species' distribution. Using *proportion of suitable habitat in protected areas* as a gauge has two principal limitations: 1) for a species with a large total area of suitable habitat, a relatively smaller proportion of protected habitat may be sufficient, especially if genetic variation within the species is not large and/or the geographic locations of protected areas for that species are well distributed; and 2) for species with a miniscule total suitable habitat area, a relatively large proportion of protected habitat could be insufficient, especially if the species has a low tolerance to human disturbance.

Nevertheless, we believe this study is important both for its fine scale of analysis and because it investigates actual wildlife species of conservation concern, rather than relying on endemism or range limitations to indicate vulnerability. As is shown in Fig. 2, many species of conservation concern have a larger total suitable habitat area than do species which are not of conservation concern, and many species not of conservation concern have a smaller suitable habitat area than do species of conservation concern. The overlaps of histograms in Fig. 2

indicate situations where total suitable habitat size is a poor proxy for vulnerability and, therefore, shows the importance of looking at direct measures of conservation concern in addition to synthetic indices. In some cases, wildlife species may have very large range sizes and suitable habitat, but are still vulnerable to extinction due to other factors—such as human persecution (e.g., Mexican wolf; *Canis lupus baileyi* Nelson & Goldman), bioaccumulation of toxins, such as lead (e.g., California condor; *Gymnogyps californianus* Shaw), or niche requirements, such as roosting caves (e.g., big free-tailed bat; *Nyctinomus macrotis* Gray). Even though these species may suffer from some stressors not directly related to habitat, protection of suitable habitat in conservation reserves may limit their exposure to these other stressors—such as hunting or toxins. That said, we found that there *is* a relationship between total suitable habitat and vulnerability, and that stands to reason. Species with limited amounts of habitat are generally at a higher level of risk from habitat conversion or degradation.

It is also clear from our results that highly protected areas in the contiguous U.S. are contributing greatly to the preservation of habitat for species of conservation concern—although not as much as they could be if their locations were always targeted specifically to capture habitats for SCC. Over 67% of wildlife species of conservation concern (363 of 537 species) have < 20% of their total suitable habitat in highly protected areas, and over 44% of wildlife SCC (237 of 537 species) have < 10% of their habitat in highly protected areas. This pattern is seen across all taxonomic classes. Our estimation of the contribution of highly protected areas to species' suitable habitats may even be an overestimation, as total potential suitable habitat has been reduced greatly in unprotected areas over the last few centuries (Ellis et al., 2013). The high proportion of a species' habitat within highly protected areas may be due to the conversion of once-natural lands to agriculture and urban development outside of protected areas.

Because the ultimate goal is to increase representation of habitat for species of conservation concern, we gave special attention to those species that are currently poorly represented in the protected-area system (< 20% of habitat). In theory, these are the species that are most vulnerable to habitat loss and degradation, as a greater proportion of their habitat is unprotected and subject to land conversion and resulting loss of habitat area. These are the species at the bottom fifth of the y-axis panels in Fig. 4.

In addition, the wildlife species of conservation concern that have large suitable habitat areas may benefit less from new protected-area designations than those with small suitable habitat areas. There are two possible reasons for this: 1) newly designated areas may not greatly increase the overall *proportion* of habitat that is highly protected, given that the total suitable habitat area is so large, and 2) loss of habitat may not be the primary driver of vulnerability, as a large amount of suitable habitat already exists for that species. If we assume that one or both of those conditions are met, we may be better served by focusing on species with relatively small total suitable habitat areas, because those species are more likely to benefit from new conservation designations (Jenkins et al., 2015). As a convenient, albeit arbitrary, cutoff we classified as "small area of habitat" those species with < 10,000 km^2 total suitable habitat, with the assumption that the designation of new protected areas targeted at them could produce greater conservation gain because, all else being equal, it would produce a greater proportional gain in habitat protected. Therefore, we gave special attention to those species as well.

And finally, we analyzed conservation opportunity (as opposed to dollar cost) because we are interested in the ability to designate conservation lands by Congressional law, Presidential declaration, or administrative policy, in addition to fee-simple purchase or conservation easement. Legal, executive, or policy changes may have the largest and most immediate impact because over 30% of the contiguous U.S. is public land (249,275,398 ha) (USGS Gap Analysis Program, 2018). Areas in GAP 3 or 4 status are generally public land or have some degree of non-conversion status that warranted them to be placed in the Protected Area Database. We consider these lands to have great conservation opportunity. In Fig. 4, we have graphed one way of determining conservation priority: a combination of species that are poorly represented in the protected-area system that also have small suitable habitat areas and that have a large (public-land) opportunity for conservation—91 species of conservation concern. If those species' suitable habitats are overlaid on a single map of the U.S., one can see the areas where one could make the largest conservation gains by protecting habitat (Fig. 5). Whether one is interested in richness of all species of conservation concern (panel A), SCC that are poorly represented in highly protected areas (panel B), poorly represented SCC with small habitat areas (panel C), or those that are poorly represented with small habitats and large conservation opportunity (panel D), these heat maps can direct conservation biologists to the most important areas for species conservation.

In fact, these heat maps could be used to prioritize the importance of public lands that are "in the pipeline" for elevated conservation designations, such as US Forest Service roadless areas. One could rank every USFS roadless area by its importance for capturing habitat for species of conservation concern. This type of study could be used to advocate for new Wilderness designations, for example, or to inform the revision of federal land management plans. Conservation of public lands, however, involves garnering sufficient political will and social acceptance, whereas private land conservation often relies simply on funding and willing landowners. Thus, if private land conservation seems more feasible, one could use heat maps (A, B, and C in Fig. 5) for prioritizing where to establish conservation easements or purchase land to prevent urban development or land conversion.

Human population growth and subsequent pressure for development and extraction of natural resources will make protected areas increasingly vital to conserve biological diversity. Future recommendations for additions to the protected-area system should strongly consider the positive effects on species of conservation concern, especially those that are currently poorly represented in highly protected areas. Our results include important summary statistics on suitable habitat area, species' representation in highly protected areas, and opportunities for conservation among individual species of conservation concern. These results ultimately provide insights into priorities for conservation designations that either rely on the purchase of land or conservation easements by willing property owners or require sufficient political will to enhance protections on public land. Results shown here can be used immediately to identify high-priority lands for acquisition from willing property owners or lands managed by federal and state agencies where elevating the conservation status would protect vulnerable species from future habitat loss.

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CRediT authorship contribution statement

Matthew S. Dietz: Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Supervision, Project administration. **R. Travis Belote**: Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing. **Josh Gage**: Methodology, Software, Formal analysis, Data curation. **Beth A. Hahn:** Conceptualization, Methodology, Supervision, Funding acquisition.

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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