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What drives at-risk species richness? Environmental factors are more influential than anthropogenic factors or biological traits

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Abstract

Species at risk of extinction are not uniformly distributed in space. Concentrations of threatened species may occur where threatening processes are intense, in refuges from those processes, or in areas of high species diversity. However, there have been few attempts to identify the processes that explain the distribution of at-risk species. Here, we identified the relative importance of biological traits, environmental factors, and anthropogenic stressors in driving the spatial patterns of both total and at-risk species richness of North American mammals and birds. Environmental factors are the predominant drivers of both total and at-risk species richness. Strikingly, the directions of variable relationships differ substantially between models of total and at-risk species richness. Understanding how environmental gradients differentially drive variation in total and at-risk species richness can inform conservation action. Moreover, our approach can predict shifts in at-risk species concentrations in response to projected environmental change and anthropogenic stressors.

KEYWORDS
anthropogenic factors, at-risk species, biological traits, birds, environmental correlates, mammals, North America, species richness, variable importance

1 | INTRODUCTION

Extinction can be an idiosyncratic process. Responses to threatening processes by different taxa in different regions are variable (Batista, Gouveia, Silvano, & Rangel, 2013), whilst the implementation and success of conservation actions are often substantially influenced by social and economic factors (Knight, Cowling, Difford, & Campbell, 2010). Nonetheless, there is widespread recognition that conservation planning and policy cannot account for the idiosyncratic nature of every vulnerable population's plight (Franklin, 1993). From the placement of protected areas, to investment in mitigating the fragmenting effects of linear infrastructure, policy-makers and conservation practitioners must often be guided by patterns in the distribution of vulnerable biodiversity. As a result, conservation practitioners require a comprehensive understanding of the location of, and threats to, biodiversity, in order to make informed choices about the relative costs, benefits, and likely success of different conservation actions (Brooks et al., 2006). Identifying where concentrations of threatened species occur, and which processes drive their occurrence, will enable conservation practitioners to ascertain the conservation actions that will deliver the best returns for biodiversity (Wilson et al., 2005).

Ultimately, biodiversity loss is driven by extrinsic, habitat-level threatening processes (Wilson et al., 2005). Anthropogenic threats, such as increasing human population density, resource extraction and climate change have all been linked with extinction risk (Cardillo et al., 2004). Biological attributes of species can determine their resilience to

threatening processes, and substantial effort has been dedicated to identifying those species-specific traits most associated with extinction risk (Cardillo et al., 2008; Purvis, Gittleman, Cowlishaw, & Mace, 2000). Additionally, the characteristics of an environment may predispose species in a given area to threatening processes (Davies et al., 2006). Energy availability is thought to drive increases in resource availability (Hawkins et al., 2003) and speciation rates (Rohde, 1992), increasing the number of species that can become at-risk, or that are predisposed to rarity. Traditionally, studies of spatial variation in extinction risk control for the effects of species richness by modelling the proportion of species in an environment classified as threatened (Davies et al., 2006). However, the environmental gradients that drive total species richness may operate differently for at-risk species richness (Moura, Villalobos, Costa, & Garcia, 2016). To understand the drivers of the distribution of at-risk species richness, we need to: (a) establish the role of environmental factors, anthropogenic threats, and biological traits; and (b) identify how the drivers of at-risk species richness differ from those that determine the size of the species pool—something yet to be considered in spatial analyses of extinction risk (Davies et al., 2006).

The processes driving threatened species richness are strongly scale-dependent (Keil et al., 2018) and different scales of enquiry offer advantages and disadvantages. Studies of extinction risk at global or biogeographic realm extents (Cardillo et al., 2008; Davies et al., 2006) offer important insights into what is driving large-scale, irreversible changes (Keil et al., 2018); however, their spatial grain is too coarse to account for the localized changes that must precede global-scale change. In contrast, smaller scale studies can uncover the drivers of finer-resolution changes, which is crucial for informing landscape management that seeks to foster species persistence; however, conclusions drawn from small-scale studies may also lack wider conservation application (Baldwin et al., 2018; Bonnot, Thompson, Millspaugh, & Jones-Farrand, 2013). Regional-scale studies offer a compromise between understanding the fine-scale processes leading to biodiversity loss and having generalizable conservation outcomes. Furthermore, regional-scale studies performed at the extent at which national land management agencies operate, allow for the identification of priority areas on which to focus resources, whilst promoting cooperation and sharing of these resources (Baldwin et al., 2018).

Here, we aim to identify the drivers of both at-risk and total species richness. To do this we ask whether variation in at-risk and total species richness can be explained by spatial variation in environmental, anthropogenic, and biological trait parameters. By comparing the drivers of at-risk and total species richness, we attempt to develop a more comprehensive understanding of what determines concentrations of at-risk species, independent of what drives the size of the species pool. We use data on the threat status and distributions of a large number of bird and mammal species that occur across the contiguous United States (CONUS). Examining both birds and mammals allows us to explore whether the variables predicting the spatial pattern of extinction risk are consistent across taxa.

2 | METHODS

2.1 | Species data

The spatial distributions across CONUS of 499 and 228 species of birds and mammals, respectively, were obtained from BirdLife International and NatureServe (2016) for birds and from IUCN (2016) for mammals. Data were available as spatial polygons of distributional boundaries, which were intersected with a grid of ~25 × 25 km (250 mi^2) cells (hereafter referred to as the "grid"). Where a species' range polygon intersected with a grid cell, the species was treated as present within that cell. Extinction risk ranks were obtained from NatureServe (http://www.natureserve.org/), with each species assigned a conservation status based on a 5-level ordinal scale: critically imperilled (G1), imperilled (G2), vulnerable (G3), apparently secure (G4), and demonstrably secure (G5). We used these national assessments of conservation status, as the IUCN classifications were designed for global assessments and therefore pose certain problems when used at a national scale (Gärdenfors, Hilton-Taylor, Mace, & Rodríguez, 2008). The use of standard ranking criteria makes these ranks comparable across birds and mammals. Under these criteria 16 bird species and 38 mammal species were classified as at-risk (G1, G2, or G3).

Species' trait data were collated from published data sources for a suite of biological traits (Tables S2 and S3) previously shown to correlate with species' extinction risk (Cardillo et al., 2008; Gaston & Blackburn 1995; Purvis et al., 2000). A list of species included in the analyses and sources of species' trait data can be found in the supporting information (Appendices S1 and S2). We calculated the mean (or modal in the case of categorical variables) value for each trait, for all species occurring in each grid cell.

2.2 | Environmental and anthropogenic covariates

We obtained data on eight environmental covariates, all previously shown to be good explanators of species richness (Luo et al., 2012). Data on five bioclimatic variables were derived from the gridded surface meteorological dataset of Abatzoglou (2013); mean annual temperature and precipitation, total annual solar radiation, and seasonality in both temperature and precipitation. Mean elevation and its standard deviation were derived from the National Elevation Dataset. A

measure of land cover diversity was calculated using the 2011 U.S. Geological Survey's National Land Cover Database (NLCD; Homer et al., 2015).

Anthropogenic influence was assessed using three variables. Using the NLCD, we calculated the area of each cell that was covered by land classified as intensively used by humans. We estimated the mean human population density within each cell from the U.S. Department of Commerce, Bureau of Census (2015), as an additional index of human influence. Using the Protected Area Database (Conservation Biology Institute, 2012), we calculated the total area of land receiving some form of protection from transformation. All environmental and anthropogenic explanatory variables were calculated at the grid resolution.

2.3 | Modelling species richness

We used random forests (RFs) to assess the potential of the environmental, anthropogenic and trait covariate sets, to explain spatial patterns in both total and at-risk species richness. For a given taxon, we fitted separate models to both the total number of species and the total number of species classified as at-risk (G1, G2, or G3) occurring in a cell. To account for spatial autocorrelation (SAC) we used a "blocking" method, whereby we split the data into ten sampling blocks based on ecoregions (Olson et al., 2001: http://www.worldwildlife.org/science/data). We fitted the models to nine of the ten sampling blocks and tested performance on the omitted block using R^2. This process was repeated ten times, resulting in ten RF models of both total and of at-risk species richness for each taxon. Models were fitted using the "randomForest" package in *R* (Liaw & Wiener, 2002).

Variable importance for each response (total richness, at-risk richness) and taxon (birds, mammals) was calculated using a permutation accuracy measure (Strobl, Boulesteix, Zeileis, & Hothorn, 2007) using the 10 RF models. To enable comparison between models and taxa, the relative variable importance was calculated by dividing the importance of each individual variable by the summed importance across all variables. To prevent bias towards categories with more variables, the mean relative variable importance was taken for each of three broad variable categories: biological traits, environment, and anthropogenic variables. We used repeated measures ANOVAs to test for significant differences in both individual and mean categorized variable importance among birds and mammals for both model responses.

To assess variable relationships, we made predictions to a data set where all but the focal variable were held at their mean (or modal) value. We repeated this for each of the ten models for the four combinations of response and taxon. To aid comparison of variable relationships, all predictions were scaled to have a mean of zero and a standard deviation of one. All anal-

yses were carried out in R 3.3.1 (R Development Core Team, 2016). Where mean metrics of model fit are given, these are accompanied by standard deviations (SD). Additional details on covariates and methods for model fitting, accounting for SAC, and assessing model fit are given in the supporting information.

3 | RESULTS

Models fitted to total and at-risk bird species richness explained a moderate amount of variation in observed richness patterns (total species richness: mean $R^2 = 0.67$, ±0.23, at-risk species richness: mean $R^2 = 0.58$, ±0.22, Figures 1a and b). Models fitted to total and at-risk mammal species richness explained a large amount of the variation in the observed richness patterns (total species richness: mean $R^2 = 0.84$, ±0.10, at-risk species richness: mean $R^2 = 0.87$, ±0.07, Figures 1c and d).

Environmental variables were significantly more important than either anthropogenic variables or biological traits for explaining both total and at-risk bird species richness (Figure 2, Table S4). There were, however, no significant differences in the importance of individual variables when comparing models of total and at-risk bird species richness (Paired Wilcoxon test: $V = 7546$, $P = 0.39$, Figure 2). For mammals, environmental variables were also significantly more important than both anthropogenic factors and biological traits for explaining total species richness, and of significantly greater importance than anthropogenic factors for explaining at-risk species richness (Figure 3, Table S4). There were, however, no significant differences in the importance of individual variables between models of total and at-risk mammal species richness (Paired Wilcoxon test: $V = 9055$, $P = 0.98$, Figure 3).

In several cases, partial relationships between individual variables and total species richness differed from those with at-risk species richness (Figure 4). For both birds and mammals, anthropogenic land use was negatively related to total species richness, but positively related to at-risk species richness. The area of protected land showed a positive relationship with both bird and mammal at-risk species richness, whilst the relationship with total species richness was hump shaped for both taxa. For birds, environments with more seasonality in precipitation supported lower total species richness but greater at-risk species richness. Whilst there is a limited relationship between diversity of elevation and total species richness, more elevationally diverse areas supported more at-risk species. There were substantial differences in the partial relationships between individual variables and total and at-risk bird species richness for all biological trait variables (Figure 4f and Figure S1l-r). For mammals, the greatest number of at-risk mammal species occurred at the
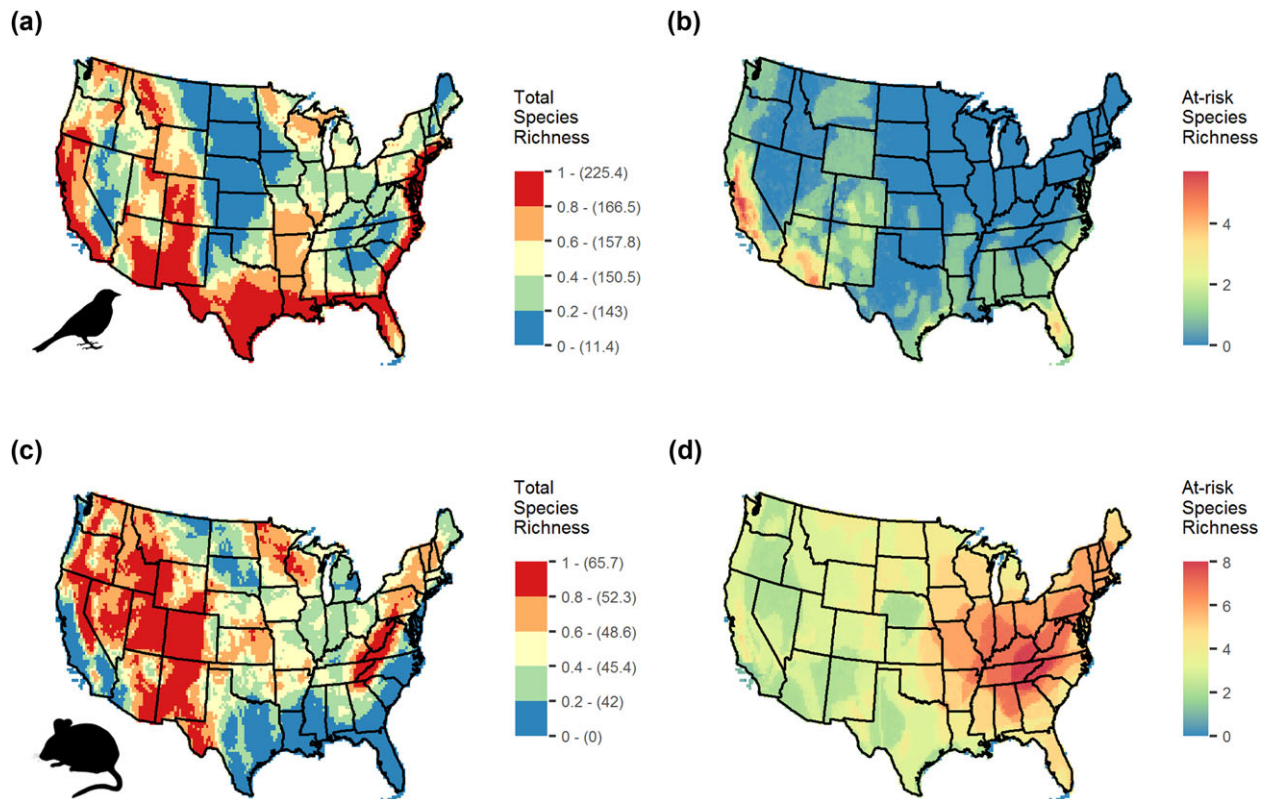
FIGURE 1 Model predicted distributions of total (a) and at-risk (b) bird species richness and total (c) and at-risk (d) mammal species richness. Note the different scales for each panel. Total species richness is shown in quantiles, with associated species counts indicated in brackets, whilst at-risk species richness is on a continuous scale

lowest elevations, but the greatest total species richness occurred at the highest elevations (Figure 4i).

4 | DISCUSSION

Our results demonstrate, at a near-continental scale, that abiotic environmental parameters are generally the most important drivers of variation in both total and at-risk species richness of both birds and mammals. Significantly, our models also show that, despite the similar importance of each variable in explaining total and at-risk species richness, there are striking differences in the effects of these variables. We discuss our findings in light of the processes driving spatial patterns of extinction risk and the utility of our analyses for conservation practitioners.

4.1 | The biological and spatial factors associated with extinction risk

The predominant drivers of at-risk species richness are the same as those driving the size of the species pool. In areas with greater total species richness, niche space is likely to be more finely partitioned, leading to more naturally rare species, prone to imperilment (Rohde, 1992). However, this similarity in variable importance belies crucial differences in the nature

of their effects on patterns of total and threatened species richness, especially for birds. For example, although total bird species richness showed a limited relationship with elevational diversity, at-risk bird species richness increased. By enabling persistence and diversification through geographic isolation and providing refuges from adverse environmental conditions, areas with high levels of topographic heterogeneity could promote the occurrence of narrow range endemic species, which are more naturally prone to extinction (Stein, Gerstner, & Kreft, 2014).

For mammals, relationships between the explanatory variables and total and at-risk species richness were more consistent. However, richness of threatened mammals was higher at low elevations, despite overall richness increasing with elevation. This may be linked to habitat loss and degradation associated with human development pressures along southeastern U.S. coastal habitats (Oli, Holler, & Wooten, 2001) and low elevation, early-seral, and open plant communities in the arid and semiarid regions of the western United States (Kofron & Villablanca, 2016), both of which may disproportionately affect the small mammal communities that inhabit those environments.

For birds and mammals, both anthropogenic land use and area of protected land had contrasting effects on the richness of total and at-risk species richness. For example, total species
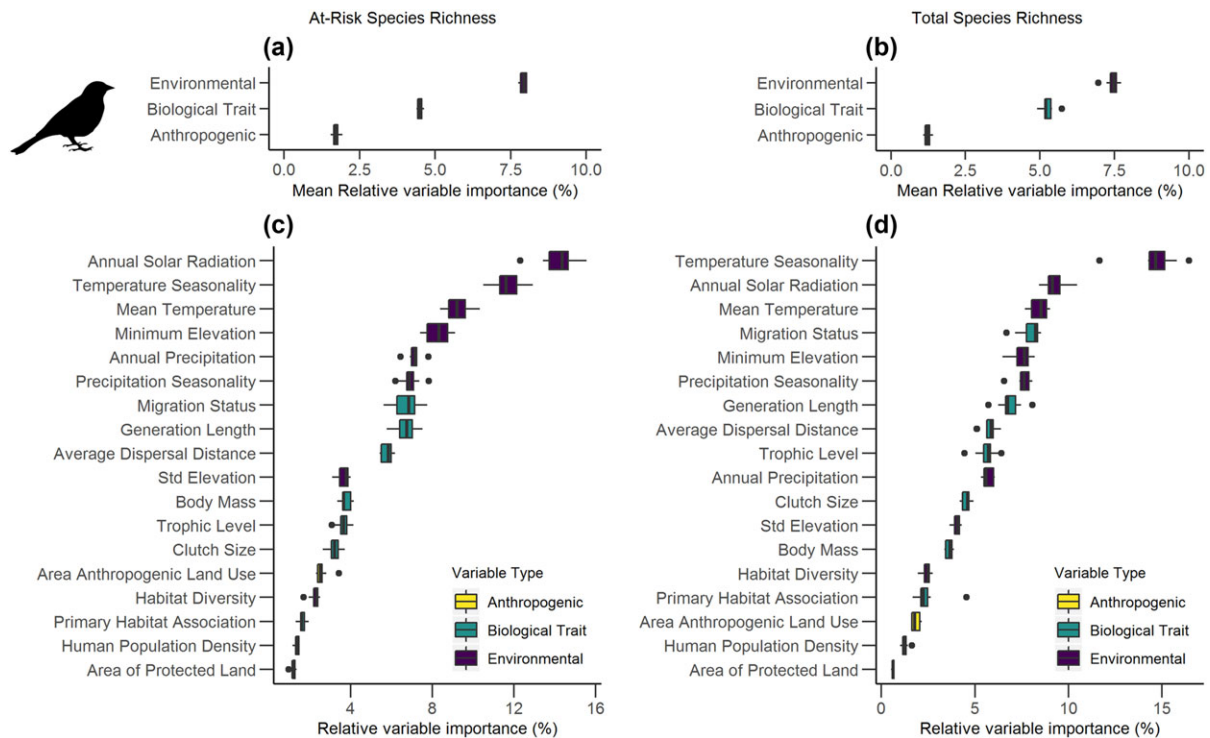
FIGURE 2 Relative variable importance from the 10 random forest models fitted to explain the distribution of the total number (G1–G5) and the total number of at-risk (G1, G2, and G3) bird species across CONUS. The mean variable importance for each category is shown for both at-risk (a) and total (b) species richness. Individual variable importance scores are also shown for at-risk (c) and total (d) species richness. The line across each box indicates the median and the box boundaries indicate the interquartile range (IQR). Whiskers identify extreme data points that are not more than 1.5 times the IQR on both sides; the dots are more extreme outliers

richness in both taxa declined with the area of anthropogenic land use, whilst the richness of at-risk species increased. Human activities and associated land use changes often lead to habitat loss and fragmentation, increasing the threats to which species are exposed, and resulting in a greater number of at-risk species but a lower number of species overall (Pautasso, 2007). Area of protected land showed a positive relationship with at-risk species richness, implying that protected areas are acting as habitat refugia, enabling the persistence of threatened species in areas with limited anthropogenic influence. Meanwhile, area of protected land showed a hump-shaped relationship with total species richness. This is consistent with the idea that protection often targets areas with high remaining species richness but marginal economic value, such as areas of high elevation or low soil productivity (Scott et al., 2001).

Our measures of spatial variation in biological traits are relatively coarse, potentially underrepresenting their importance in influencing at-risk species richness. Nevertheless, our results show biological traits to be more important than anthropogenic factors for determining at-risk species richness for both birds and mammals. Differences between taxa in the importance of biological traits could be a consequence of relative dispersal abilities, affecting species' capacity to explore the surrounding environment and adjust distributions accord-

ingly (Moura et al., 2016). Good dispersers are more likely to be at equilibrium with conditions, whilst poor dispersers are more likely to be restricted by abiotic barriers to movement (Arita & Rodríguez, 2004). Non-volant mammals are generally less vagile than birds, potentially explaining why biological traits are relatively more important for mammals than birds. Additionally, the differences between the importance of environmental factors, anthropogenic stressors, and biological traits for birds and mammals could relate to their different sensitivities to threatening processes. For example, birds have been shown to be more sensitive to the impacts of climate change than mammals, whereas mammals are more sensitive to the impacts of overexploitation (Ducatez & Shine, 2016). Overexploitation has a direct effect on species, with the effect greatest for species with larger body masses, and slower life histories, indicating why biological traits may be more important for mammals than for birds (González-Suárez et al., 2013).

4.2 | The utility of extinction risk studies

Given the lack of congruence in the distributions of at-risk species richness between taxonomic groups, choosing where to focus action, and what those actions should be, can be a predicament for conservation planners. By understanding the
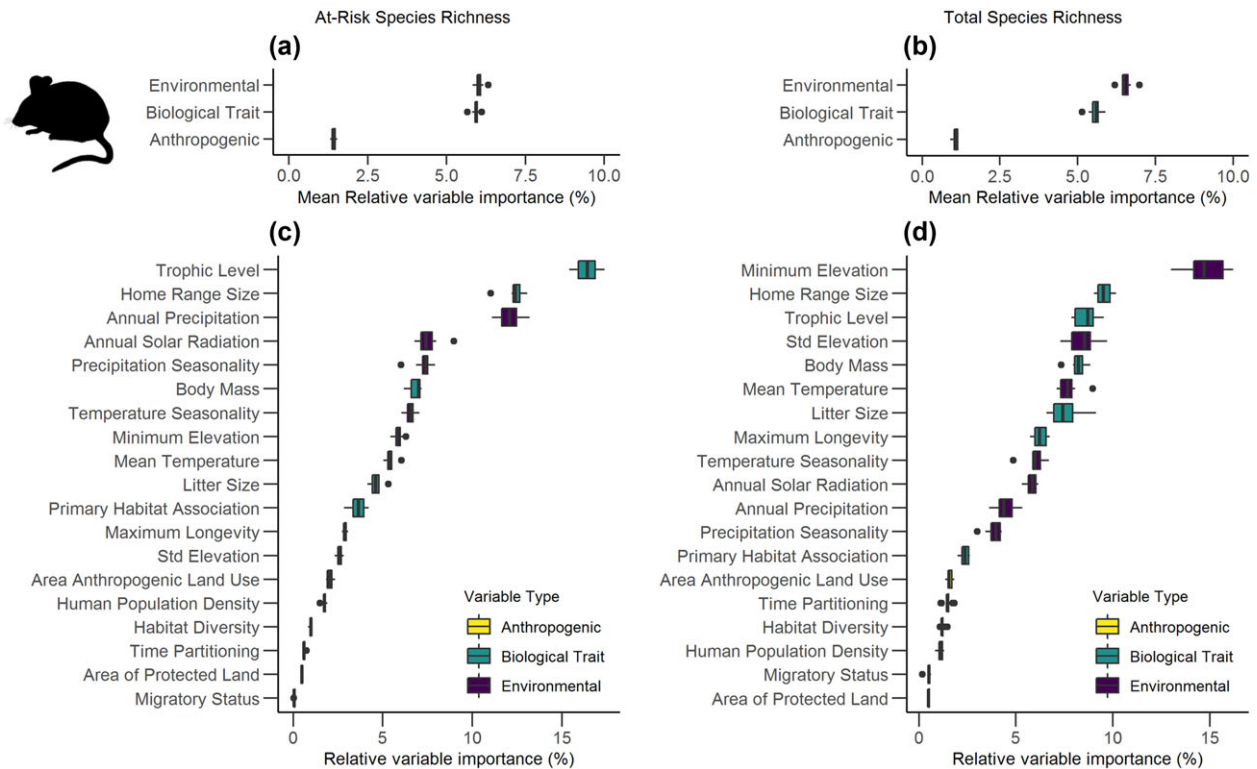
FIGURE 3 Relative variable importance from the 10 random forest models fitted to explain the distribution of the total number (G1–G5) and the total number of at-risk (G1, G2, and G3) mammalian species across CONUS. The mean variable importance for each category is shown for both at-risk (a) and total (b) species richness. Individual variable importance scores are also shown for at-risk (c) and total (d) species richness. Interpretation of box and whiskers is as for Figure 2

location of and the threats to biodiversity, we are better able to evaluate the relative costs and benefits of different conservation actions (Wilson et al., 2005). Here, we comment on the implications of our findings, and the utility of our approach for four areas of practical conservation.

Large-scale conservation relies heavily on the establishment of new protected areas (Pimm, Jenkins, & Li, 2018). Protected areas, however, are often established in areas with low opportunity costs, limiting the potential benefits for biodiversity (Tesfaw et al., 2018). By combining spatially explicit information on the occurrence of a large collection of species, with potential drivers associated with extinction risk, our approach guards against siting reserves in areas of low stakeholder conflict with little biodiversity conservation benefit and can identify factors that should be addressed in conservation plans associated with reserve establishment.

Another pragmatic consideration relates to the high incidence of threatened biodiversity on private lands (Groves et al., 2000). Many governments now supplement publicly owned resources with funded conservation programs on private grounds (Gordon, Langford, White, Todd, & Bastin, 2011) or enter into public–private partnerships that plan for species conservation while maintaining private landowner land use flexibility (Langpap & Kerkvliet, 2012). The approach we have presented here can help to guide

locations for public–private partnerships and to identify the most appropriate local conservation. For example, the link between dispersal ability and at-risk species richness indicates the importance of management strategies that promote functional connectivity in landscapes where mammal species are at risk. Our correlative approach is, of course, vulnerable to identifying noncausal processes. With cautious interpretation, however, the results still offer insight into the processes driving at-risk species richness. For instance, we point to our interpretation of the relationship between at-risk mammal species richness and minimum elevation, which suggests a role for human development pressures in low lying coastal and shrubland areas.

Our approach also yields conservation recommendations for the management of existing public lands. Although these lands are "protected," many of the agencies responsible for their stewardship operate under a multiple-use mandate, permitting resource extraction activities like timber harvesting, livestock grazing, and mining. Using the U.S. Forest Service as an example, management of their lands is guided by the 2012 Planning Rule (USDA, Forest Service, 2012) that defines the requirements for developing and revising land resource management plans on National Forests and Grasslands. These plans are required to provide the ecological conditions necessary to maintain species of conservation
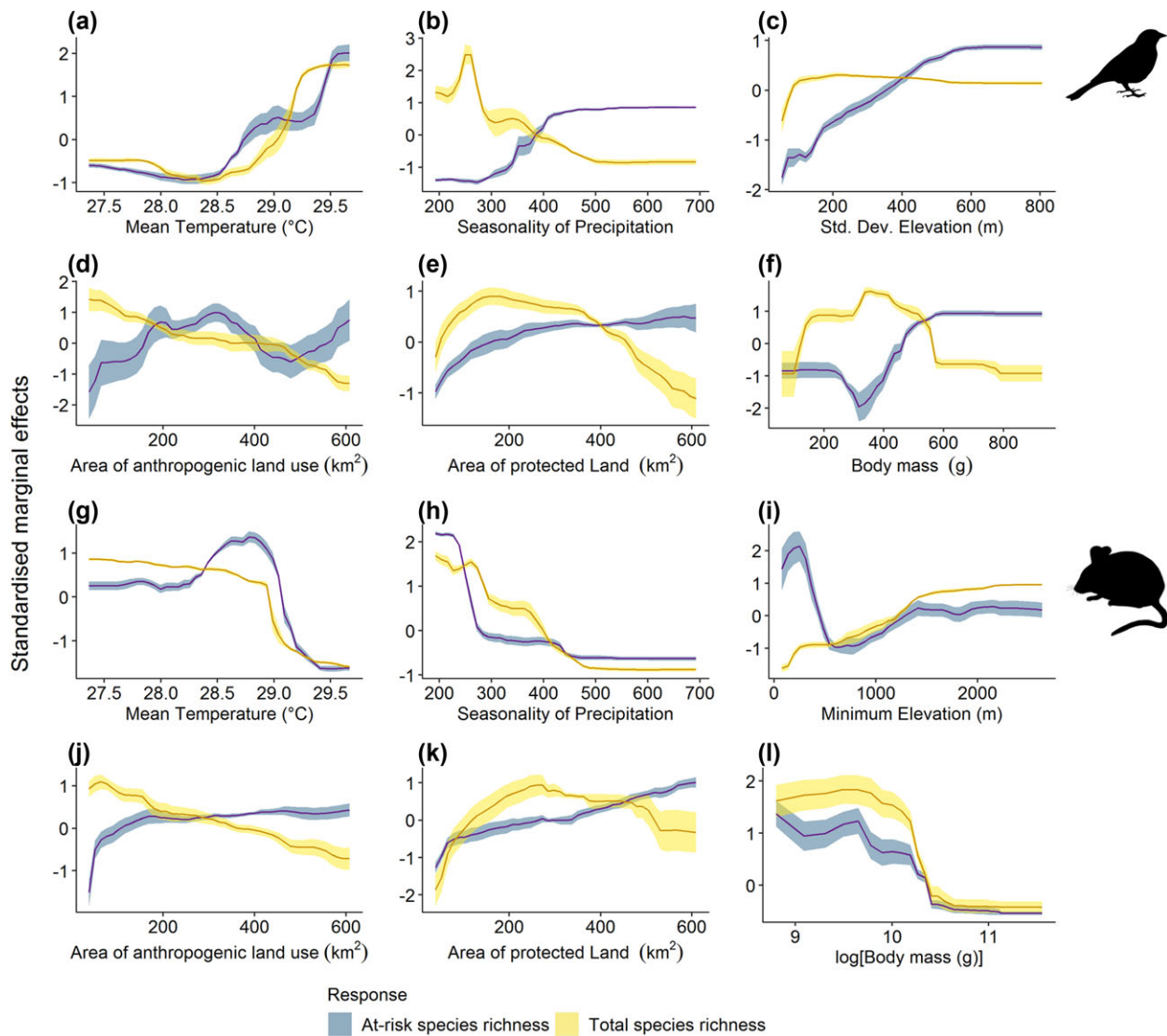
FIGURE 4 Relationships between variables and the predicted number of at-risk (blue lines) and total number (yellow lines) of birds (a–f) and mammals (g–l) in a grid cell. The lines show the mean predictions, with other variables held at their mean values, from across the 10 random forests. Shaded areas are the standard deviations around those means. To aid comparison, predictions have been scaled to have a mean of one and a standard deviation of zero. Relationship plots for all individual variables can be found in the supporting information (Figures S1 and S2)

concern. The observation unit of our approach is, in most cases, of sufficient resolution to describe the heterogeneity of at-risk species occurrence within a National Forest. Models identifying the important drivers of concentrations of these species can inform decisions regarding what proportions of National Forests should be dedicated to species conservation and which can contribute to the provisioning of ecosystem services.

Finally, in an era of rapid global change, it would be naïve to assume that regions targeted for conservation under current conditions would remain immutable. Our approach can be coupled with projections of environmental attributes and anthropogenic stressors to anticipate where spatially

explicit targeting for species conservation might shift in the future.

Successful conservation planning must occur regionally or across whole landscapes, as this is the scale at which the ultimate political and economic drivers of threatening processes take place. Natural resource agencies and conservation organizations, however, often only work within their own jurisdictions, which can lead to diffuse and uncoordinated efforts and less comprehensive conservation action (Aycrigg et al., 2016). If biodiversity is to be fully protected in the face of climate change, urban expansion, wildfires and other large-scale threatening processes, conservation efforts must incorporate landscape-scale strategies alongside the

species-by-species and site-specific conservation strategies that currently dominate efforts to stem extinction (Likens & Lindenmayer, 2012), particularly in the United States (Evans et al., 2016). By assessing the drivers of threat at a national scale, our approach can help to inform a comprehensive strategy for systematic and resilient habitat conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.