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RESEARCH ARTICLE

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Climate, food and humans predict communities of mammals in the United States

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Abstract

Aim: The assembly of species into communities and ecoregions is the result of interacting factors that affect plant and animal distribution and abundance at biogeographic scales. Here, we empirically derive ecoregions for mammals to test whether human disturbance has become more important than climate and habitat resources in structuring communities.

Location: Conterminous United States.

Time Period: 2010–2021.

Major Taxa Studied: Twenty-five species of mammals.

Methods: We analysed data from 25 mammal species recorded by camera traps at 6645 locations across the conterminous United States in a joint modelling framework to estimate relative abundance of each species. We then used a clustering analysis to describe 8 broad and 16 narrow mammal communities.

Results: Climate was the most important predictor of mammal abundance overall, while human population density and agriculture were less important, with mixed effects across species. Seed production by forests also predicted mammal abundance, especially hard-mast tree species. The mammal community maps are similar to those of plants, with an east–west split driven by different dominant species of deer and squirrels. Communities vary along gradients of temperature in the east and precipitation in the west. Most fine-scale mammal community boundaries aligned with established plant ecoregions and were distinguished by the presence of regional specialists or shifts in relative abundance of widespread species. Maps of potential ecosystem services provided by these communities suggest high herbivory in the Rocky Mountains and eastern forests, high invertebrate predation in the subtropical south and greater predation pressure on large vertebrates in the west.

Main Conclusions: Our results highlight the importance of climate to modern mammals and suggest that climate change will have strong impacts on these communities. Our new empirical approach to recognizing ecoregions has potential to be applied to expanded communities of mammals or other taxa.

KEYWORDS
climate, macroecology, mammal communities, masting, species distribution models

1 | INTRODUCTION

Conserving biodiversity in the age of Earth's sixth mass extinction (Ceballos et al., 2015) will require understanding the basic properties of plant and animal communities, including the effects of biotic and abiotic factors on their distribution and abundance, as well as evaluating the recent impacts of human development. Species distributions and patterns of abundance for both plants and animals reflect many processes that operate at biogeographic scales, including climate, geomorphology, habitat complexity, palaeogeography and human impacts (Myers et al., 2000). However, widely used biogeographic classes, including ecoregions (Olson, 2001), forest types (Ruefenacht et al., 2008) and community classifications (Jennings et al., 2009), are typically defined by the distribution of plants. Accordingly, much of our understanding of large-scale biogeographic drivers focus on how climate, habitat variables (including soils and drainage) and human influence (e.g., forest harvest, agricultural practices) affect these plant ecoregions (Turner et al., 2001). Similar knowledge of vertebrates has lagged because of the difficulty measuring the abundances of multiple animal species at representative scales.

Plant communities offer many of the critical resources needed by mammals and are likely a key determinant of their distribution and abundance. If vertebrate biogeography tracks plant formations, then animals either respond to the same influences or are driven by bottom-up forces. On the other hand, animals are more than the food they eat and their dynamic behaviours such as movement and thermoregulation could result in different biogeographic patterns than plants, especially in response to human disturbance and resource supplementation. In North America, ecoregions are defined along climatic and topographic gradients reflecting the vegetative communities in deserts, plains, highlands, tundra and seven forest types (Omernik & Griffith, 2014). Previous tests have found mixed results when using these ecoregions to explain bird and mammal distributions by predicting areas of high species turnover from animal range maps, with no support when considering only North American species (McDonald et al., 2005), but stronger support at the global scale (Smith et al., 2018). However, these two studies were conducted by matching high-level biogeographic patterns of diversity and both recognized the importance of additional research to identify the specific mechanisms underlying observed ecoregion patterns.

A historical perspective on the most important ecological drivers for mammals indicates that prehistoric biogeography in North America was strongly shaped by climate and then later by colonizing humans (Alroy, 2001). Human societies continue to exert large impacts on modern mammal populations, extirpating predators from large areas and driving substantial community changes along urban-wild gradients, as sensitive species are restricted to wildlands, while anthrophilic species thrive near people (Parsons et al., 2018). However, the relative importance of human factors in comparison to climate in modern populations has not been addressed at the large scale needed to encompass meaningful climatic variation. Mammals also depend on plant communities for cover and food. Green vegetation forms the base of the food web, along with tree mast (i.e., seeds, fruits, nuts) crops that feed diverse guilds of granivores and frugivores (Martin et al., 1951). If food and climate drive the patterns of distribution and abundance of mammals, we would expect plant ecoregions to structure mammal communities. However, if human factors are now the most important influence driving these patterns, we would predict a homogenization of mammal communities across areas with similar levels of human development (McKinney, 2006). Understanding the relative importance of these factors is critical for conserving biodiversity in the face of climate change and human population growth.

In this study, we examine a large compilation of mammal abundance estimates at a continental scale that represent the full range of climatic and human disturbance levels of the continental United States: hot to cold, wet to dry and urban to wild (Figure S1). Together, these data allow us to quantify the biogeography of mammals by mapping the ecological communities of 25 of the most common, larger terrestrial mammals of the conterminous United States, compare them to regions based on plants and identify potential mechanisms underlying ecoregion boundaries by comparing the extent to which these communities are shaped by climate, habitat and human disturbance. The relative importance of these factors on mammal species today has important implications for managing biodiversity on a warming, drying continent with a growing human population and footprint. Additionally, these larger mammals play important ecological roles that can cascade through ecosystems (Terborgh, 2010) and we use our maps to predict the relative strength of their resulting ecological impacts across the United States.

2 | MATERIALS AND METHODS

We used models of relative abundance from collaboratively collected camera trap data from 424 array sites using a standardized sampling design to predict mammal communities, which we then grouped based on similarity and mapped across the country. An overview of our approach is provided in Figure 1 and the steps are also identified in sub-headings.

2.1 | Camera trap data (1)

We collected camera trap data from across the United States by combining data from Snapshot USA (Cove et al., 2021; Kays, Cove, et al., 2022), Carolina Critters (Lasky et al., 2021) and other data sets from (Figure S1). To reduce the problem of uneven sampling we thinned the data from North Carolina and Virginia to be similar to the camera densities from other regions by randomly selecting 400 locations within each 3-degree grid cell. All cameras were set at ~0.5 m height and without bait. A variety of camera models were used, but all had fast (<0.5 s) trigger times and other features that made their data comparable. Some cameras were set on hiking trails or dirt roads and this was noted. We initially aimed to include data from Canada but found much of it was collected with cameras set higher on trees (to account for snowfall of cameras left in remote areas for long time periods), which failed to reliably detect smaller species. Cameras were set to take multiple pictures for each trigger event and immediately retrigger and we combined these into one sequence with a 60 s independence interval, which ensures temporal independence of detections (Kays

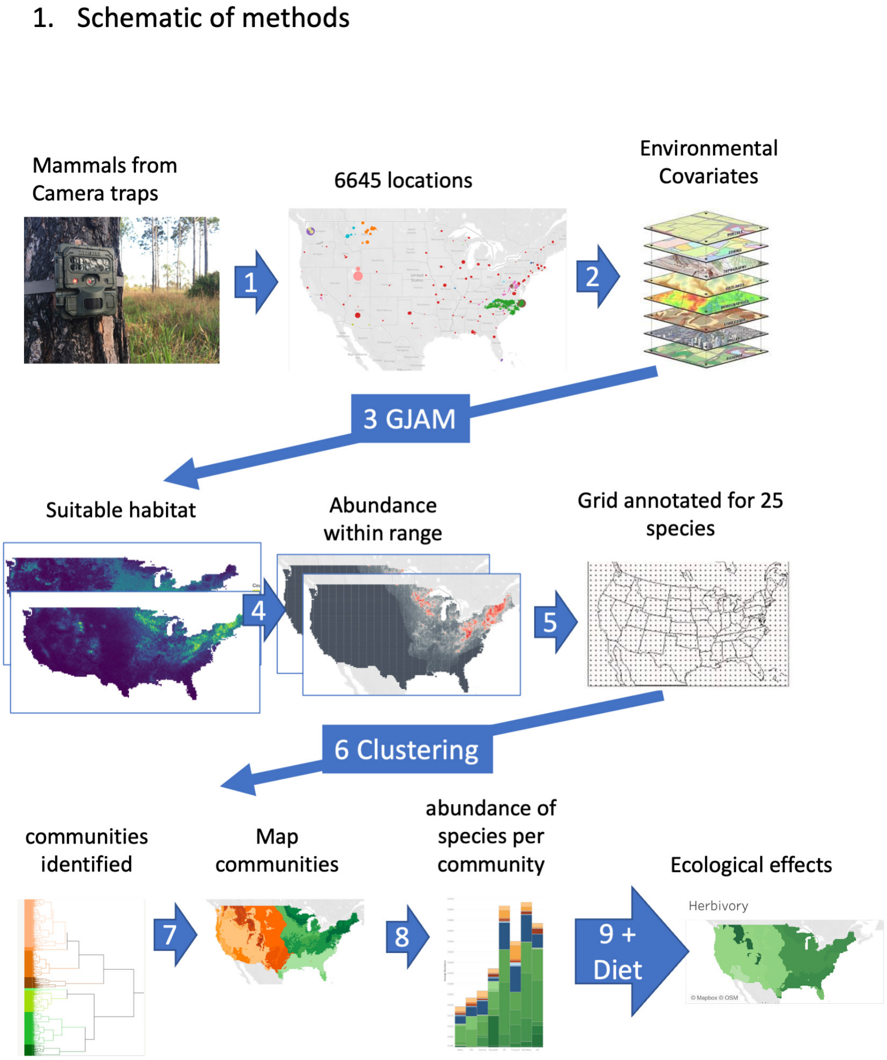

FIGURE 1 An overview of our approach for mapping mammal communities in North America. (1) We acquired relative abundance data for 25 mammal species across 6645 sites monitored by camera traps (2) annotated them with environmental covariates and (3) used GJAM to predict their potentially suitable habitat. We then (4) used range maps to trim out areas not used and (5) annotated a grid of points with the predicted relative abundance for all species. We used these mammal community data in a (6) hierarchical clustering algorithm to create 8 broad and 16 narrow clusters, which (7) could then be mapped, (8) characterized by their typical mammal abundances and (9) combined with diet and body size information to extrapolate ecological impacts.

& Parsons, 2014). We used the number of independent detections at a camera site as a measure of relative abundance for a species, standardizing for the amount of time a camera was in place, essentially comparing detection rate across sites for a species. We then adjusted these measurements to account for differences in detection area for species of different sizes (Rowcliffe et al., 2011). While local animal movement rates can also affect detection rate (Broadley et al., 2019), if cameras are set in standardized way it can still provide an index of relative abundance that can be compared across sites and species (Hofmeester et al., 2019) that is correlated with absolute density (Parsons et al., 2017). It is likely that the relationship between detection rate and true abundance is different across species, but our models compare the relative abundance of one species at a time, avoiding those complications. In total, we collected data from sites monitored by 6447 cameras across 424 arrays (i.e., study sites) representing 688.4 camera-years of survey effort.

We initially focused on 26 terrestrial, broad-ranging mammal species that are large enough to be well surveyed by camera traps, can be indisputably identified from images and which were well covered in our data with a minimum size cut-off based on performance of preliminary model runs (Table S1). The smallest sample size was for grey wolves with 109 detections by 55 cameras across 16 study areas. We excluded species that were not sampled well because they are primarily aquatic or because they are difficult or impossible to tell apart on camera trap pictures (i.e., *Sylvilagus*, *Neotoma*, *Glaucomys*, Kays, Lasky, et al., 2022). Our sampling is thus somewhat biased towards the larger, more common, more widespread species, although it does include small species like chipmunks and rare species like wolves and cougar.

2.2 | Covariates (2)

We selected environmental covariates to describe the physical, vegetative, climatic and human aspects of habitats sampled with camera traps (Table 1). We zero-centred and standardized all covariates. We initially included a larger number of covariates and removed those that were correlated ($r \geq 0.6$; except annual temperature and rainfall which were correlated at 0.63). We used the MASTIF model to estimate the production of seeds and fruit by

TABLE 1 Covariates used in GJAM models.

Type	Name	Source	Description	Scale	Year	Ref.
Human	Human population size	GPW V4	Number of people	1 km^2	2020	Center for International Earth Science Information Network (2018)
Climate	Temp	MERRAclim	Annual Mean Temperature (degree Celsius multiplied by 10)	2.5 arcminutes	2000s decade	Vega et al. (2017)
Climate	Precipitation	MERRAclim	Annual Precipitation	2.5 arcminutes	2000s decade	Vega et al. (2017)
Climate	Aridity index	ENVIREM	Degree of water deficit below water need	30 arc seconds	Current	Title and Bemmels (2018)
Terrain	Terrain	Terrain Ruggedness Index	Difference between central pixel and surrounding cells	1 km	Current	Amatulli et al. (2018)
Habitat	Shrub	IUCN Habitats	% of area that was shrub	1 km^2	2015	Jung et al. (2020)
Habitat	AgCombo	IUCN Habitats	% of area that was pasture or arable	1 km^2	2015	Jung et al. (2020)
Habitat	Grass01	IUCN Habitats	Scored 1 if % of area in grass was >30%	1 km^2	2015	Jung et al. (2020)
Habitat	Hard Mast, Big Nut Mast, Conifer Mast, Fruit tree mast	MASTIF	Estimated production of each type of mast (kg/ha) weighted by the amount of forest in 1 km^2	1 km^2	2015	Clark et al. (2019) and Jung et al. (2020)

Note: Acronyms are MASTIF = mass inference and prediction, GPW V4 = gridded population of the world, version 4, Merraclim = modern-era retrospective analysis for research and applications climate, ENVIREM = environmental rasters for ecological modelling, IUCN = international union for conservation of nature.

trees at each camera location (Clark et al., 2019). Seeds were classified into four categories: hard mast, big nut, conifer, soft mast (Table S2). The MASTIF data are estimates of typical mast production for a site given the forest composition (species, size, age), but do not account for year-to-year variation. Because MASTIF sites (170,000 forest inventory plots) were not at the exact same locations as our cameras, we took an average of the three MASTIF sites closest to the camera trap that were in the same forest type (Ruefenacht et al., 2008). Because these fruits only come from forested land, we then multiplied that value by the total % forest cover within 1 km^2 (Jung et al., 2020) to get a measure of the amount of mast available to mammals around a camera site. This process resulted in four measures of forest cover weighted by the amount of mast (hard, soft, big nut, or conifer) they were likely to produce.

2.3 | Modelling community abundance (3–5)

We used a generalized joint attribute model GJAM (Clark et al., 2017) to predict the relative abundance of 26 mammal species at the community scale based on the covariates described above. This multivariate approach extends single-species distribution models by considering relationships among the community members through a correlation matrix from the residuals. The model accepts response variables that may be measured in different ways (i.e., continuous or discrete), representing all observations as continuous through the latent vector $\boldsymbol{\omega}_i$, which, in this case, represents counts per effort (detection rate) for each species up to S at camera trap i, where $\boldsymbol{\omega}_i$ is given by:

$$\boldsymbol{\omega}_i \sim \mathrm{MVN}(\boldsymbol{\mu}_i, \boldsymbol{\Sigma}) \quad (1)$$

where $\boldsymbol{\mu}_i$ is a vector of means of length S and $\boldsymbol{\Sigma}$ is an $S \times S$ covariance matrix which quantifies the residual correlation between species that is not taken up by the mean structure of the model. These residual correlations reflect species co-occurrence patterns not explained by environmental predictors which could be due to model mis-specifications, missing covariates, or species interactions.

The mean structure $\boldsymbol{\mu}_i$ is modelled as a function of environmental predictors following:

$$\boldsymbol{\mu}_i = \boldsymbol{\beta}' \boldsymbol{X}_i \quad (2)$$

where $\boldsymbol{\beta}$ is a $Q \times S$ matrix of slope coefficients associated with each species and each predictor up to length Q in design matrix $\boldsymbol{X}_i$.

The output of the model predicts the relative abundance of each species at the observation (camera trap) scale and includes a species-by-species covariance matrix with measures of the sensitivity of each species to each covariate. We ran our model within a Bayesian framework using non-informative priors via the gjam package (v 2.6.2, Clark & Taylor-Rodriquez, 2021) in program R (R Core Team, 2023), achieving convergence after 40,000 iterations with a burn-in of 10,000 iterations. The relative importance of each covariate was determined through a sensitivity analysis that integrates the change in the model performance to removal of each covariate (Brynjarsdóttir & Gelfand, 2014).

As a measure of relative abundance for each species, we used the number of detections from a camera trap and the amount of time a camera was in place as a measure of effort (i.e., detection rate). To make this abundance measure more comparable across species, we accounted for the fact that larger species are detected by camera traps over larger areas by dividing the abundance by the mass-adjusted area surveyed by each camera following (Rowcliffe et al., 2011):

$$\text{Area} = 1.65 \times \text{mass}^{0.33} \tag{3}$$

To evaluate the utility of mast-weighted measures of forest cover, we ran two versions of the model, one with % forest cover within 1 km unweighted by mast and one with % forest cover within 1 km weighted by the four mast types, respectively. Both models included all other covariates. We used DIC values to compare the performance of these two models.

We used a regular 10 km grid of points across the country to predict relative abundance of each species to unsampled areas based on covariate values at each grid point. We ran our prediction using the predictGJAM routine in the GJAM package which allows species-specific prediction while accounting for community-level variance–covariance relationships (i.e., multivariate prediction; Clark & Taylor-Rodriquez, 2021). We used the resulting predictions to make habitat suitability maps for each species across the country. The prediction maps from GJAM show where potentially suitable habitat occurs, but the species may not actually live in all these areas due to dispersal limitations or other factors not included in our model. Therefore, we used range maps (IUCN, 2020; USDA, 2022) to trim these habitat suitability predictions to only include areas each species is known to inhabit. These predicted measures were then annotated onto a 10 km grid of points across the country, predicting the relative abundance of all members of the mammal community we modelled. At this point we excluded the North American porcupine (*Erethizon dorsatum*) from the analysis because of a poor fit between their predicted and actual distribution, resulting in 25 modelled species.

2.4 | Describing communities and ecological impacts (6–9)

We used hierarchical clustering (JMP, SAS, Cary, NC, USA) to group sites with similar mammal communities, based on the predicted relative abundance of each species. We used these to describe a number of clusters chosen to represent coarse ($n=8$) and fine ($n=16$) scaled groupings to roughly align with the level of detail in the level I and level II ecoregions (Omernik & Griffith, 2014). We compared the match of these communities with plant derived ecoregions using a 10 km grid of points annotated to level I and level II ecoregions (Omernik & Griffith, 2014). We then mapped the location of these clusters and calculated the average relative abundance for each species in each region. Following the approach of two recent papers (Parsons et al., 2022; Ramirez et al., 2021), we calculated the potential relative ecological impact of each species as a consumer of plants or prey based on their activity at a site, their body size and their diet. We calculated a scaled measure of species activity by combining the camera trap data detection rate (predicted from GJAM already scaled by survey area for each species), average group size and average amount of time spent in front of the camera:

$$D_{sj} = \left(\frac{n_{sj}}{D_j}\right) * t_s * g_s \tag{4}$$

where D_{sj} is the scaled activity of species s at camera location j, n_{sj} is the total count of species s on camera j divided by the expected detection area of a camera based on body size of species s and D_j is the total number of days camera j ran. t_s is the average amount of time species s spent in front of camera traps in seconds and g_s is the average group size of species s on camera traps. We used detection rates predicted from the GJAM model, which already account for differences in camera detection area based on body size (this correction was made to data used in GJAM). Because of the fact that the group size and time in front of the camera were not available for all datasets, we calculated average values for each species from the Snapshot USA data (Cove et al., 2021; Kays, Cove, et al., 2022).

Next, we used this measure of animal activity at a site to estimate their potential ecological impacts by adding information on body size and diet following:

$$I_{sv} = M_s \times p_{sv} \times d_{sj} \tag{5}$$

where M_s is the metabolically active tissue (species average $\text{kg}^{0.75}$; Kleiber, 1947 in species s), p_{sv} is the percent of the diet of species s made up of items from trophic level v and d_{sj} is the average scaled species activity in front of a camera (Equation 4). Data on species mass and diet were drawn from the PANTHERIA and CARNIDIET databases (Jones et al., 2009; Middleton et al., 2021). We used the more detailed data in CARNIDIET to classify the proportion of a species diet that was large or small prey for the carnivores (15-kg cut-off). We quantified the proportion of their dietary items that were large or small prey while excluding trace dietary items (<15% volume per sample). This ecological impact metric expresses in an index of the kg of mammal biomass supported by potential feeding on a given food type, weighted by the time spent in a given area.

3 | RESULTS

Camera traps at 6645 locations documented 215,722 visits made by 25 focal mammal species (Table S1, which also has scientific names for all species). Our GJAM models including measures of forest seed production performed much better (many fewer Deviance

Information Criterion (DIC) points) than models using the simpler measure of forest cover. The GJAM model converged well, with stable beta chains and most species had good model performance (Table S3). Using a sensitivity analysis, we identified climate variables as being the most important factors, followed by a combination of habitat, terrain and human factors (Figure 2a).

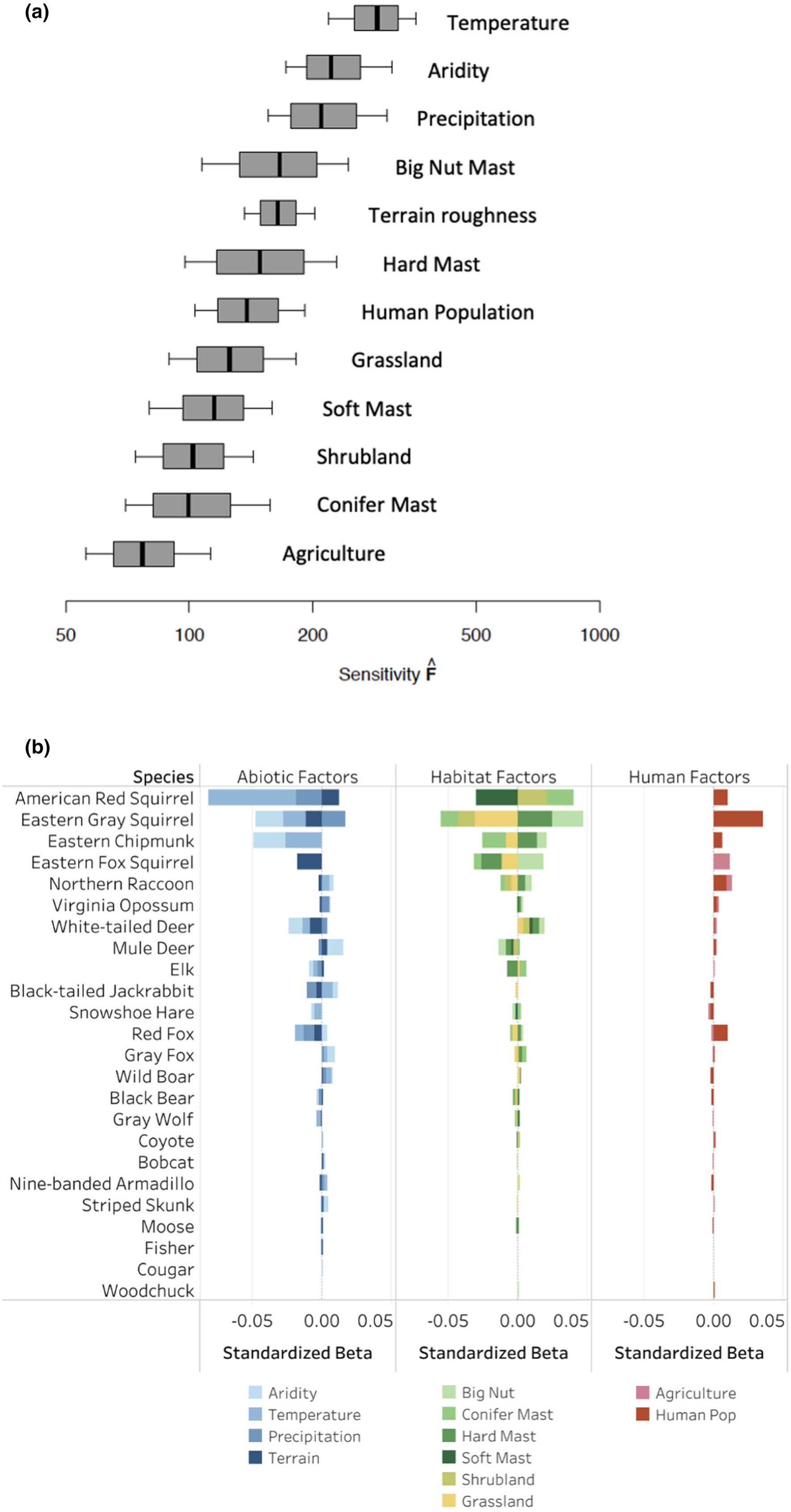

FIGURE 2 Model results for generalized joint attribute model of mammal abundance based on 11 covariates. (a) The sensitivity of the full community model to each covariate, showing that climate variables are the most important (highest sensitivity). This sensitivity measure is designed to evaluate covariate importance among multiple response variables and multiple continuous predictors (15). (b) The β values for the significant (95% credible intervals not overlapping zero) covariates for each species' model showing the direction and magnitude of effects (see Table S2 for all values). The dark line shows the median value, the grey boxes show the lower and upper quartile and the whiskers show 1.5 the interquartile range.

Estimated relationships between the relative abundance of individual species and environmental conditions followed expectations based on species biology (Figure 2b, Figure S2, Table S4). For example, Eastern grey squirrels had a strong positive relationship with human population size, as did other well-known anthrophilic species (e.g., northern raccoon, red fox, eastern chipmunk, Virginia opossum, white-tailed deer) and black-tailed jackrabbit, wild pigs and snowshoe hare had the strongest negative relationship with human population size. Forest cover weighted by the type and amount of seeds they produce was important in explaining the distribution of a number of species, especially squirrels. Hard mast production was positively associated with abundance of eastern grey squirrels, eastern chipmunks and American red squirrels, but negatively associated with eastern fox squirrels. Big nuts were positively associated with eastern grey and eastern fox squirrels, while conifer mast was positively associated with American red squirrel abundance. Although none of these relationships were surprising, taken together, they do allow us to predict the relative abundance of each species across the United States (Figure S3), enabling new insights into community structure and potential ecological impacts.

3.1 | Clustering communities

Our clustering analysis on the predicted relative abundance of mammals throughout a 10km grid of points across the conterminous United States shows the hierarchical divisions of mammal communities, with the first split being between the eastern and western United States (Figure 3, Figure S4). The eastern United States is then split latitudinally, with the four coarse community clusters being subtropical, southeast, midwest and northeast. The western communities also divide into four groups, but the patterns appear to be driven more by precipitation than latitude. There is a broad western and central plains group, one around the extreme hot areas of the southwest and another in the extreme cold parts of the Rocky Mountains. These patterns broadly match those of ecoregions defined around plant communities (Figure S1), with 82% of the area of the 8-community mammal map matching up with the respective Level I ecoregion and 62% of the 16-community map matching up with Level II ecoregions (Table S5).

The differences between the eight primary communities are shown by the expected average relative abundance for species (Figure 4, Figure S4). The east–west split is most obviously associated with higher relative abundance overall in the east, driven especially by many squirrels, northern raccoons and white-tailed deer. Those species are present in some parts of the west, but are much less abundant and mule deer replace white-tailed deer in these drier western regions. The Rocky Mountain community is the most divergent in the west and has by far the lowest northern raccoon abundance. A number of species were characteristic of one or two regions (e.g., abundant in one or two regions, but rare or absent elsewhere) including elk in the Rocky Mountains, black-tailed jackrabbits in the southwest and wild pigs and nine-banded armadillos in the southeast. There was also a suite of cold-adapted

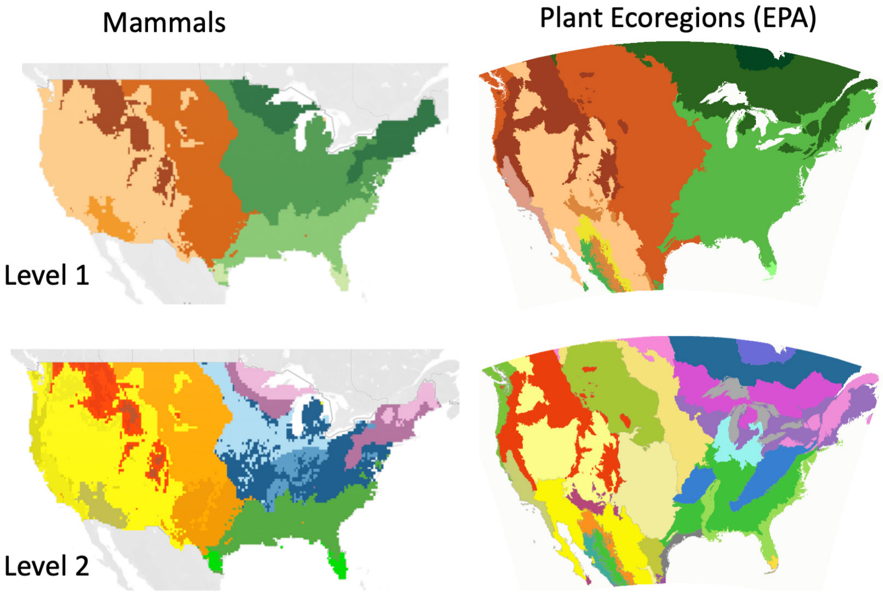

FIGURE 3 Comparing mammal regions to the level 1 US Environmental Protection Agency (EPA) ecoregions (Omernik & Griffith, 2014) shows a very good match for the Great Plains, Northern Forest and Subtropical zone. The Eastern Temperate Forest region is split into 2 for mammals while the general western mammal region includes 4 plant ecoregions. The Rocky Mountains mammal region matches the northwestern forested mountains, in part, but does not include the Sierra Nevada range. The southwest mammal region is not recognized in plant regions. At the more detailed level, the split of western and Great Plains regions generally matches between plants and mammals, as does the split of Northeast into 2 regions (except the lower peninsula of Michigan which clusters with the Midwest mammals). The split of the Rockies and Midwest each into 3 regions is not matched by the plant ecoregion.

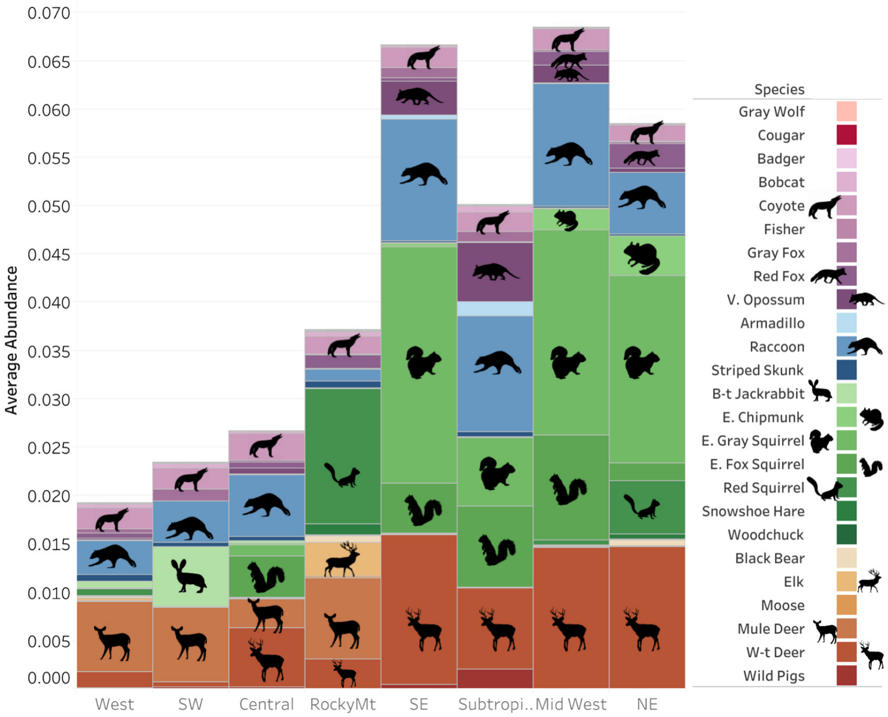

FIGURE 4 Average species' relative abundances across the eight communities with species colour coded as large carnivores in red (although they are so relatively rare they are hard to see), small carnivores in purple, insectivores in blue and herbivores in green (small) or brown (large). Animal silhouettes are provided for the most common species to help distinguish colour gradients. Abundances for the more detailed 16 communities are shown in Figure S5.

species that were most abundant in the Rocky Mountains and northeast forests including moose and snowshoe hares. Finally, several broad-ranging species were present in many different regions, but had variable abundance across space, which helped distinguish communities.

The finer scale differences that distinguish the 16 communities tended to be due to minor differences in relative abundance (Figure S4). The western region is split into three groups with fewer Virginia opossums in zone 1, more northern raccoons in zone 2 and fewer black-tailed jackrabbits but more black bears and bobcats in zone 3. The central region is split into two with more typical warm-tolerant species (i.e., grey fox, Virginia opossum, nine-banded armadillo, wild pigs, black-tailed jackrabbit) in the south and more cold-adapted species (i.e., elk, red fox, red squirrel) in the northern zone (5). Mule deer and Eastern fox squirrels were more abundant in zone 5, while Eastern grey squirrels were more abundant in zone 6. The Rocky Mountains are also split into three regions with a periphery (7), northern core (8) and southern core (9), with differences driven especially by increases in red squirrel and elk abundance and decreases in racoons in higher and more southerly mountains. The Midwest zone is split into three due mostly to differences in squirrels, with zone 12 having more eastern fox squirrels, zone 14 having more eastern grey squirrels and zone 13 having similar but very high levels of both. Virginia opossums are more abundant in zone 13, while zone 14 had higher levels of American black bears, bobcats and grey foxes that also comprised portions of the Mid-Atlantic. Finally, the northern forests split into two zones, with the cold-adapted species (i.e., snowshoe hare, moose, grey wolf) being more common in the northern zone (15) and less cold-adapted species (i.e., Eastern grey squirrel, eastern fox squirrel, racoon, Virginia opossum) being more common in the southern zone (16).

3.2 | Ecological impacts

We can represent spatially explicit ecological impacts by mapping the relative strength of the ecological roles played by common mammals across the country based on their typical abundance, time spent in front of the camera, weight and diet (Figure 5). Potential herbivory pressure is driven by the larger ungulates and is the highest in the Rocky Mountains that are home to elk and abundant mule and white-tailed deer, followed by eastern regions with high numbers of white-tailed deer. Similarly, the potential ecological impact of invertebrate consumers is also driven by the three largest-bodied species: American black bears, wild pigs and northern raccoons. The addition of nine-banded armadillos in the subtropical region helps give it the highest overall invertebrate predation pressure. Northern raccoons are by far the most abundant predator of small prey and they drive community-wide patterns of small prey predation pressure in the east, while predation pressure from other predators on small prey remains consistent across regions. Finally, predation pressure on large prey (>15 kg) is highest in the Rocky Mountains where cougars and grey wolves are most abundant. Coyotes hunt far fewer large prey than wolves or cougars, but their abundance across the country makes them the most important risk to large prey in many regions.

4 | DISCUSSION

We empirically derived communities of mammals based on patterns of abundance and found them strikingly similar to well-known ecoregions created from plant communities (Figure 3, Table S5). More than just pattern matching, our niche models give insight into the ecological mechanisms underlying these communities. We

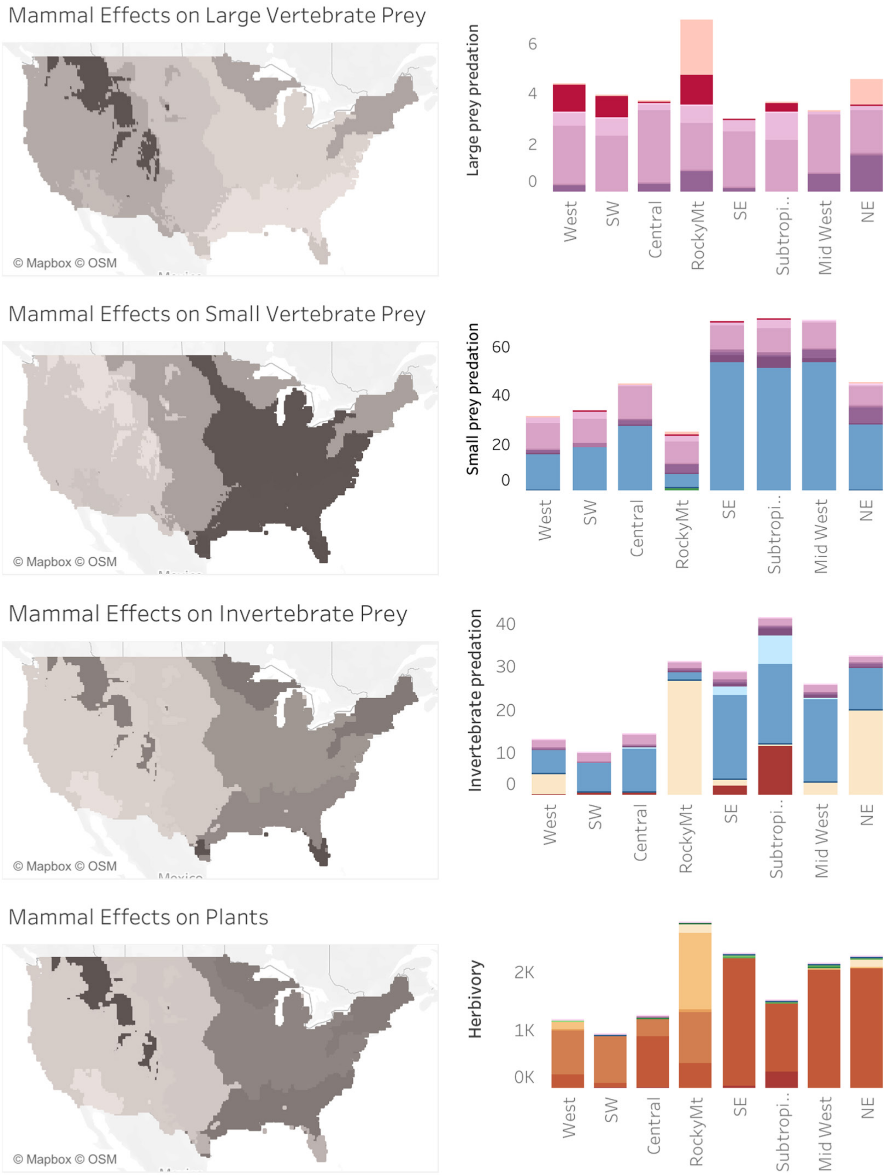

FIGURE 5 Relative strength of ecological impacts of mammals mapped out per coarse region (left side) and per species (right side) as predators on large vertebrate prey, small vertebrate prey, invertebrates or herbivores on plants. These indices of potential ecological impact combine aspects of each species' relative abundance, body size and diet (units: [kg mammals]*[time at a site]/day/m^2). Darker grey colours indicate stronger effects, with regional values and the relative contribution of species shown on graphs to the right. This ecological impact metric is an index of mammal biomass (kg) supported by potential feeding on a given food type, weighted by the time spent in a given area.

found that climate variables are the most important influencers, driving a primary split between the eastern and western United States and producing secondary divisions along temperature gradients in the east and precipitation gradients in the west that parallel those seen in plant ecoregions. Food production by forests is also an important predictor of abundance, especially larger hard mast producing trees that have a long coevolutionary history with mammals (Stapanian & Smith, 1978). Anthropogenic disturbance to the landscape is correlated with mammal abundance in contrasting ways for different species, but it is not presently affecting mammal communities to the extent observed with climate and food. The resulting patterns of mammal abundance, especially of larger species, have ecological consequences due to differences in the potential for herbivory and predation across the continent.

Three climatic covariates (precipitation, temperature, aridity) were the most important predictors of abundance across the mammal communities we modelled (Figure 2a). Although climate has been linked to major evolutionary events in the history of North American mammals (1), no studies have evaluated its importance on contemporary mammal distributions in comparison with habitat and human factors. These effects can also be seen when considering the community maps and graphs of relative abundance, where overall mammal abundance is higher in wetter regions (e.g., east and Rocky Mountains) and where latitudinal change in zones (e.g., zones 14–16) reflect species turnover and addition of more abundant cold-adapted species (i.e., snowshoe hare, moose). Our models suggest that climate change will have strong impacts on the composition of mammal communities and we are able to quantify these relationships to predict those effects for 25 species (Table S4).

Human factors (population density, agriculture) were less important than climate, but still had strong impacts on mammal abundance, although in contrasting ways, showing how some species successfully occupy urbanized spaces while others do not. Human population density was important for 68% of species, with a positive relationship for 11 species and negative for 6 species (Figure 2b, Tables S2 and S4). Agriculture was strongly negatively correlated with abundance for four carnivore species and snowshoe hare, but positively associated with eight species of herbivores and omnivores (Figure 2b, Table S2). The simplistic covariates we were able to use for this large scale analysis represent a more complex relationship and additional variance could likely be explained with more information on hunting by humans and recreation patterns (Kays et al., 2017), effects of historical extirpations (Laliberte & Ripple, 2004) and more nuanced information about the types and intensities of agricultural developments (Caldwell & Klip, 2023). Nonetheless, our data encompass the full range of variation of human footprint, from cities to farmland to wilderness (Figure S1), allowing us to broadly compare the importance of humans to other factors.

The seeds and fruits produced by trees represent food for many mammal species and new large-scale estimates of their production (Clark et al., 2019) allowed us to relate them to animal abundance over broad scales for the first time, providing substantially better predictions than using simple measures of forest cover. The largest seeds (big nuts: *Carya* and *Juglans*) and other hard masting species were the most important (Figure 2, Figure S2). This approach of quantifying the potential value of a forest by the density of different kinds of seeds it produces also has modelling advantages over using categorical forest types. For the seed and fruit eating species, these relationships probably reflect direct benefits of the trees producing food for these mammals. The importance of mast for other species, such as predators, was lower, but still important by reflecting other aspects of habitat quality (i.e., prey abundance) associated with mast production. We grouped tree species into four broad categories that reflect mammal feeding preferences (Table S4, Figure S6), but expect more nuanced relationships could be discovered through more fine-scale dietary categories related to species' known dietary preferences (Moller, 1983).

Ecological maps are key for many aspects of conservation, including supporting biodiversity and red list assessments, predicting carbon dynamics and assessing disease risk (Gatti et al., 2021). Our ecological maps provide a unique perspective, not only because they are specific to mammal communities, but also because they provide the basis for quantifying the relative ecological impact of mammals across these zones. Our results show strong regional differences in mammalian herbivory and predation on small prey (e.g., ~2× higher in much of the eastern United States than some western regions). These maps also show that parts of the Rocky Mountains have high levels of herbivory and predation on large prey. Whether the higher absolute herbivory translates into higher pressure per plant would depend on plant abundance and defences, which are clearly different across the United States (e.g., sparse, well-defended desert plants vs. abundant leafy eastern deciduous forests). These results also emphasize the ecological importance of common large species over smaller rare species of the same guild, with animals like coyotes, northern raccoons and white-tailed deer having the overall largest roles across the continent. We hope these results will be useful in generating hypotheses about the mechanisms underpinning ecological impacts that can be tested with field experiments (e.g., herbivory; Rosin et al., 2017, predation risk Schuttler et al., 2016).

One drawback of our study is that it only included 25 species of mammals and future work could improve analyses by adding more species and understudied habitats. Despite collecting one of the largest camera trap datasets ever published, many species remained data deficient, limiting our ability to model their abundance at a continental scale and in undersampled regions in the western United States. Adding more camera data through standardized surveys (Cove et al., 2021), common repositories (Ahumada et al., 2019), or integrating other types of mammal datasets (Pacifici et al., 2017), could help meet this goal. Expanding the species included in analyses could change the resulting mammal communities identified, especially through the addition of species endemic to small regions. However, our work does include the most common large mammals, which have the strongest ecological impacts (Figure 5, Equation 5), so we expect fewer changes to those maps of ecological function. Our work is also limited by having only one model per species, thus forcing the same ecological relationships across an entire species' range and not explicitly considering species interactions. Most wide-ranging species probably have some variation in their ecology due to local adaptation or subspecific genetic variation (Pease et al., 2022; Rollinson et al., 2021) and accounting for this would improve local abundance predictions.

This work shows the potential for continental-scale estimates of animal abundance through large collaborations (Cove et al., 2021; Kays, Cove, et al., 2022), data standards and sharing tools (Ahumada et al., 2019) and the growing diversity of relevant ecological data (i.e., mast production Clark et al., 2019). Our results show that the patterns of modern mammal communities, as with plant ecoregions, are driven by climate and are relatively stable across broad landscapes despite substantial variability in human densities and infrastructure. This finding also highlights the potential impact of rapid climate change (Shukla et al., 2019) to these communities and raises questions about the ability of plant and animal communities to keep pace without active management. Ecoregions have proven a useful tool for mapping existing patterns and we see potential for our empirical niche-driven approach to be extended to document changes in near real time (Kays & Wikelski, 2023) and offer predictions useful for conservation management about where species are likely to do best in future conditions.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All camera trap data are publicly available through the references cited in Figure S1.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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