

PRIMARY RESEARCH ARTICLE

Predicted climate-induced reductions in scavenging in eastern North America

Courtney J. Marneweck¹  | Todd E. Katzner²  | David S. Jachowski¹

¹Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA

²U.S. Geological Survey, Forest & Rangeland Ecosystem Science Center, Boise, ID, USA

Correspondence

Courtney J. Marneweck, Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA.
Email: cmarnew@clemson.edu

Funding information

US Department of Agriculture

Abstract

Scavenging is an important function within ecosystems where scavengers remove organic matter, reduce disease, stabilize food webs, and generally make ecosystems more resilient to environmental changes. Global change (i.e., changing climate and increasing human impact) is currently influencing scavenger communities. Thus, understanding what promotes species richness in scavenger communities can help prioritize management actions. Using a long-term dataset from camera traps deployed with animal carcasses as bait along a 1881 km latitudinal gradient in the Appalachian Mountains of eastern USA, we investigated the relative impact of climate and humans on the species richness and diversity of vertebrate scavengers. Our most supported models for both mammalian and avian scavengers included climatic, but not human, variables. The richness of mammalian and avian scavengers detected was highest during relatively warm (5–10°C) and dry (100–150 mm precipitation) winters, when food was likely limited and both reliance on and detection of carrion was high. The diversity of mammalian and avian scavengers detected was highest under drier conditions. We then used these results to project the future species richness of scavengers that would be detected within our sampling area and under the climate scenario of 2070 (emissions level RCP8.5). Our predictions suggest up to 80% and 67% reductions, respectively, in the richness of avian and mammalian scavengers that would be detected at baited sites. Climate-induced shifts in behavior (i.e., reduction in scavenging, even if present) at this scale could have cascading implications for ecosystem function, resilience, and human health. Further, our study highlights the importance of conducting studies of scavenger community dynamics within ecosystems across wide spatial gradients within temperate environments. More broadly, these findings build upon our understanding of the impacts of climate-induced adjustments in behavior that can likely have negative impacts on systems at a large scale.

KEYWORDS

avian, diversity, future climate, human, mammalian, richness, scavenging

1 | INTRODUCTION

Complex networks of ecological interactions maintain biodiversity (Bascompte et al., 2006). Scavenging is one such network within

food webs, although it is often underappreciated (Moleón et al., 2014; Wilson & Wolkovich, 2011). Scavenging species are valuable members of ecosystems as they stabilize food webs (DeVault et al., 2003; Wilson & Wolkovich, 2011) and remove decaying organic

matter (Ćirović et al., 2016; O'Bryan et al., 2018), which ultimately reduces disease transmission (O'Bryan et al., 2018; Ogada et al., 2012) and promotes nutrient recycling (Gharajehdaghipour et al., 2016; Payne & Moore, 2006; Wilson & Read, 2003). Communities with species-rich assemblages of scavengers are also suggested to have higher ecosystem stability due to the complex networks of pathways within the food web (Moleón, Sánchez-Zapata, Margalida, et al., 2014; Sebastián-González et al., 2016), meaning that these systems could be more resilient to environmental changes.

Global change (i.e., changing climate and increasing human impact) may alter important ecological interactions (Sebastián-González et al., 2019). It is suggested that vertebrate scavenger species richness is strongly negatively affected by humans (Sebastián-González et al., 2019). In some environmental settings, higher human population density can reduce scavenger richness and diversity due to habitat fragmentation and fatality from conflict or road deaths (Crooks et al., 2011; Hagen et al., 2012; McKinney, 2008; Planillo et al., 2018; Sebastián-González et al., 2019; Treves & Karanth, 2003). Conversely,

TABLE 1 A priori hypotheses that could explain the effect of climatic and anthropogenic variables on the richness and diversity of vertebrate scavenger species detected at camera traps placed over a 1881-km latitudinal gradient during winter in the Appalachian Mountains of eastern North America. The direction indicates its effect on scavenger species richness and diversity, where ↑ = increase and ↓ = decrease

Hypothesis	Conditions	Direction	Justification
<i>Climatic</i>			
Snowpack	Cold and wet	↑	Low winter temperature increases reliance on valuable protein, but deep snow makes it difficult to find and/or physically access live prey or non-carrion food items (Needham et al., 2014; Selås & Vik, 2006; Watson et al., 2019), increasing richness and diversity of species scavenging
Physiological tolerance	Cold and dry	↓	Cold and arid conditions are difficult for many species to physically tolerate and thus persist (Currie et al., 2004). So, there will be fewer species present, decreasing richness and diversity of species scavenging
Dry snow drought	Cold and dry	↑	A dry snow drought occurs when there is a lack of winter precipitation (Harpold et al., 2017). Low winter temperature increases reliance on valuable protein, but the lack of precipitation affects many food sources, making it difficult to find sufficient live prey or non-carrion food items (Brown et al., 2006; Dierauer et al., 2019), increasing richness and diversity of species scavenging
Warm snow drought	Warm and wet	↑ ↓	A warm snow drought occurs when there is a lack of snow accumulation due to increased temperature and/or early snow melts (Harpold et al., 2017). Under these mild winter conditions, fewer herbivore starvation mortalities occur (Wilmers & Getz, 2005) which could lead to higher reliance on the fewer available carcasses, increasing richness and diversity of species scavenging. Conversely, these conditions may facilitate live-prey or other food acquisition, lessening the reliance on scavenging, decreasing richness and diversity of species scavenging
Interkingdom competition	Warm and wet	↓	Increased microorganism and invertebrate activity can lead to vertebrates being outcompeted and carcasses not persisting long enough to be utilized (DeVault et al., 2004; Ray et al., 2014), decreasing richness and diversity of species scavenging
Compounded snow drought	Warm and dry	↑	The cumulative effect of low precipitation (dry snow drought) and early snow melts (warm snow drought) can lead to difficulty in finding sufficient live prey or non-carrion food items (Brown et al., 2006; Dierauer et al., 2019), increasing richness and diversity of species scavenging
Stability	Variable	↓	High variation in local climate makes it difficult for many species to adapt to local conditions, as well as physically tolerate these fluctuations and thus persist in the area (Currie et al., 2004; Ricklefs, 2004), so there will be fewer species present and thus fewer species scavenging decreasing richness and diversity of species scavenging
<i>Anthropogenic</i>			
Provisioning	Higher human density	↑	Species exploit resources provided by humans (Lambertucci et al., 2009; Newsome et al., 2015), increasing richness and diversity of species scavenging
Conflict	Higher human density	↓	Habitat fragmentation and mortality from conflict or road deaths will lead to human avoidance (Crooks et al., 2011; Planillo et al., 2018; Sebastián-González et al., 2019; Treves & Karanth, 2003), decreasing richness and diversity of species scavenging

carrion provisioning in areas of high human density (e.g., from hunting, livestock, roadkill) could lead to increased vertebrate scavenger species richness and diversity (Lambertucci et al., 2009; Newsome et al., 2015). Thus, alternative scenarios imply that scavenging could become more prevalent under future human impact, maintaining higher scavenger species richness in some areas.

Many nominal predators switch from hunting to scavenging when conditions make it difficult to find live prey, such as during winter at temperate latitudes (Needham et al., 2014). Winter in temperate ecosystems is typically a period of high energetic demand and low food availability (Young, 1976) and, consequently, both obligate and facultative scavengers rely heavily on carrion during winter to gain valuable protein (Crabtree & Sheldon, 1999; Needham et al., 2014; Peers et al., 2018).

There are several potential hypotheses that could explain how scavenging rates are influenced by climate during winter in temperate regions (Table 1). All these climate hypotheses relate to temperature (i.e., cold or warm winters) and precipitation (i.e., wet or dry winters). Average winter conditions in temperate regions are snowy (i.e., cold and wet), but snow droughts (Harpold et al., 2017) are becoming more common. A warm snow drought occurs when the amount of winter precipitation is average, but the winter temperature is above-average (i.e., warm and wet), causing early season snow melts (Harpold et al., 2017). Deep snow can make it difficult to find or physically access live prey or non-carrion food items (Needham et al., 2014; Selås & Vik, 2006; Watson et al., 2019), increasing reliance on scavenging (i.e., the snowpack hypothesis). On the other hand, warm snow droughts can reduce carrion availability due to fewer winter starvation mortalities (Wilmers & Getz, 2005) and, although these conditions reduce carcass availability, they may also facilitate live-prey or other food acquisition, lessening the reliance on scavenging.

Both facultative and obligate scavengers rely heavily on scavenging during temperate winters, but these winters are becoming milder and are predicted to continue this trajectory into the near future (IPCC, 2014; Romero-Lankao et al., 2014). Therefore, understanding the mechanisms driving scavenging behavior during this time of high reliance is of great importance (Williams et al., 2015). Furthermore, the rate of human development and climate change differs across the globe, so it is also important to understand the potential additive effect of these factors on scavenging communities. For example, Sebastián-González et al. (2019)'s global review found a strong impact of humans, but not climate, on the species richness of scavengers. Yet, the majority of studies included were in areas of relatively high human impact and, as noted by the authors, were unbalanced in space and lacked representation from a range of biomes (Sebastián-González et al., 2019). Therefore, more studies are needed at the biome or regional scale across a range of human impacts and climates to fully understand the effects of global change on scavenging species. Further, understanding the influence of human disturbance and climate on scavenging communities is important in temperate ecosystems, particularly during winter when reliance on scavenging is expected to be highest.

To understand how climatic conditions and human disturbance influence scavenger communities, we evaluated support for the

competing climatic and anthropogenic hypotheses we outlined above (Table 1) on richness and diversity of both mammalian and avian scavengers. Data for this study were collected during winter months from a latitudinal gradient of temperate conditions in the greater Appalachian region of the eastern USA. We then used these data to parameterize models investigating potential changes in scavenger species richness that could be expected from climate change in our study area in 50 years' time.

2 | MATERIALS AND METHODS

2.1 | Study area

A large group of community scientists established and operated a camera trap network of >180 sites during the winters of 2008–2017 in the greater Appalachian region of the eastern USA (Jachowski et al., 2015). This effort created an extensive dataset with samples from across the entire latitudinal gradient of the Appalachian Mountain range from Alabama to Maine, and over multiple winters. This region goes from sub-tropical/warm temperate to cold temperate/boreal and thus encompasses a large gradient of winter severity. For example, average January high and low temperature in Mobile, southern Alabama is 16 and 4°C, respectively, with, on average, 0-cm snow (U.S. Climate Data, 2020). In contrast, average January high and low temperature in Caribou, northern Maine is -7 and -17°C, respectively, with on average 64 cm of snow (U.S. Climate Data, 2020). As this project expanded greatly in 2013, we considered input data from all sites used pre-2013 as well as from sites post-2013 that had been active for more than one winter. From here, we then created species accumulation curves for each site using the R package *vegan* (Oksanen et al., 2019) and excluded individual site winters that did not reach an asymptote. Ultimately, this left us with $n = 129$ sites (100% MCP of study area 716,982 km²; 31°–44°; 1,881 km distance, mean elevation of 571 m [range = 1–1221 m]; Appendix S1). Our study region was heavily forested, with relatively low human impact (see Section 2.4 below).

Sites were located on a mix of private and public land and, in collaboration with landowners, each site was fitted with a non-invasive motion-sensitive camera trap (multiple brands were used) set to record an image with a delay of ≥ 1 min between images. Each site was baited with carrion, usually the carcass of a white-tailed deer (*Odocoileus virginianus*) but sometimes of domestic or feral livestock, which was secured to the ground and replaced when depleted. Monitoring at sites was standardized with a uniform protocol where volunteers visited sites weekly to check cameras and replace carcasses that were largely consumed (for more details, see Jachowski et al., 2015).

Not every site was monitored for each of the 9 years of the study (Table A1.1), so our final dataset included 10,953 survey effort days across 231 individual site winters and ~3 million images. The cameras remained active exclusively during winter months (November–April)

to coincide with the period when mammalian and avian carnivores are likely at their physiological limits due to cold weather and limited food sources. We assumed that this timing would increase the likelihood of observing scavenging, non-hibernating carnivores at the carcasses. In addition, by focusing on a period when American black bears (*Ursus americanus*) are generally inactive and thus not dominant at carcasses (Allen et al., 2014; Gámez-Brunswick & Rojas-Soto, 2020) the cameras likely provide the fullest possible picture of the scavenging community at each site.

2.2 | Species identification

To extract information about the scavenger species' presence at each site, two experienced team members classified the daily presence or absence of each species per site from photographs. We subsequently consolidated this to record the presence-absence of each species per site per winter season. Due to the difficulty in differentiating *Corvus* species (e.g., fish crow [*C. ossifragus*], American crow [*C. brachyrhynchos*], and common raven [*C. corax*]) in camera trap images, we collapsed these species into *Corvus* spp. We considered only scavengers in the final analyses (i.e., those that incorporate meat in their diet); by-catch species such as white-tailed deer walking in front of the camera, and domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*) were not included. While we acknowledge domestic dogs can have important role in scavenging, we did not observe free-ranging dogs in our study, only those accompanying community members. Further, to strengthen our inference, we retained for analysis only species that were detected at >3 individual site winters. To calculate our responses of species richness and diversity, we used the *vegan* package in R (R Core Team, 2020) with the *specnumber* function to calculate the species richness, and the *diversity* function to calculate the Shannon diversity metric (which takes into account the richness and the proportional abundance of species—inferred from the number of images) at each site for each winter season.

2.3 | Predictor variables

All our climate hypotheses are based on combinations of temperature and precipitation (see Table 1 for full list and descriptions). Thus, we used the Google Earth Engine (GEE) data catalogue “PRISM Daily Spatial Climate Dataset AN81d” (Daly et al., 2015) to extract climate data using the R package *rgee* (Aybar et al., 2020). This dataset includes daily measures of temperature (°C) and total daily precipitation (mm; rain and melted snow) for the USA, assimilated from many weather stations across the country and interpolated to create a smooth raster. We extracted the mean temperature and mean daily precipitation for each site over the winters' study dates. We did the same for the standard deviation (SD) of both the temperature and precipitation. We then calculated the temperature seasonality ($SD \times 100$) and precipitation seasonality (SD/mean , i.e., coefficient

of variation) at each site as measures of climate stability (as defined in the WorldClim global dataset; WorldClim, 2020). This resulted in one value of each mean temperature, mean precipitation, temperature seasonality, and precipitation seasonality for each site each winter.

We also evaluated the role of several potential anthropogenic influences on scavenging, using datasets available on GEE (Table 1), extracted relative to each camera site. Ultimately, due to strong correlation between variables, we retained only human population density (details of other variables and correlations can be found in Appendix S2: human impact). We downloaded data on human population density (people/km²) from the GEE dataset “WorldPop Global Project Population Data” (WorldPop and Center for International Earth Science Information Network, 2020).

2.4 | Statistical analysis

Because the species observed in our study exhibit a variety of behaviors (e.g., aerial vs. terrestrial foraging, small vs. large home ranges), we evaluated the performance of the full global model with all predictors at several spatial grains (5, 20, and 100 km radius buffers) around the camera sites. This approach allowed us to explore which scale would best explain species richness and diversity (similar to Egan et al., 2020). We also evaluated if we should combine mammals and birds as one scavenging community or model them separately. Results from these exploratory analyses led us to select a 100 km radius buffer around each site for our predictor variables and to model mammals and birds separately. Details of these selection and evaluation procedures can be found in Appendix S2.

We created four a-priori sets of candidate generalized linear mixed-effects models to investigate support for the hypothesized influences of climate and humans on responses of (1) mammalian richness; (2) mammalian diversity; (3) avian richness; and (4) avian diversity using the R package *lme4* (Bates et al., 2015). We included site as a random variable in all models to account for repeated years of data from a single site. We checked for multicollinearity between predictor variables using spearman's correlation coefficient and variance inflation factors, where we retained all variables with $r < 0.6$ and $VIF < 2$ (Zuur et al., 2010). Moreover, as latitude was correlated with both temperature and precipitation, we did not retain this variable in any of our models. We also considered the potential quadratic effect of our variables, by comparing the adjusted R^2 of singular variable linear models with those of their quadratic counterparts (i.e., linear model with two variables, one being the square of the other). As none of the quadratic models showed improvement performance over the linear, we did not retain or report any quadratic effects in our models. Because mammalian and avian richness are described by count data, we constructed our models with a Poisson distribution. Because data for mammalian and avian diversity are continuous and they met assumptions about normality, we modeled these data with a Gaussian distribution. We modeled main effects as well as relevant

interactions and additive effects (Table A2.3) to investigate their potential effect on our four response variables.

Each of the four model sets included 11 models derived from the hypotheses about climate and humans on scavenging (for a full list of candidate models see Table A2.3). To identify the best model(s) in each candidate model set, we used model selection based on Akaike's information criterion adjusted for small sample size (AIC_c) using the R package *MuMIn* (Barton, 2020), where models within $2 \Delta AIC_c$ of the top model were considered important (Burnham & Anderson, 2002). We plotted the top models for each of the four responses using packages *visreg* (Breheny & Burchett, 2017) and *ggplot2* (Wickham, 2016), where we used these plots to estimate optimal climates for scavenging (i.e., the temperature and precipitation supporting the highest species richness).

2.5 | Projecting current and future species richness

We used the predictors included in the top models explaining species richness to project the current species richness of mammalian and avian scavengers over the extent of our study area in the eastern USA. To do this, we first created species distribution models (SDMs) using the species presence at each site and rasters of the current climate predictors of winter temperature and winter precipitation extracted from the WorldClim database (WorldClim, 2020). Due to the nature of our data (i.e., baited sites), these SDMs should not be interpreted as traditional SDMs that imply occurrence, but rather interpreted as the distribution describing the probability of a species scavenging on carrion. We created SDMs using all algorithms available (for list see Schmitt et al., 2017) and retained those with the best performance, evaluated via the area under the curve (AUC). Next, we created a single ensemble SDM using the three best performing algorithms for estimating separately the species richness for mammals and for birds. For mammals these were the algorithms MARS (multivariate adaptive regression splines), CTA (classification tree analysis), and SVM (support vector machines; all $AUC > 0.90$), and for birds these were MARS, CTA, and RF (random forests; all $AUC > 0.85$). We did this using the R package *SSDM* (Schmitt et al., 2017) and the *PRR.pSSDM* method which uses a probability ranking

rule to estimate species richness based on the decreasing probability of presence calculated by the SDMs. Ultimately, this process allowed us to estimate species richness across an area using species presence data and climate. As our data were collected from a subset of many species' full distribution ranges, to ensure appropriate inference we constrained predictions based on these SDMs to our study area (Barbet-Massin et al., 2010; Thuiller et al., 2004).

Using the *project* function of *SSDM*, we reprojected the ensemble SDM described above with new predictors of the future winter temperature and future winter precipitation extracted from the WorldClim database (WorldClim, 2020). This process considered the climate where the species were present and creates a new projection of where species would be present based on the future climate. As the WorldClim data are only available for 50 and 70 years into the future and projected future climate data are limited in accuracy (Bedia et al., 2013), we extracted data for the year 2070 (i.e., in 50 years' time), under emissions level RCP8.5. The individual SDM maps showing the probability of scavenging (and confidence) for each species under current and future climate scenarios are displayed in Figures A3.1–A3.21. Finally, we used the *overlay* function of the *raster* package (Hijmans, 2020) to subtract the future species richness projection from the current species richness projection in order to estimate species loss or gain per pixel over our study area. We extracted all data for predictor variables, performed all analyses, and created all figures using R version 4.0.1 (R Core Team, 2020).

3 | RESULTS

3.1 | Mammalian scavengers

Of the 12 mammalian species identified, coyotes (*Canis lupus*), gray foxes (*Urocyon cinereoargenteus*), and red foxes (*Vulpes vulpes*) had the largest ranges across latitude (Table A3.1; Figures A3.3, A3.5, A3.8). Eastern spotted skunks (*Spilogale putorius*) had the smallest range, occurring only in the mid-latitudes (Table A3.1; Figure A3.9). The winter climate that facilitated the highest species richness was 5–10°C and 100–150 mm total precipitation (Figure 1a). The

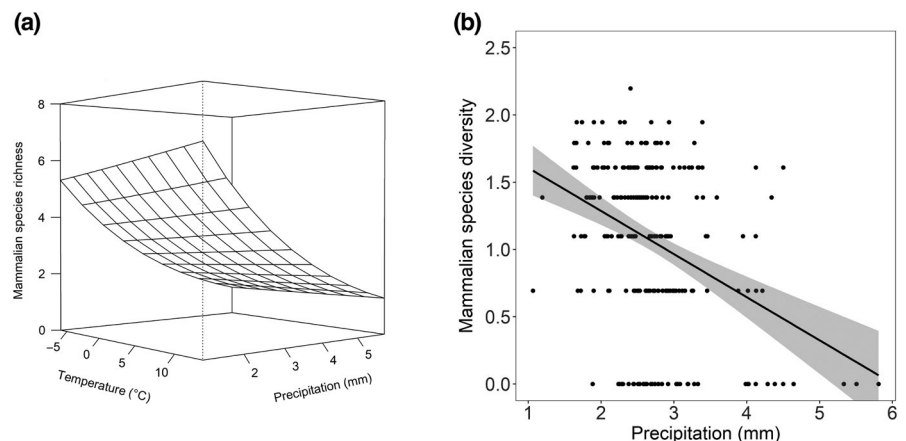


FIGURE 1 The effect of (a) mean daily temperature and mean daily precipitation on species richness of mammalian scavengers, and (b) mean daily precipitation on species diversity of mammalian scavengers in the Appalachian region of the eastern USA for the winter periods between 2008 and 2017

highest richness of mammalian scavengers at any given site was nine, with the highest richness occurring in mid-latitudes 35°–45° (Figure 2a).

The models best predicting species richness of mammalian scavengers included mean precipitation and the additive effect of mean precipitation and mean temperature (Figure 1a; Table 2; Tables A3.2 and A3.3). Mean precipitation also had an important influence on mammalian scavenger species diversity (Figure 1b; Table 2; Tables A3.2 and A3.3). In line with the compounded snow drought hypothesis, species richness and diversity were highest under dry conditions, especially if also warm (Figure 1). There were no anthropogenic factors retained in our top candidate models.

We observed a reduction in the predicted scavenging by mammal species throughout our study area over the next 50 years (Figure 2a,b). For the speciose mid-latitude portion of our study area, our future projection predicts a reduction of scavenging by six mammal species by 2070 (i.e., 67% decrease; Figure 2c). In these scenarios, the mean probability of detecting coyotes, bobcats, and striped skunks scavenging within our study area decreased the most (by 34%, 30%, and 27%, respectively; Table A3.1; Figures A3.2, A3.3, A3.10). Our ensemble SDM had a species richness error (i.e., the difference between the predicted and observed species richness) of 2.2 for both the current and future projections.

3.2 | Avian scavengers

We identified 11 avian scavenging species across our study region (Table A3.1; although *Corvus* spp. represents multiple species, meaning there were likely 13 scavenging species). Of these, bald eagles (*Haliaeetus leucocephalus*), *Corvus* spp., golden eagles (*Aquila chrysaetos*), red-tailed hawks (*Buteo jamaicensis*), and turkey vultures (*Cathartes aura*) occurred across the largest ranges of latitude (Table A3.1; Figures A3.11, A3.15, A3.16, A3.19, A3.21). Like mammals, the winter climate that facilitated the highest species richness was 5–10°C and 100–150-mm total precipitation (Figure 3a). The highest

richness of avian scavengers at any given site was 10, with the highest richness again occurring in mid-latitudes 35°–45° (Figure 2d).

The models best predicting species richness of avian scavengers contained mean precipitation and the interaction between mean precipitation and mean temperature (Table 2; Tables A3.2 and A3.3). In support of the compounded snow drought hypothesis, avian species

TABLE 2 Model coefficients for the top models (i.e., $\Delta AIC_c < 2$) when investigating the effects of climatic and anthropogenic variables on the species richness and diversity of mammalian and avian scavengers in the Appalachian region of the eastern USA. For the full list and model selection output, see Tables A3.2 and A3.3

Model	Estimate	SE	95% CI
<i>Mammalian scavengers</i>			
Species richness			
1. Mean precipitation	-0.228	0.047	-0.321 to -0.140
2. Mean precipitation + Mean temperature	-0.238	0.049	-0.334 to -0.140
	0.010	0.012	-0.013 to 0.033
Species diversity			
1. Mean precipitation	-0.292	0.060	-0.409 to -0.174
<i>Avian scavengers</i>			
Species richness			
1. Mean precipitation	-0.142	0.049	-0.238 to -0.048
2. Mean precipitation + mean temperature + Mean precipitation*mean temperature	-0.029	0.083	-0.190 to 0.137
	0.063	0.040	-0.014 to 0.144
	-0.023	0.014	-0.051 to 0.003
Species diversity			
1. Mean precipitation	-0.146	0.045	-0.234 to -0.056

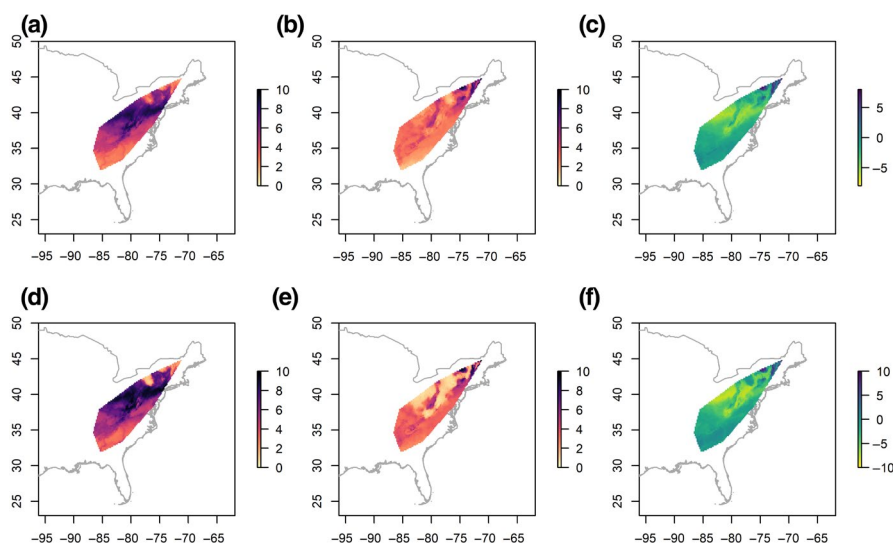
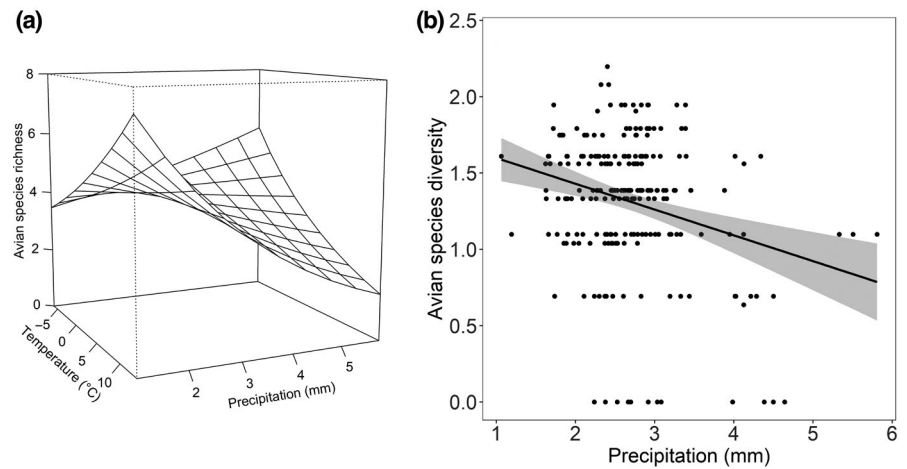


FIGURE 2 The (a) current, (b) future, and (c) net change in the species richness of mammalian scavengers, and the (d) current, (e) future, and (f) net change in the species richness of avian scavengers. Models are based on the climatic variables mean winter temperature and mean winter precipitation as found in our top models. The grey line marks the USA country border [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 The effect of (a) the interaction of mean daily precipitation and mean daily temperature on species richness of avian scavengers, and (b) mean daily precipitation and on species diversity of avian scavengers in the Appalachian region of the eastern USA for the winter periods between 2008 and 2017



richness was highest under warm and dry conditions (Figure 3a). In addition, in support of the snowpack hypothesis, avian species richness was also high under cold and wet conditions (Figure 3a). As was the case for mammals, there were no anthropogenic factors retained in our top candidate models. For avian species diversity, the most influential predictor was mean precipitation (Table 2; Tables A3.2 and A3.3). Partly supporting the dry snow drought and compounded snow drought hypotheses, diversity was higher during drier winters (Figure 3b).

Our models predict a reduction in the predicted scavenging by avian species throughout our study area over the next 50 years (Figure 2d,e). For the speciose mid-latitude region, our future projection predicts a reduction of scavenging by as many as eight fewer species by 2070 (i.e., 80% decrease; Figure 2f). The species for which probability of scavenging is projected to decrease the most between now and 2070 were turkey vultures, *Corvus* spp., and red-tailed hawks (by 38%, 37%, and 37%, respectively; Table A3.1; Figures A3.15, A3.19, A3.21). Our ensemble SDM had a species richness error of 2.5 for both the current and future projections.

4 | DISCUSSION

In this study, we found support for a climatic effect on scavenger species richness and diversity. Scavenging by the most mammalian and avian species was observed during dry and warm winters. The future winter climate for the eastern USA is projected to become warmer and wetter (Dai, 2013; Romero-Lankao et al., 2014), and we show that these future conditions will shift toward the outside of the optimal climate band for facilitating scavenging (i.e., toward too warm and too wet). This could lead to the southeastern USA in particular losing the benefits associated with high scavenging rates, an outcome that could ultimately compromise ecological function (DeVault et al., 2003; Sebastián-González et al., 2016; Wilson & Wolkovich, 2011). Our results highlight an overall reduction in the frequency of scavenging in the lower latitudes of our study area into the future, suggesting the behavior of the species present will change but also parallels other findings that suggest many species

distributions are shifting poleward with the climate (Buckley et al., 2018; Chen et al., 2011; Hastings et al., 2020). Our findings also support observations from other regions that suggest climate change can have complex and context-specific influences on vertebrate scavengers (Hidasi-Neto et al., 2019; Olson et al., 2016; Peers et al., 2020; Selva et al., 2005; Stiegler et al., 2020).

For mammals, our results support the compounded snow drought hypothesis, where species were more reliant on scavenging during relatively warm and dry winters (5–10°C and 100–150 mm). These climatic conditions likely facilitate both the dependence on carcasses and their accessibility. Colder, sub-zero temperatures can freeze carcasses solid, and deep snow can further limit smaller mammals' ability to access carrion (Peers et al., 2020). A frozen carcass is also likely more difficult to smell, and therefore locate, as low temperature delays decomposition (Moleón et al., 2014). Thus, above zero temperatures and a lack of snow likely increases both detection and accessibility of carrion for mammals and thus facilitates detection of higher scavenger species richness. Our findings are consistent with other observations that scavenging rates in a boreal region were higher in warmer winters, with Canada lynx (*Lynx canadensis*) being most likely to scavenge at ~10°C (Peers et al., 2020). In contrast, much warmer and wetter conditions can make other food sources more available (Maignan et al., 2008) which could ultimately lessen the reliance on scavenging. Many mammalian facultative scavengers are also generalists and compensate for periodic shortages of regular food items by shifting their diet (Dell'Arte et al., 2007; Swingen et al., 2015; Van Dijk et al., 2008). Under warmer and wetter conditions (i.e., outside the optimal climate for scavenging we found in our study), many species may be able to access other food items and, under these conditions, our cameras recorded lower species richness of scavengers. Mammalian species diversity was also higher during dry winters. As with richness, we suggest that these climatic conditions likely facilitate both the dependence on carcasses and their accessibility which ultimately increases the abundance of individuals scavenging as well as the species richness that the cameras detect.

As was the case for mammals, we also detected the most bird species scavenging during warm and dry winters (5–10°C and

100–150 mm), supporting the compounded snow drought hypothesis. Deep snow can restrict smaller birds' access to carrion (Selva et al., 2005). Thus, above zero temperatures and a lack of snow may increase the accessibility of carrion and facilitate higher species richness. We also found fairly high richness during cold and wet winters, which likely represents the increased detection from above and against snowy landscapes of the large carrion we used (Moreno-Opo et al., 2015; Selva et al., 2005). Further, because energetic needs are high during these cold snowy conditions, facultative avian scavengers may be more reliant on scavenging as well. Alternatively, it may be more difficult to find small mammalian prey when they are covered by snow (i.e., in the subnival environment); similarly, North American vultures eat fewer carcasses of small prey when snow is deep (Yahner et al., 1986). However, we observed that owls, one of the facultative scavengers in our system, were most likely to be detected scavenging when in moderate winter conditions (mean 2°C and 3 mm). This lends support to our increased carcass detectability hypothesis rather than our small mammal availability hypothesis. Avian species diversity was higher when winters were drier, partly supporting the dry snow drought and compounded snow drought hypotheses. Most of the bird species in this study are migratory, typically moving south to overwinter in warmer areas while some southerly located individuals remain sedentary. Considering that birds' migration distances and timing have been changing with the climate (Brisson-Curadeau et al., 2019; McCaslin & Heath, 2020; Studds & Marra, 2011), the lower diversity during dry winters may represent an interruption in migration departure or progress, whereby not all individuals move at the same time and take advantage of southerly scavenging opportunities due to fluctuations in migration timing.

Our future projection suggests a reduction in the number of mammalian species cameras would detect scavenging across our study area. The mean winter climate for our study area is predicted to increase by 5°C and 54 mm of winter precipitation by 2070 (WorldClim, 2020). Our findings could mean that mammals will remain in these areas, but only scavenge in the northern parts of their range where the climate makes this necessary. Alternatively, these species may be shifting ranges into higher latitudes altogether, following the suitable climate (Chen et al., 2011; Levinsky et al., 2007). Our models suggest that coyotes, bobcats, and striped skunks are especially less likely to be detected scavenging in the eastern USA in the future. These species are all widely distributed generalists (Helgen & Reid, 2016; Kays, 2018; Kelly et al., 2016) so a predicted reduction in scavenging is consistent with the notion that they are more able to find alternative food under predicted climatic scenarios.

Like mammals, our projection suggests a reduction in the number of avian species detected scavenging across our study area in the future. However, unlike mammals, this may be due to migration shifts rather than an ability to find alternative food during future milder winters. In North America, migratory raptors have displayed a northward shift in their distribution and have been arriving earlier over time, consistent with a warming climate (Huntley et al., 2006; McCaslin & Heath, 2020; Sullivan et al., 2016; Therrien et al., 2017). Our results are consistent with changes in behavior such that

migrating species would not be travelling as far south under future climate scenarios. Turkey vultures, *Corvus* spp., and red-tailed hawks had the largest decreases in probability of scavenging in our study area into the future. As widely distributed generalists, *Corvus* spp. likely mirror the mammalian response by utilizing other available food sources. Similarly, as red-tailed hawks are permanent residents across most of the region, they also can easily switch to alternative food. In contrast, as an obligate scavenger, turkey vultures can only make small shifts to their diet. Thus, our modeling suggests that the distribution of this species could be shifting or expanding, consistent with reports of turkey vulture populations expanding northward over time (Sauer et al., 2017). As our sites were mainly located at higher elevations, our reduction in turkey vulture probability of scavenging could also represent them moving to lower elevation/coastal regions. However, it is also possible that under warmer and wetter winters, turkey vultures focus on an alternative food source as they have a wider diet breadth of carrion than black vultures (*Coragyps atratus*) and they frequently utilize human garbage dumps (Ballejo et al., 2018; Noreen & Sultan, 2021) and small mammal prey (Yahner et al., 1986).

In a global review, and in contrast to our findings, Sebastián-González et al. (2019) found only human impact to negatively affect scavenger species richness. Because several, smaller-scale studies have found climate to be important (Peers et al., 2020; Selva et al., 2005; Stiegler et al., 2020), our study emphasizes the need for regional studies to fully understand the influence of global change on scavenging within different regions. The interpretation of our results also suggests several avenues for future study. For example, we did not evaluate the interactions between the mammalian and avian guilds, a topic which requires further study in general (Terraube & Bretagnolle, 2018). Scavenging mammals and birds can have several facilitating or excluding interactions (Prior & Weatherhead, 1991; Sebastián-González et al., 2016; Vucetich et al., 2004). However, in this study, the mammalian and avian guilds were mostly separated by nocturnal and diurnal niches respectively, so we think it is unlikely for any direct interactions to have a significant effect on our results. Moreover, group size can also influence which species are the dominant scavengers, and we have observed instances where a single bald eagle is clearly dominant over a single raven, but also that large groups of corvids can displace bald eagles. Also regarding the different guilds, we were unable to measure species-specific consumption rates. Although preliminary data suggest one deer carcass to be removed within 11.09 ± 1.95 days in our study area (Marneweck et al., unpublished data), more information on specific consumption rates per species are required to fully understand scavenging efficiency, group size, and community composition. Therefore, the additive effect of group size on scavenging efficiency should be considered an important avenue for future research. Furthermore, interactions between carcass degradation and climate may also occur, where future warmer and wetter climate may break down carcasses in the absence of vertebrate scavengers. Thus, research on alternative pathways for carcass decomposition in the future with this predicted loss in scavenger species richness would be informative. We

also did not evaluate the physiological processes underlying species' responses to the environment (Gamiel et al., 2020) and, most importantly, using range-restricted occurrence data to study climate-induced changes in species richness may lead to an underestimate of the suitable climatic space (Barbet-Massin et al., 2010; Thuiller et al., 2004). This means that our suitability forecasts may be less extreme than predicted, due to an underestimation of suitable climate space. Nevertheless, even with our forecasts tempered, our results suggest that the future frequency of scavenging by many species in the lower latitudes of our study region is likely to be reduced.

Our findings highlight the importance of considering potential climate-induced alterations in behavior that could have cascading effects on ecosystem structure. The loss of vertebrate scavenger richness and diversity reduces the number of pathways in the food web, which could lead to a decrease in ecosystem resilience. Although there may be mechanisms to compensate for this loss, ultimately, carcasses will still be present on the landscape in the future and scavenging of some type will still be an important ecosystem service. The predominant large herbivore in this ecosystem, white-tailed deer, are expected to persist or even increase in abundance across eastern North America in the future (Chitwood et al., 2015; Dawe & Boutin, 2016; Johnston & Schmitz, 1997). Thus, even with an expected decline in overwinter mortality under future climate conditions (Wilmers & Getz, 2005), carcasses will still be present on the landscape. It is also possible that carcass presence under warm and wet conditions in the future may lead to an increased disease risk to humans (O'Bryan et al., 2018; Ogada et al., 2012). Attention placed on the conservation of species-rich scavenger communities, especially vultures that facilitate rapid carcass removal, is therefore likely important to retain the functional role of scavenging in eastern North America (Gutiérrez-Cánovas et al., 2020; Sebastián-González et al., 2016). Although a great deal of attention is placed on species extinction risk and distribution changes as a result of changing climate (Chen et al., 2011; Thomas et al., 2004), a reduction in scavenging highlights the impact of climate-induced adjustments in behavior that could have negative impacts at a large scale in a temperate ecosystem.

ACKNOWLEDGEMENTS

We would like to thank the many hundreds of volunteers who maintained camera traps over the duration of this study. Without their remarkable efforts, this study would not have happened. Many of them are acknowledged by name in the Appalachian Eagles Annual Report, available from T. Katzner. In addition, T. Miller, K. O'Malley, K. Heyden, S. Somershoe, C. Todd, C. Martin, T. Salo, C. Kelly, D. Cuthrell, D. Brinker, E. Soehren, and S. Allen assisted with coordination of the camera-trapping effort. T. Ortiz and L. Rhea collated and organized many of the images. In addition, we thank S. Harris, L.S. Hawthorne, and J. Rodrigue for collating data from the images. Financial support for data collection was provided in part by the West Virginia University Division of Forestry, the US Department of Agriculture Forest Service Northern Research Station, a private donor, and many natural resource agencies that supported their

staff time collecting these data. The authors declare no conflict of interests. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in article Supporting Information.

ORCID

Courtney J. Marneweck  <https://orcid.org/0000-0002-5064-1979>

Todd E. Katzner  <https://orcid.org/0000-0003-4503-8435>

REFERENCES

- Allen, M. L., Elbroch, L. M., Wilmers, C. C., & Wittmer, H. U. (2014). Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. *PLoS One*, *9*, e102257. <https://doi.org/10.1371/journal.pone.0102257>
- Aybar, C., Wu, Q., Bautista, L., Yali, R., & Barja, A. (2020). rgee: An R package for interacting with Google. *Earth Engine Journal of Open Source Software*, *5*, 2272. <https://doi.org/10.21105/joss.02272>
- Ballejo, F., Lambertucci, S. A., Trejo, A., & De Santis, L. J. M. (2018). Trophic niche overlap among scavengers in Patagonia supports the condor-vulture competition hypothesis. *Bird Conservation International*, *28*, 390–402. <https://doi.org/10.1017/S0959270917000211>
- Barbet-Massin, M., Thuiller, W., & Jiguet, F. (2010). How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? *Ecography*, *33*, 878–886. <https://doi.org/10.1111/j.1600-0587.2010.06181.x>
- Barton, K. (2020). MuMIn: Multi-model inference (version 1.43.17). <https://CRAN.R-project.org/package=MuMIn>
- Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, *312*, 431–433. <https://doi.org/10.1126/science.1123412>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software*, *67*, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bedia, J., Herrera, S., & Gutiérrez, J. M. (2013). Dangers of using global bioclimatic datasets for ecological niche modeling. Limitations for future climate projections. *Global and Planetary Change*, *107*, 1–12. <https://doi.org/10.1016/j.gloplacha.2013.04.005>
- Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*, *9*, 56–71. <https://doi.org/10.32614/RJ-2017-046>
- Brisson-Curadeau, É., Elliott, K. H., & Côté, P. (2019). Factors influencing fall departure phenology in migratory birds that bred in northeastern North America. *The Auk*, *137*, 1–14. <https://doi.org/10.1093/auk/ukz064>
- Brown, O. J. F., Field, J., & Letnic, L. (2006). Variation in the taphonomic effect of scavengers in semi-arid Australia linked to rainfall and the El Niño southern oscillation. *International Journal of Osteoarchaeology*, *16*, 165–176. <https://doi.org/10.1002/oa.833>
- Buckley, L. B., Khaliq, I., Swanson, D. L., & Hof, C. (2018). Does metabolism constrain bird and mammal ranges and predict shifts in response to climate change? *Ecology and Evolution*, *8*, 12375–12385. <https://doi.org/10.1002/ece3.4537>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). Springer Science & Business Media.
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate

- warming. *Science*, 333, 1024–1026. <https://doi.org/10.1126/science.1206432>
- Chitwood, M. C., Lashley, M. A., Kilgo, J. C., Moorman, C. E., & Deperno, C. S. (2015). White-tailed deer population dynamics and adult female survival in the presence of a novel predator. *The Journal of Wildlife Management*, 79, 211–219. <https://doi.org/10.1002/jwmg.835>
- Ćirović, D., Penezić, A., & Krofel, M. (2016). Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. *Biological Conservation*, 199, 51–55. <https://doi.org/10.1016/j.biocon.2016.04.027>
- Crabtree, R. L., & Sheldon, J. W. (1999). Coyotes and canid coexistence in Yellowstone. In T. W. Clark, A. P. Curlee, S. C. Minta, & P. M. Kareiva (Eds.), *Carnivores in ecosystems: The Yellowstone experience* (Vol. 1, pp. 127–163). Yale University Press.
- Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2642–2651. <https://doi.org/10.1098/rstb.2011.0120>
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J.-F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E., & Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134. <https://doi.org/10.1111/j.1461-0248.2004.00671.x>
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3, 52–58. <https://doi.org/10.1038/NCLIMATE1633>
- Daly, C., Smith, J. I., & Olson, K. V. (2015). Mapping atmospheric moisture climatologies across the conterminous United States. *PLoS One*, 10, e0141140. <https://doi.org/10.1371/journal.pone.0141140>
- Dawe, K. L., & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and Evolution*, 6, 6435–6451. <https://doi.org/10.1002/ece3.2316>
- Dell'Arte, G. L., Laaksonen, T., Norrdahl, K., & Korpimäki, E. (2007). Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecologica*, 31, 276–281. <https://doi.org/10.1016/j.actao.2006.12.007>
- DeVault, T. L., Brisbin Jr., I. L., & Rhodes Jr., O. E. (2004). Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. *Canadian Journal of Zoology*, 82, 502–509. <https://doi.org/10.1139/Z04-022>
- DeVault, T. L., Rhodes, O. E. Jr, & Shivik, J. A. (2003). Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, 102, 225–234. <https://doi.org/10.1034/j.1600-0706.2003.12378.x>
- Dierauer, J. R., Allen, D. M., & Whitfield, P. H. (2019). Snow drought risk and susceptibility in the western United States and southwestern Canada. *Water Resources Research*, 55, 3076–3091. <https://doi.org/10.1029/2018wr023229>
- Egan, M., Day, C., Katzner, T., & Zollner, P. (2020). Relative abundance of coyotes influences gray fox occupancy across the eastern United States. *Canadian Journal of Zoology*, 99(4). <https://doi.org/10.1139/cjz-2019-0246>
- Gámez-Brunswick, C., & Rojas-Soto, O. (2020). The effect of seasonal variation on the activity patterns of the American black bear: An ecological niche modeling approach. *Mammalia*, 84, 315–322. <https://doi.org/10.1515/mammalia-2019-0017>
- Gamliel, I., Buba, Y., Guy-Haim, T., Garval, T., Willett, D., Rilov, G., & Belmaker, J. (2020). Incorporating physiology into species distribution models moderates the projected impact of warming on selected Mediterranean marine species. *Ecography*, 43, 1–17. <https://doi.org/10.1111/ecog.04423>
- Gharajehdaghpour, T., Roth, J. D., Fafard, P. M., & Markham, J. H. (2016). Arctic foxes as ecosystem engineers: Increased soil nutrients lead to increased plant productivity on fox dens. *Scientific Reports*, 6, 1–7. <https://doi.org/10.1038/srep24020>
- Gutiérrez-Cánovas, C., Moleón, M., Mateo-Tomás, P., Olea, P. P., Sebastián-González, E., & Sánchez-Zapata, J. A. (2020). Large home range scavengers support higher rates of carcass removal. *BioRxiv*, 34(9), 1921–1932. <https://doi.org/10.1101/2020.02.07.938415>
- Hagen, M., Kissling, W. D., Rasmussen, C., De Aguiar, M. A. M., Brown, L. E., Carstensen, D. W., Alves-Dos-Santos, I., Dupont, Y. L., Edwards, F. K., Genini, J., & Olesen, J. M. (2012). 2 – Biodiversity, species interactions and ecological networks in a fragmented world. In U. Jacob & G. Woodward (Eds.), *Advances in ecological research* (Vol. 46, pp. 89–210). Academic Press.
- Harpold, A. A., Dettinger, M., & Rajagopal, S. (2017). Defining snow drought and why it matters. *Eos*, 98. <https://doi.org/10.1029/2017E0068775>
- Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., & Genner, M. J. (2020). Climate change drives poleward increases and equatorward declines in marine species. *Current Biology*, 30, 1572–1577.e1572. <https://doi.org/10.1016/j.cub.2020.02.043>
- Helgen, K., & Reid, F. (2016). *Mephitis mephitis*. *The IUCN Red List of Threatened Species*, eT41635A45211301. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41635A45211301.en>
- Hidasi-Neto, J., Joner, D., Resende, F., Monteiro, L., Faleiro, F., Loyola, R., & Cianciaruso, M. (2019). Climate change will drive mammal species loss and biotic homogenization in the Cerrado Biodiversity Hotspot. *Perspectives in Ecology and Conservation*, 17, 57–63. <https://doi.org/10.1016/j.pecon.2019.02.001>
- Hijmans, R. J. (2020). raster: Geographic data analysis and modeling (version 3.3-13). <https://CRAN.R-project.org/package=raster>
- Huntley, B., Collingham, Y. C., Green, R. E., Hilton, G. M., Rahbek, C., & Willis, S. G. (2006). Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, 148, 8–28. <https://doi.org/10.1111/j.1474-919X.2006.00523.x>
- IPCC. (2014). *Climate change 2014: Synthesis report*. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC.
- Jachowski, D. S., Katzner, T., Rodrigue, J. L., & Ford, W. M. (2015). Monitoring landscape-level distribution and migration phenology of raptors using a volunteer camera-trap network. *Wildlife Society Bulletin*, 39, 553–563. <https://doi.org/10.1002/wsb.571>
- Johnston, K., & Schmitz, O. (1997). Wildlife and climate change: Assessing the sensitivity of selected species to simulated doubling of atmospheric CO₂. *Global Change Biology*, 3, 531–544. <https://doi.org/10.1046/j.1365-2486.1997.00093.x>
- Kays, R. (2018). *Canis latrans* (errata version published in 2020). *The IUCN Red List of Threatened Species*. eT3745A163508579. <https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T3745A163508579.en>
- Kelly, M., Morin, D., & Lopez-Gonzalez, C. A. (2016). *Lynx rufus*. *The IUCN Red List of Threatened Species*. eT12521A50655874. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T12521A50655874.en>
- Lambertucci, S. A., Speziale, K. L., Rogers, T. E., & Morales, J. M. (2009). How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodiversity and Conservation*, 18, 2063–2074. <https://doi.org/10.1007/s10531-008-9573-3>
- Levinsky, I., Skov, F., Svenning, J.-C., & Rahbek, C. (2007). Potential impacts of climate change on the distributions and diversity patterns of European mammals. *Biodiversity and Conservation*, 16, 3803–3816. <https://doi.org/10.1007/s10531-007-9181-7>
- Maignan, F., Bréon, F., Vermote, E., Ciais, P., & Viovy, N. (2008). Mild winter and spring 2007 over western Europe led to a widespread early vegetation onset. *Geophysical Research Letters*, 35, 1–6. <https://doi.org/10.1029/2007GL032472>
- McCaslin, H. M., & Heath, J. A. (2020). Patterns and mechanisms of heterogeneous breeding distribution shifts of North American

- migratory birds. *Journal of Avian Biology*, 51, e02237. <https://doi.org/10.1111/jav.02237>
- McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11, 161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Meyer, J., Anderson, B., & Carter, D. O. (2013). Seasonal variation of carcass decomposition and gravesoil chemistry in a cold (Dfa) climate. *Journal of Forensic Sciences*, 58, 1175–1182. <https://doi.org/10.1111/1556-4029.12169>
- Moleón, M., Sánchez-Zapata, J. A., Margalida, A., Carrete, M., Owen-Smith, N., & Donazar, J. A. (2014). Humans and scavengers: The evolution of interactions and ecosystem services. *BioScience*, 64, 394–403. <https://doi.org/10.1093/biosci/biu034>
- Moleón, M., Sánchez-Zapata, J. A., Selva, N., Donazar, J. A., & Owen-Smith, N. (2014). Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews*, 89, 1042–1054. <https://doi.org/10.1111/brv.12097>
- Moreno-Opo, R., Trujillano, A., & Margalida, A. (2015). Optimization of supplementary feeding programs for European vultures depends on environmental and management factors. *Ecosphere*, 6, 1–15. <https://doi.org/10.1890/ES15-00009.1>
- Needham, R., Odden, M., Lundstadsveen, S. K., & Wegge, P. (2014). Seasonal diets of red foxes in a boreal forest with a dense population of moose: The importance of winter scavenging. *Acta Theriologica*, 59, 391–398. <https://doi.org/10.1007/s13364-014-0188-7>
- Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24, 1–11. <https://doi.org/10.1111/geb.12236>
- Noreen, Z., & Sultan, K. (2021). A global modification in avifaunal behavior by use of waste disposal sites (waste dumps/rubbish dumps): A review paper. *Pure and Applied Biology*, 10, 603–616. <https://doi.org/10.19045/bspab.2021.100062>
- O'Bryan, C. J., Braczkowski, A. R., Beyer, H. L., Carter, N. H., Watson, J. E. M., & McDonald-Madden, E. (2018). The contribution of predators and scavengers to human well-being. *Nature Ecology & Evolution*, 2, 229–236. <https://doi.org/10.1038/s41559-017-0421-2>
- Ogada, D. L., Torchin, M. E., Kinnaird, M. F., & Ezenwa, V. O. (2012). Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology*, 26, 453–460. <https://doi.org/10.1111/j.1523-1739.2012.01827.x>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Peter Solymos, M., Stevens, H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community ecology package* (version R package version 2.5-6). <https://CRAN.R-project.org/package=vegan>
- Olson, Z. H., Beasley, J. C., & Rhodes, O. E. (2016). Carcass type affects local scavenger guilds more than habitat connectivity. *PLoS One*, 11, e0147798. <https://doi.org/10.1371/journal.pone.0147798>
- Payne, L. X., & Moore, J. W. (2006). Mobile scavengers create hotspots of freshwater productivity. *Oikos*, 115, 69–80. <https://doi.org/10.1111/j.2006.0030-1299.14899.x>
- Peers, M. J. L., Konkolics, S. M., Lamb, C. T., Majchrzak, Y. N., Menzies, A. K., Studd, E. K., Boonstra, R., Kenney, A. J., Krebs, C. J., Martinig, A. R., McCulloch, B., Silva, J., Garland, L., & Boutin, S. (2020). Prey availability and ambient temperature influence carrion persistence in the boreal forest. *Journal of Animal Ecology*, 89, 2156–2167. <https://doi.org/10.1111/1365-2656.13275>
- Peers, M. J., Majchrzak, Y. N., Konkolics, S. M., Boonstra, R., & Boutin, S. (2018). Scavenging by snowshoe hares (*Lepus americanus*) in Yukon, Canada. *Northwestern Naturalist*, 99, 232–235. <https://doi.org/10.1898/NWN18-05.1>
- Planillo, A., Mata, C., Manica, A., & Malo, J. E. (2018). Carnivore abundance near motorways related to prey and roadkills. *The Journal of Wildlife Management*, 82, 319–327. <https://doi.org/10.1002/jwmg.21384>
- Prior, K. A., & Weatherhead, P. J. (1991). Competition at the carcass: Opportunities for social foraging by turkey vultures in southern Ontario. *Canadian Journal of Zoology*, 69, 1550–1556. <https://doi.org/10.1139/z91-218>
- R Core Team. (2020). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ray, R.-R., Seibold, H., & Heurich, M. (2014). Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. *Animal Biodiversity and Conservation*, 37, 77–88. <https://doi.org/10.32800/abc.2014.37.0077>
- Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7, 1–15. <https://doi.org/10.1046/j.1461-0248.2003.00554.x>
- Romero-Lankao, P., Smith, J. B., Davidson, D. J., Diffenbaugh, N. S., Kinney, P. L., Kirshen, P., Kovacs, P., & Ruiz, L. V. (2014). North America. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. M. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 1439–1498). Cambridge University Press.
- Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski Jr., D. J., Pardieck, K. L., Fallon, J. E., & Link, W. A. (2017). *The North American Breeding Bird Survey, results and analysis 1966–2015*. USGS Patuxent Wildlife Research Center.
- Schmitt, S., Pouteau, R., Justeau, D., de Boissieu, F., & Birnbaum, P. (2017). SSDM: An R package to predict distribution of species richness and composition based on stacked species distribution models. *Methods in Ecology and Evolution*, 8, 1795–1803. <https://doi.org/10.1111/2041-210X.12841>
- Sebastián-González, E., Barbosa, J. M., Pérez-García, J. M., Morales-Reyes, Z., Botella, F., Olea, P. P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donazar, J. A., Cortés-Avizanda, A., Selva, N., Lambertucci, S. A., Bhattacharjee, A., Brewer, A., Anadón, J. D., Abernethy, E., Rhodes, O. E., ... Sánchez-Zapata, J. A. (2019). Scavenging in the anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. *Global Change Biology*, 25, 3005–3017. <https://doi.org/10.1111/gcb.14708>
- Sebastián-González, E., Moleón, M., Gibert, J. P., Botella, F., Mateo-Tomás, P., Olea, P. P., Guimarães, P. R., & Sánchez-Zapata, J. A. (2016). Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. *Ecology*, 97, 95–105. <https://doi.org/10.1890/15-0212.1>
- Selås, V., & Vik, J. (2006). Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897–1976. *Journal of Zoology*, 269, 299–308. <https://doi.org/10.1111/j.1469-7998.2006.00048.x>
- Selva, N., Jędrzejewska, B., Jędrzejewski, W., & Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology*, 83, 1590–1601. <https://doi.org/10.1139/z05-158>
- Stiegler, J., Von Hoermann, C., Müller, J., Benbow, M. E., & Heurich, M. (2020). Carcass provisioning for scavenger conservation in a temperate forest ecosystem. *Ecosphere*, 11, 1–13. <https://doi.org/10.1002/ecs2.3063>
- Studds, C. E., & Marra, P. P. (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3437–3443. <https://doi.org/10.1098/rspb.2011.0332>
- Sullivan, A. R., Flaspohler, D. J., Froese, R. E., & Ford, D. (2016). Climate variability and the timing of spring raptor migration in eastern North America. *Journal of Avian Biology*, 47, 208–218. <https://doi.org/10.1111/jav.00692>

- Swingen, M. B., DePerno, C. S., & Moorman, C. E. (2015). Seasonal coyote diet composition at a low-productivity site. *Southeastern Naturalist*, 14, 397–404. <https://doi.org/10.1656/058.014.0219>
- Terraube, J., & Bretagnolle, V. (2018). Top-down limitation of mesopredators by avian top predators: A call for research on cascading effects at the community and ecosystem scale. *Ibis*, 160, 693–702. <https://doi.org/10.1111/ibi.12581>
- Therrien, J.-F., Lecomte, N., Zgirski, T., Jaffré, M., Beardsell, A., Goodrich, L. J., Bêty, J., Franke, A., Zlonis, E., & Bildstein, K. L. (2017). Long-term phenological shifts in migration and breeding-area residency in eastern North American raptors. *The Auk: Ornithological Advances*, 134, 871–881. <https://doi.org/10.1642/AUK-17-5.1>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature0212>
- Thuiller, W., Brotons, L., Araújo, M. B., & Lavorel, S. (2004). Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, 27, 165–172. <https://doi.org/10.1111/j.0906-7590.2004.03673.x>
- Treves, A., & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17, 1491–1499. <https://doi.org/10.1111/j.1523-1739.2003.00059.x>
- U.S. Climate Data. (2020). U.S. climate data; monthly averages. <https://www.usclimatedata.com/>
- van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H., & Landa, A. (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology*, 77, 1183–1190. <https://doi.org/10.1111/j.1365-2656.2008.01445.x>
- Vucetich, J. A., Peterson, R. O., & Waite, T. A. (2004). Raven scavenging favours group foraging in wolves. *Animal Behaviour*, 67, 1117–1126. <https://doi.org/10.1016/j.anbehav.2003.06.018>
- Watson, J. W., Vekasy, M. S., Nelson, J. D., & Orr, M. R. (2019). Eagle visitation rates to carrion in a winter scavenging guild. *The Journal of Wildlife Management*, 83, 1735–1743. <https://doi.org/10.1002/jwmg.21760>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.
- Williams, C. M., Henry, H. A., & Sinclair, B. J. (2015). Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90, 214–235. <https://doi.org/10.1111/brv.12105>
- Wilmers, C. C., & Getz, W. M. (2005). Gray wolves as climate change buffers in Yellowstone. *PLoS Biology*, 3, e92. <https://doi.org/10.1371/journal.pbio.0030092>
- Wilson, D., & Read, J. (2003). Kangaroo harvesters: Fertilising the rangelands. *The Rangeland Journal*, 25, 47–55. <https://doi.org/10.1071/RJ03007>
- Wilson, E. E., & Wolkovich, E. M. (2011). Scavenging: How carnivores and carrion structure communities. *Trends in Ecology & Evolution*, 26, 129–135. <https://doi.org/10.1016/j.tree.2010.12.011>
- WorldClim. (2020). *Global climate data*. <http://www.worldclim.org>
- WorldPop and Center for International Earth Science Information Network. (2020). Global high resolution population denominators project. www.worldpop.org. <https://doi.org/10.5258/SOTON/WP00674>
- Yahner, R. H., Storm, G. L., & Wright, A. L. (1986). Winter diets of vultures in southcentral Pennsylvania. *Wilson Bulletin*, 98, 157–160.
- Young, R. A. (1976). Fat, energy and mammalian survival. *American Zoologist*, 16, 699–710. <https://doi.org/10.1093/icb/16.4.699>
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Marneweck CJ, Katzner TE, Jachowski DS. Predicted climate-induced reductions in scavenging in eastern North America. *Glob Change Biol*. 2021;27:3383–3394. <https://doi.org/10.1111/gcb.15653>