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Disturbance type and species life history predict mammal responses to humans

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Abstract

Human activity and land use change impact every landscape on Earth, driving declines in many animal species while benefiting others. Species ecological and life history traits may predict success in human-dominated landscapes such that only species with "winning" combinations of traits will persist in disturbed environments. However, this link between species traits and successful coexistence with humans remains obscured by the complexity of anthropogenic disturbances and variability among study systems. We compiled detection data for 24 mammal species from 61 populations across North America to quantify the effects of (1) the direct presence of people and (2) the human footprint (landscape modification) on mammal occurrence and activity levels. Thirty-three percent of mammal species exhibited a net negative response (i.e., reduced occurrence or activity) to increasing human presence and/or footprint across populations, whereas 58% of species were positively associated with increasing disturbance. However, apparent benefits of human presence and footprint tended to decrease or disappear at higher disturbance levels, indicative of thresholds in mammal species' capacity to tolerate disturbance or exploit human-dominated landscapes. Species ecological and life history traits were strong predictors of their responses to human footprint, with increasing footprint favoring smaller, less carnivorous, faster-reproducing species. The positive and negative effects of human presence were distributed more randomly with respect to species trait values, with apparent winners and losers across a range of body sizes and dietary guilds. Differential responses by some species to human presence and human footprint highlight the importance of considering these two forms of human disturbance separately when estimating anthropogenic impacts on wildlife. Our approach provides insights into the complex mechanisms through which human activities shape mammal communities globally, revealing the drivers of the loss of larger predators in human-modified landscapes.

KEYWORDS
anthropogenic disturbance, carnivore, conservation, environmental filter, human footprint index, human-wildlife coexistence, occupancy, traits, ungulate, wildlife

1 | INTRODUCTION

As the spatial extent and intensity of human activity expands worldwide (Larson et al., 2016; Venter et al., 2016), it is increasingly critical to understand how animal communities respond to anthropogenic disturbance (Gallo et al., 2017; Magle et al., 2016; Parsons et al., 2018). Disturbance effects on animal distribution and activity are typically assumed to be negative (Belote et al., 2020; Dirzo et al., 2014), yet for some species, human activities confer benefits as well as costs. These trade-offs are particularly common for mammals, as greater resource availability and reduced competition or predation in human-dominated landscapes (Bateman & Fleming, 2012; Moll et al., 2018) may offset the impacts of habitat loss and exposure to anthropogenic mortality (Hill et al., 2020; Sévêque et al., 2020). At the community level, the differential responses of species to human disturbance may have a filtering effect (Aronson et al., 2016; Santini et al., 2019), such that only species with "winning" combinations of ecological and life history traits (i.e., those suited to coexistence with humans) will persist in disturbed environments (Pineda-Munoz et al., 2021). Human disturbance may, therefore, reshape mammal communities in ways that are predictable from suites of species traits, with implications for both single-species conservation efforts and broader patterns of ecosystem functioning (Estes et al., 2011; Schmitz et al., 2018).

Anthropogenic activity involves multiple distinct stressors, which may interact with species traits to determine the net effect of human influence on mammal behavior and habitat use. Recent work (Doherty et al., 2021; Nickel et al., 2020) demonstrates that two broad types of human disturbance—direct human presence

(e.g., recreation, hunting; Kays et al., 2017; Naidoo & Burton, 2020) and human footprint on the landscape (e.g., habitat fragmentation, development; Smith et al., 2019; Suraci et al., 2020; Venter et al., 2016)—have different and often opposing effects on mammals, likely because these two disturbance types represent distinct sets of filters that interact differently with species traits. For instance, mammal body size and trophic position may determine whether the immediate presence of humans induces fear responses that result in reduced habitat use and suppressed activity (Clinchy et al., 2016; Ordiz et al., 2019; Suraci, Clinchy, et al., 2019) or whether human presence leads to indirect benefits through relaxed predation/competition (Berger, 2007; Muhly et al., 2011). Species traits may similarly determine mammal responses to human footprint. Species with large space requirements may be more negatively impacted by habitat loss and fragmentation (Crooks et al., 2017; Ripple et al., 2014), whereas those with higher dietary flexibility may benefit from increased resource availability in modified landscapes (Bateman & Fleming, 2012; Newsome & Van Eeden, 2017). Across disturbance types, suites of traits may be strongly related to both the likelihood that a species will occur in areas of high human influence (Aronson et al., 2016; Evans et al., 2011; Santini et al., 2019), as well as the intensity with which a species uses such areas when present (e.g., the number of individuals present and/or the frequency with which a site is visited; Lewis et al., 2015; Moll et al., 2018; Suraci, Clinchy, et al., 2019), potentially allowing ecologists to predict shifts in mammal community structure and species interactions with increasing disturbance intensity.

However, variation among populations may obscure the link between species-level traits and measured responses to human disturbance. Within a given mammal species, populations frequently vary in the intensity or directionality of their response to a given disturbance type depending on local conditions, including habitat productivity and exposure to anthropogenic mortality (Belote et al., 2020; Kays et al., 2017; Moreno-Rueda & Pizarro, 2009; Sévêque et al., 2020). Indeed, studies of recreation impacts in protected areas commonly report contrasting responses to human presence by different populations of the same species (Bateman & Fleming, 2017; Patten & Burger, 2018; Reed & Merenlender, 2008; Reilly et al., 2017), and use of developed areas may also vary among populations based on trade-offs between anthropogenic threat and resource availability (Bateman & Fleming, 2012; Carlos et al., 2009). Therefore, elucidating general patterns in mammal responses to human disturbance requires explicitly accounting for variation among populations as well as across species.

Here, we examine the link between mammal species traits and responses to human disturbance at the continental scale, hypothesizing that species with particular combinations of trait values are more negatively impacted by human influence. Specifically, we hypothesized that larger, more carnivorous species and those with slower life history strategies (i.e., longer maturation periods, slower reproductive rates) are more negatively affected by both human presence and human footprint, given that these species are typically more likely to come into conflict with humans (Oriol-Cotterill et al., 2015; Ripple et al., 2014) and may experience higher rates of anthropogenic mortality (Darimont et al., 2015; Hill et al., 2020). To test our hypotheses, we compiled camera trap data for 24 medium-to-large ungulate and carnivore species from 61 study areas across North America (Figure 1a), which collectively represent a substantial proportion of the North American range for all mammal species in our analysis. Each camera trapping project deployed cameras across gradients of both human presence (Figure 1b) and human footprint (Figure 1c), covering a broad range of both disturbance types, from undeveloped, remote landscapes to well used parks and urban centers. Our analysis addresses two objectives. We first quantify mammal species responses to human disturbance across North America, incorporating variation among populations of the same species to determine the net effect of human presence and human footprint on habitat use and activity levels for each species. We then model mammal responses to anthropogenic disturbance as a function of species ecological and life history traits to discern the mechanistic drivers of human influence on mammal communities.

2 | MATERIALS AND METHODS

2.1 | Camera trapping projects and species

We compiled data from 61 camera trapping studies (here after, "projects") from across the continental United States, Canada, and Mexico, representing 3212 unique camera locations sampled for a total of 454,252 trap days. Details of each camera trapping project are presented in Table S1. Projects were conducted between 2007 and 2019, ranged in spatial extent between 0.4 and 61,506 km^2 ($\bar{x}$ ± SD = 3473.1 ± 9834.9), deployed camera traps at three to 487 unique camera sites ($\bar{x}$ ± SD = 52.6 ± 87.6) and operated for between 63 and 106,480 trap days ($\bar{x}$ ± SD = 7446.7 ± 17,488.5). Although the specific locations across North America sampled in this study were driven by the availability of existing camera trap data sets, we endeavored to cover a large and representative proportion of the continent and to focus on areas with overlapping mammal species composition. We focused our analyses on 24 medium-to-large mammal species in the orders *Artiodactyla* and *Carnivora* that were reliably identifiable from camera trap images and which represented three trophic guilds: herbivores, omnivores, and carnivores (Table S2). We only included those species that were detected by at least three camera trapping projects and with a total of at least 100 independent detections to ensure convergence of occupancy models (see below). Due to data limitations, we treated eastern and western spotted skunks (*Spilogale putorius* and *Spilogale gracilis*) as a single species. We considered different camera trapping projects to approximate separate populations of each focal species, while acknowledging that there may be some overlap among adjacent projects.

We used the geographic location of each camera site to standardize the spacing between sites by (i) treating groups of camera sites within 10 m of each other as a single site and (ii) subsampling

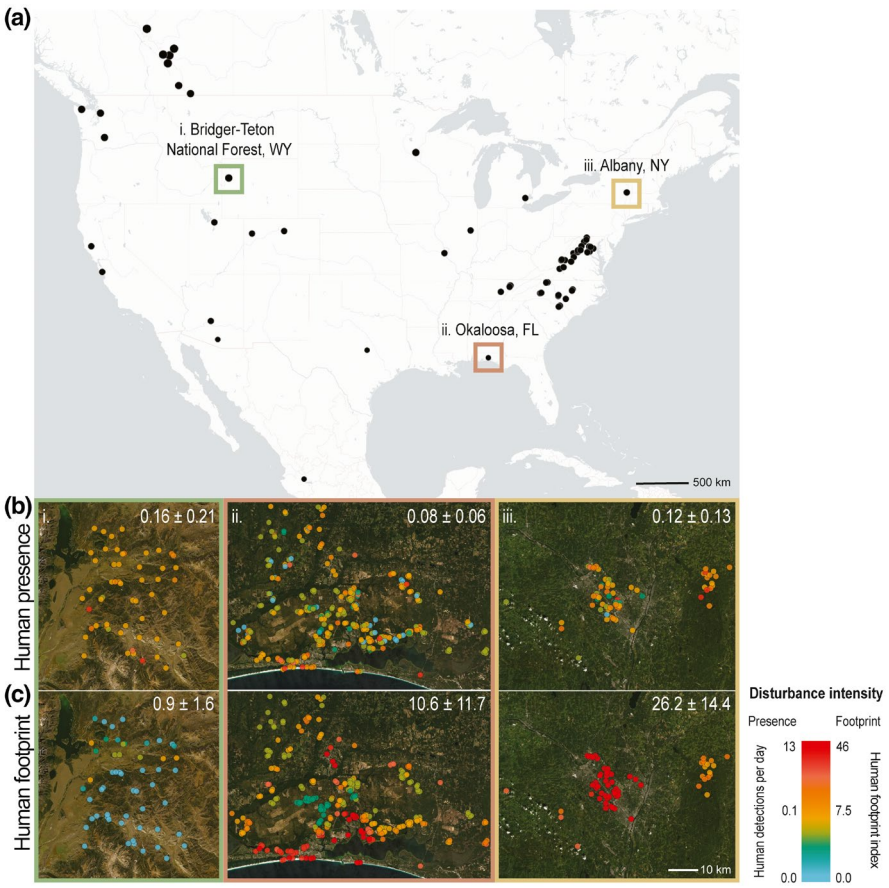

FIGURE 1 Continental-scale assessment of mammal responses to human disturbance. (a) Locations of 61 camera trap projects across North America are shown. Projects ranged from undeveloped but heavily used protected areas (i) through mosaics of developed and undeveloped land (ii) to urban centers (iii). Within each project, camera sites spanned a gradient of both (b) human presence and (c) human footprint. The color of each camera site (point) in b and c represents human detections per day and the Human Footprint Index value, respectively, at that location (both color gradients on the log scale). Mean ± SD disturbance levels are shown for the three example projects [Colour figure can be viewed at wileyonlinelibrary.com]

camera sites such that each site was at least 500 m from its nearest neighbor. For the latter step, when two or more camera sites were within 500 m of each other, we retained the site with the longest sampling duration. Because data on camera activity and camera failures were inconsistently recorded across projects, we used detection (i.e., photograph) time stamps to algorithmically identify breaks in camera activity of greater than 4 weeks (28 days). We considered these to be likely camera failures, and the durations of these activity breaks were therefore subtracted from the total trap days for the corresponding camera site. Averaged across all camera sites, these breaks in activity accounted for 4.6% (±12.3% SD) of the total time a camera was deployed across the study.

2.2 | Estimating human presence and human footprint

We estimated human presence as the detection rate (i.e., detections per trap day) of humans at each camera site. Human detections included all people on foot, bicycles, and motorized vehicles but did not include detections of domestic animals unless a person was also present in the photograph. Because the number of individuals in each photograph was inconsistently reported between projects, each detection event could include one or multiple humans, and thus, detection rates should be interpreted as groups of humans detected per trap day (Nickel et al., 2020). Detections of people on camera provide a fine-scale estimate of hotspots of human presence across a landscape (e.g., where recreational activity is highest).

Human footprint at each camera site was estimated from the Human Footprint Index (HFI), which ranges between 0 and 50 and integrates multiple anthropogenic pressures on the landscape including development, agriculture, and transportation infrastructure (Venter et al., 2016). We used the most recent (i.e., 2009) HFI map and extracted the average HFI value within a 1-km buffer around each camera site. This buffer size matches the resolution of the HFI layer itself and is comparable to the buffer size used in previous studies examining the effects of landscape context on occupancy model parameters across multiple study areas and for species with a range of movement capacities (e.g., Nickel et al., 2020; Rich et al., 2017). We note that the spatial resolution of the HFI (i.e., 1 km) may not match the optimal scale of effect of human footprint for all species considered here (Moll et al., 2020). However, this layer is among the few available at the necessary geographic extent (i.e., all of North America) and has been found to correlate strongly with wildlife behavioral responses in previous large-scale studies considering a range of mammal species (e.g., Tucker et al., 2018).

Across all projects, human presence ranged from zero people/groups per day in remote areas to more than 10 per day (max = 12.5) in heavily used protected areas and suburban neighborhoods (Figure S1a). The human footprint ranged from an HFI of zero, representing undeveloped landscapes in or near protected areas, to more than 40 (max = 46.1) in urban centers such as Detroit, Michigan,

and Albany, New York (Figure S1b). Areas of high human footprint often also have many people present (although this is not always the case, e.g., in heavily modified agricultural landscapes). However, given that camera trap detections represent a fine-scale estimate of human presence (i.e., in the immediate vicinity of the camera) and because cameras in suburban and urban landscapes were often set in locations frequented by wildlife but not by people (e.g., riparian corridors, woodlots, or private property), our measures of human presence and footprint are uncorrelated at the level of individual cameras (Pearson's $r = 0.003$, $p = 0.77$) and only weakly correlated at the project level (project-level means; $r = 0.22$, $p = 0.09$).

2.3 | Quantifying mammal responses to human disturbance via occupancy models

We fit a series of single-species occupancy models to detection data for each of the 24 focal species. Occupancy models estimate two linked parameters, occupancy probability, ψ, the probability that at least one individual of a focal species "occupies" a given site, and intensity of use, p, the probability of detecting the species at that site, given that the site is occupied (Burton et al., 2015; MacKenzie et al., 2002). When studying wide-ranging wildlife species, individuals may use multiple camera sites and may be absent from any given camera site for periods longer than the survey interval (Burton et al., 2015; Efford & Dawson, 2012; Neilson et al., 2018). We, therefore, interpret ψ as "site use" rather than occupancy per se (Kays et al., 2020). We refer to p as "intensity of use" (rather than simply "detection probability" [sensu MacKenzie et al., 2002]) to reflect the fact that the likelihood of detecting a species at a used site depends strongly on the local abundance of the species at that site (Royle, 2004; Royle & Nichols, 2003) and likely also varies with changes in individual behavior (e.g., increased crypsis or reduced activity levels where perceived mortality risk is high; Suraci, Clinchy, et al., 2019). We, therefore, use covariates on p to investigate how anthropogenic disturbance affects the frequency or intensity with which an occupied site is used (Lewis et al., 2015).

In addition to human presence and footprint, we estimated several covariates for each camera site with the potential to affect occupancy and/or intensity of use (Table S1). We calculated percent forest cover around each camera site using the 2010 Global Tree Cover database (30-m resolution; Hansen et al., 2013) and estimated net primary productivity (NPP) around each site using NASA's MODIS system annual NPP layer (500-m resolution; Running & Zhao, 2019) for 2016, the median year of all detection events in this study. Forest cover and NPP were estimated within a 1-km buffer around each camera site, matching the spatial scale at which the human footprint was estimated and capturing the landscape context experienced by animals using that camera site (Nickel et al., 2020; Rich et al., 2017). We also estimated forest cover in the immediate vicinity of each site (i.e., 100-m buffer) to capture the effects of local vegetation cover on species detection probability. Given the large number of ecoregions represented by our continental-scale data set, we elected to use forest cover and NPP as continuous proxies for habitat and ecosystem type rather than expending model degrees of freedom on several discrete habitat categories. Principal investigators for each camera trapping project provided data on whether their project baited camera sites (with either scent lures or food rewards) as well as the prevalence of legal hunting within the project area for both carnivores and ungulates. Typically, hunting data were not available for each individual camera site within a project. We, therefore, assigned each camera site to one of two hunting prevalence categories depending on hunting activity across the project area: 0 = no or only limited hunting (of carnivores and/or ungulates) within the project area, where limited hunting implies that only a subset of camera sites was located within areas where hunting was permitted/occurring; 1 = hunting occurred across the project area (i.e., at most or all camera sites, as reported by data contributors). Finally, we included the geographic location of each camera site (latitude and longitude) in our occupancy models to account for potential similarities between sites in occupancy stemming from geographic proximity (Rota et al., 2016). Several other aspects of camera deployment (e.g., camera height, whether cameras were set on trails) may affect the probability of detecting mammal species, but data on these variables were only available for a subset of camera trapping projects. We, therefore, included a random effect for each project in the occupancy models described below to accommodate variation between projects not explicitly modeled by detection covariates.

Several camera trapping projects spanned multiple seasons and years (Table S1). To satisfy the occupancy model assumption of closure to changes in site-level occupancy status during a given sampling period (Burton et al., 2015), data for each camera site were divided into seasonal sampling periods of at most 6 months: summer (March to August) and winter (September to February). We determined the total duration that each camera was active within each sampling period using the timestamp of the first and last detection event within that period. We treated each week of a given sampling period as a separate survey and modeled the number of weeks in which the focal species was detected during sampling period i at camera site j in project k as

$$y_{ijk} \sim \text{BetaBinom}\left(p_{ijk} * z_{ijk}, S_{ijk}, \rho\right)$$

$$z_{ijk} \sim \text{Bernoulli}\left(\Psi_{ijk}\right)$$

where S_{ijk} is the total number of weeks that camera site j (nested in project k) was active during sampling period i and thus available for sampling, and ρ is the overdispersion parameter of the beta-binomial distribution. We modeled y as beta-binomially distributed because preliminary analyses indicated that variation between projects led to overdispersion in detection data relative to the variability accommodated by the more standard binomial distribution, a situation that is well handled by a beta-binomial model (Gelman & Hill, 2007). The mean of the beta-binomial distribution for camera site j during sampling period i is given by the intensity of use, p, multiplied by z, the latent occupancy state of the focal species at that camera site (Royle &

Dorazio, 2008). z_{ijk} is in turn drawn from a Bernoulli distribution with probability ψ, that is, the probability that the focal species occupies camera site j during sampling period i.

Occupancy probability and intensity of use were modeled as

$$\begin{aligned}\text{logit}\left(\Psi_{ijk}\right) &= \alpha_{0jk} + \alpha_{1k}\text{Presence}_{ij} + \alpha_{2k}\text{Footprint}_j + \alpha_{3k}\text{Presence}_{ij}^2 \\ &+ \alpha_{4k}\text{Footprint}_j^2 + \alpha_5\text{Hunt}_j + \alpha_6\text{Forest\_1 km}_j + \alpha_7\text{NPP}_j \\ &+ \alpha_8\text{Season}_i + \alpha_9\text{Latitude}_j + \alpha_{10}\text{Longitude}_j\end{aligned}$$

$$\begin{aligned}\text{logit}\left(p_{ijk}\right) &= \beta_{0jk} + \beta_{1k}\text{Presence}_{ij} + \beta_{2k}\text{Footprint}_j + \beta_{3k}\text{Presence}_{ij}^2 \\ &+ \beta_{4k}\text{Footprint}_j^2 + \beta_5\text{Hunt}_j + \beta_6\text{Forest\_100 m}_j \\ &+ \beta_7\text{Bait}_j + \beta_8\text{Season}_i\end{aligned}$$

We modeled occupancy as a function of percent forest cover in a 1-km radius around the camera site to estimate the effect of local habitat type on the probability of site use, whereas detection probability was modeled as a function of forest cover in the immediate vicinity of the camera (100-m radius), as sight lines and thus the ability to detect species that are present may be reduced in more heavily forested habitats relative to open areas. For both human presence and human footprint, we fit linear and quadratic terms to test for potential nonlinear effects of increasing human disturbance on species responsiveness. Because all covariates were mean centered for direct comparison (see below for details), linear terms are interpretable independently of quadratic terms (Schielzeth, 2010). Different populations of a given mammal species may not necessarily exhibit consistent responses to human disturbance. For both ψ and p, we, therefore, allowed the intercept (α_0, β_0) and the coefficient estimates for human presence (α_1, β_1) and human footprint (α_2, β_2), as well as their quadratic terms (α_3, α_4, β_3, β_4), to vary by camera trapping project k. All project-level covariates were modeled as being drawn from a common distribution, with hyperparameters μ and σ^2 describing the mean and variance across all projects in the data set. For instance, α_{0k} was modeled as

$$\alpha_{0k} \sim N\left(\mu_{\alpha 0}, \sigma_{\alpha 0}^2\right).$$

To account for the fact that many camera sites were sampled repeatedly across multiple sampling periods, the intercepts were further modeled as camera site-level random effects, with camera site j nested in project k, that is,

$$\alpha_{0jk} \sim N\left(\alpha_{0k}, \sigma_{\alpha_k}^2\right)$$

$$\beta_{0jk} \sim N\left(\beta_{0k}, \sigma_{\beta_k}^2\right)$$

where $\sigma_{\alpha_k}^2$ is an error term describing the variance between camera sites for a given project (and likewise for $\sigma_{\beta_k}^2$).

Because a primary objective of this study was to model mammal responses to human disturbance (estimated from occupancy model coefficients) as a function of species traits, it was essential that model coefficients were comparable across species. We therefore fit identical occupancy models to each species' data (using all model terms just described) rather than attempting to identify the best model for each individual species through model comparison. All model covariates were mean-centered, and continuous covariates were scaled by two standard deviations. We centered and scaled disturbance covariates prior to subsetting the data for each single-species model such that a given value of human presence/footprint received the same standardized value in all models to ensure comparability across species. Pearson correlation coefficients (r) between all pairs of model covariates were <0.6, with the exception of latitude and longitude (r = −0.62). For each focal species, occupancy models only included data from projects that detected the species at least once.

To determine whether each human disturbance type had a net positive or negative effect on site occupancy and intensity of use for a given species, we calculated the probability that each human disturbance linear effect (i.e., α_1, α_2, β_1, and β_2 above) was more extreme (greater or less) than zero using the Bayesian posterior distribution of the coefficient estimate (referred to as the "posterior probability" of the disturbance effect). We quantified the number of species exhibiting an effect of each disturbance type by counting the species for which the posterior probability of a positive or negative effect was >0.9. This value corresponds to 80% Bayesian credible intervals around the disturbance coefficient that do not include zero and was chosen to capture species with limited sample sizes and/or high variability between populations that nonetheless exhibited a strong trend toward a positive or negative association with anthropogenic influence.

2.4 | Modeling mammal responses to disturbance as a function of species traits

A primary objective of this study was to examine how a species' traits affect its responsiveness to human disturbance while explicitly accounting for variation between populations of the same species. We therefore extracted project-level estimates for the (linear) effect of human presence and human footprint on both occupancy and detection probability (i.e., α_{1k}, α_{2k}, β_{1k}, and β_{2k} above) from each single-species occupancy model and modeled these values as a function of species traits. We modeled each of the four disturbance–response combinations (i.e., presence and footprint effects on ψ and p) separately.

For each focal species, we used the PanTHERIA database (Jones et al., 2009) to extract a suite of species traits that may affect responsiveness to human disturbance. This included several traits related to size and space use requirements, namely adult body mass, home range size, and longevity (i.e., maximum lifespan). We also extracted traits related to species reproductive strategy, including litter size, weaning age (i.e., the average age at which young become independent of their mother for nutritional needs), and age at sexual maturity (Jones et al., 2009). We used the EltonTraits database (Wilman et al., 2014) to extract data on the proportion of each of 10 diet categories in the diet of each species and used these data to calculate two dietary indices. Following Santini et al.

(2019), we used the Shannon Index to estimate dietary diversity for each species based on all 10 diet categories. We also calculated the proportion of the diet consisting of vertebrate prey as an estimate of each species' degree of carnivory (EltonTraits diet categories "vertebrate-endoderm," "vertebrate-ectoderm," "vertebrate-fish," and "vertebrate-unknown"). The proportion of vertebrate prey and scavenging in the diet was used to classify each species into three trophic guilds: herbivore (0%), omnivore (1%–50%), and carnivore (>50% vertebrate prey and scavenging). All species trait values are presented in Table S2. We conducted a principal components analysis (PCA) on all trait and dietary data and extracted the first two principal components (PC1 and PC2), which collectively accounted for 72.3% of the variation in trait values between species. We then used PC1 and PC2 as covariates in modeling species responses to human disturbance.

Our response variables in these models, that is, the effects of presence or footprint on species occupancy or detection, are themselves model estimates and are thus not perfectly observed. We, therefore, determined the posterior variance around each project-level disturbance effect size, as estimated by single-species occupancy models, and propagated this error through the multi-species trait models. We treated the "true" disturbance effect on occupancy or detection, w_{is}, as an unobserved latent variable for which we have an observed value, v_{is}, with an associated "observation" error value, $\sigma^2_{o,is}$

$$v_{is} \sim N\left(w_{is}, \sigma^2_{o,is}\right)$$

where i is a project-level disturbance effect size observation for species s. We then modeled the true, unobserved disturbance effect, w_{is}, as a function of PC1, PC2, and their interaction using a Gaussian linear model. We also included the geographic location of each project (project-level mean latitude and longitude, Table S1) in all models to account for potential similarities between projects in mammal responses stemming from geographic proximity. The linear models included a random intercept for species to account for the fact that each species' response to disturbance was estimated for several camera trapping projects. The species-level random effect was nested within family to account for the influence of taxonomic relatedness in driving similar responses between species. Other taxonomic levels were not included because there were either too few categories (only two orders, *Artiodactyla* and *Carnivora*, were represented) or too few observations per category (most genera were only represented by a single species) to estimate the random effects, inhibiting model convergence.

2.5 | Model fitting and checking

We analyzed all occupancy models (24, one for each focal species) and species trait models (4) in a Bayesian framework using the Stan programming language called through the Rstan package in R (Stan Development Team, 2020). For each model, we ran three Hamiltonian Monte Carlo (HMC) chains of either 2000 or 4000 iterations each (depending on ease of model convergence) and retained 1000 samples from the posterior distribution of each chain for inference. Following Gelman et al. (2008) and Gabry et al. (2019), we chose vague or weakly informative priors for all random variables and random starting values for each HMC chain. We confirmed convergence of HMC chains by visual inspection of trace plots and via the Gelman–Rubin statistic ("*R*-hat" values <1.1 for all parameters; Gelman, 2006) and verified the reliability of model inference following the procedure outlined by Gabry et al. (2019). We tested model fit using Bayesian *p*-values, which compare test statistics calculated from observed and expected (i.e., model-generated) data (Hobbs & Hooten, 2015). P-values were calculated using test statistics appropriate for the model distributions—for occupancy models we calculated Freeman–Tukey (Conn et al., 2018) and chi-squared statistics (Royle & Dorazio, 2008), and for the trait models we used the mean and coefficient of variation (Hobbs & Hooten, 2015). We detected satisfactory to excellent fit between model and data for all occupancy models ($0.41 \leq p \leq 0.92$; all p-values shown in Table S5) and trait models ($0.35 \leq p \leq 0.81$; all p-values shown in Table S4).

3 | RESULTS

Standardized occupancy model coefficients, summarizing the average response to disturbance across all populations of a given species, revealed that 17% of the 24 mammal species in our study (three herbivores and one carnivore) were negatively affected by human presence (i.e., the posterior probability of a negative effect of human presence on occupancy and/or intensity of use was >0.9, see Section 2). Elk (*Cervus elaphus*) exhibited reduced site occupancy with increasing human presence, whereas moose (*Alces alces*), mountain goats (*Oreamnos americanus*), and wolverines (*Gulo gulo*) exhibited reduced intensity of use (Figure 2a,b). Thirty-three percent of species were positively associated with human presence (two herbivores, two omnivores, four carnivores). Bighorn sheep (*Ovis canadensis*), black bears (*Ursus americanus*), and wolverines exhibited increased site occupancy with increasing human presence, whereas mule deer (*Odocoileus hemionus*), bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), pumas (*Puma concolor*), and wolves (*Canis lupus*) tended to increase intensity of use in areas of higher human activity (Figure 2a,b).

Human footprint had a negative effect on site occupancy and/or intensity of use for 25% of mammal species (one herbivore, one omnivore, and four carnivores), and a positive effect for 38% of species (three herbivores, two omnivores, and four carnivores). Species negatively associated with human footprint included grizzly bears (*Ursus arctos*), lynx (*Lynx canadensis*), wolves, and wolverines, all of which were less likely to occupy sites with increasing footprint and exhibited decreased intensity of use when present, whereas moose and martens (*Martes americanus*) exhibited decreased intensity of use only. Raccoons (*Procyon lotor*) and white-tailed deer (*Odocoileus virginianus*) were positively associated with human footprint in terms

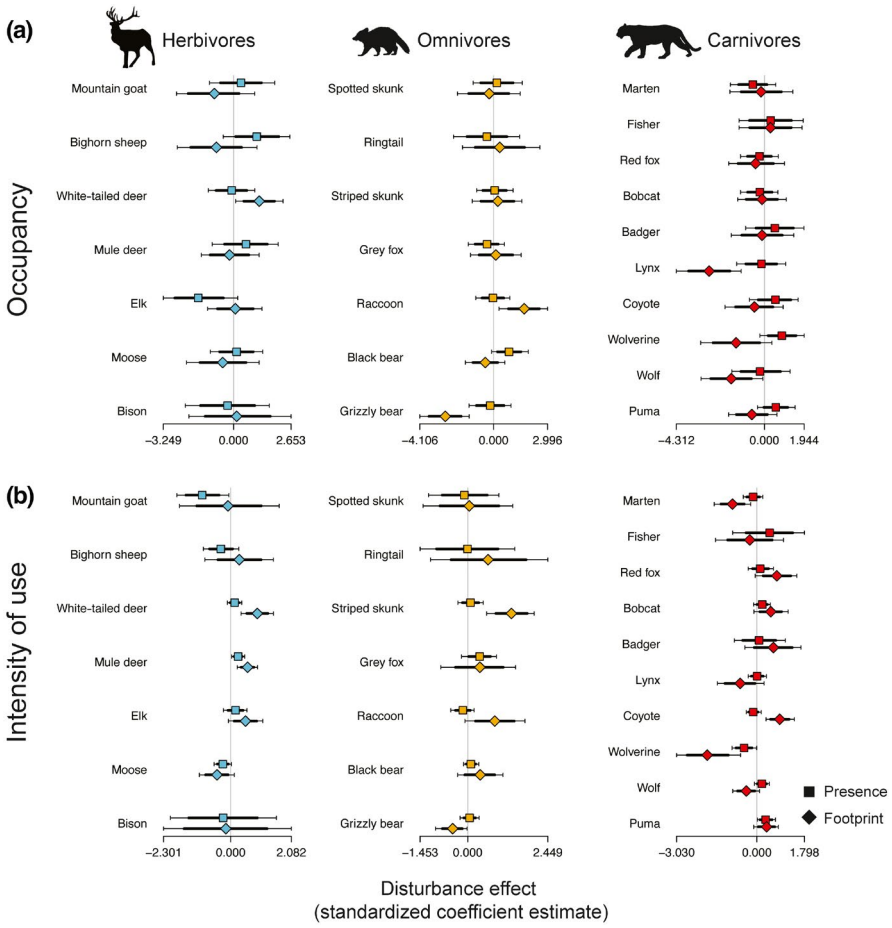

FIGURE 2 Human presence and human footprint have contrasting impacts within and among mammal species. Occupancy model coefficient estimates for the effects of human presence (square) and human footprint (diamond) on (a) site occupancy and (b) intensity of site use. Error bars are 95% (thin) and 80% (thick) Bayesian credible intervals. Coefficient estimates are grouped by trophic guild (based on percent of vertebrate prey and scavenging in the diet, see Table S2 and Section 2) [Colour figure can be viewed at wileyonlinelibrary.com]

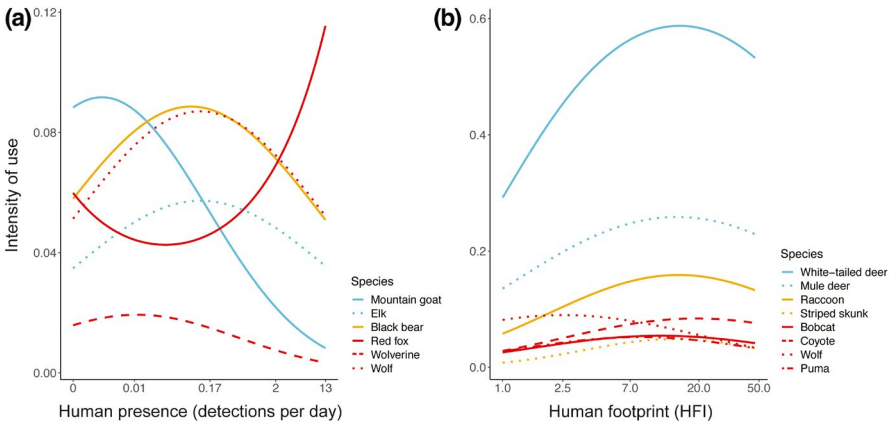

FIGURE 3 Nonlinear effects of human disturbance. Occupancy model predictions for the change in intensity of site use with increasing (a) human presence and (b) human footprint. Results are shown for species for which models estimated a >0.9 probability of a quadratic effect. Lines are color-coded by trophic guild, as shown in Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

of both occupancy and intensity of use, while elk, mule deer, striped skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), bobcats, coyotes (*Canis latrans*), and pumas all tended to use occupied sites more intensively at higher levels of human footprint (Figure 2a,b).

For several species exhibiting positive responses to disturbance, intensity of use peaked at low to intermediate values of human presence (six species, Figure 3a) or footprint (eight species, Figure 3b), indicative of thresholds in these species' capacity to tolerate disturbance or exploit human-dominated landscapes. Red foxes were the single exception, being the only species to exhibit an increasingly positive association with human presence at medium to high disturbance levels (Figure 3a). Full results for all occupancy models are shown in Figure S2.

The first two components of the PCA performed on species trait values (accounting for 72.3% of trait variation) describe axes of increasing body size with decreasing life history speed (i.e., smaller litters, slower maturation; PC1), and increasing space use with greater carnivory (PC2; Figure 4a and Table S3). Bayesian regression models revealed that the effects of human footprint on both site occupancy (Figure 4b; β = −0.22 [95% CI = −0.48,0.01]) and intensity of use (Figure 4c; β = −0.23 [−0.57,0.04]) were increasingly negative at higher values of PC1 (posterior probability of a negative slope = 0.97

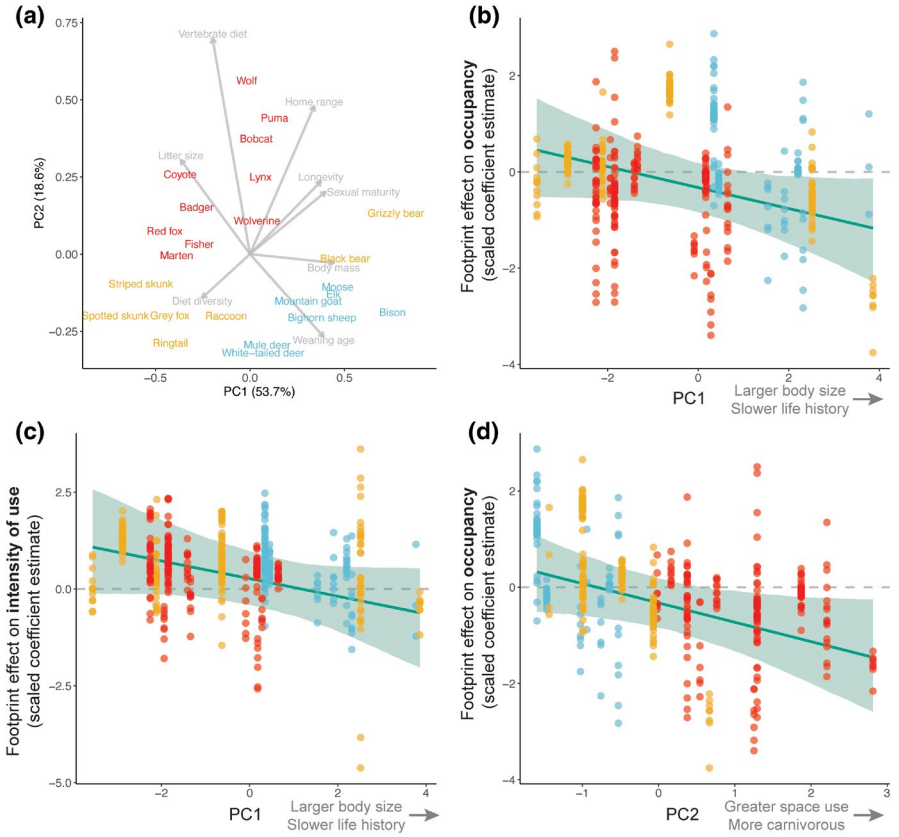

FIGURE 4 Species traits predict responses to human footprint. (a) Biplot of the principal components analysis performed on species trait data, with each mammal species plotted based on its values of the first two principal components (PC1—larger body size and slower life history and PC2—greater space use and more carnivorous). Factor loadings for each trait are shown in gray (see also Table S3). Mammal responses to human footprint were increasingly negative with increasing values of PC1 for both (b) site occupancy and (c) intensity of use. Occupancy responses to footprint (d) were also negatively associated with PC2. Data points in b–d are population-level estimates of each species' response to human footprint, where values above zero (dashed line) indicate a positive response (i.e., increased occupancy or intensity of use with increasing footprint) and those below zero indicate a negative response. Solid lines and shaded areas are the estimated slope and 95% Credible Intervals from hierarchical linear models (see also Table S4). Data in all plots are color-coded by trophic guild, as shown in Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

and 0.95, respectively; Table S4), indicating that larger, longer-lived mammal species and those with slower maturation and reproductive rates are less likely to occur in modified landscapes and are less active when present. Human footprint also had an increasingly negative effect on occupancy (but not intensity of use; Table S4) for species with higher PC2 values (Figure 4d; β = −0.40 [−0.76, −0.04]; probability of a negative slope = 0.99), indicating that species with more carnivorous diets and larger home ranges are less likely to use a given site as landscape modification increases. We did not detect a relationship between human presence and species traits in their effects on site occupancy or intensity of use (Bayesian regression; posterior probability of a negative slope ranged between 0.33 and 0.85 for all relationships; Table S4).

4 | DISCUSSION

By bringing together data on activity and habitat use from mammal populations across North America, our study provides a comprehensive understanding of mammal responses to human disturbance. We found that species' ecological and life history traits were strong predictors of their responses to human footprint on the landscape, confirming our hypothesis that larger, more carnivorous, and slower reproducing species are more negatively affected by human landscape modification. Contrary to our expectations, however, species traits were not strongly related to their responses to human presence, highlighting the importance of considering these two forms of human disturbance separately when estimating anthropogenic impacts on wildlife (Nickel et al., 2020; Sévêque et al., 2020).

Our occupancy model estimates revealed relatively few overall "winners" and "losers", that is, species that tended to respond positively or negatively across disturbance types. Instead, most species exhibited differing, and frequently opposing, responses to human presence and footprint (Figure 2a,b). This pattern was previously reported for mammals in a single study area (Nickel et al., 2020), and our results suggest this is a common feature of human–mammal interactions across North America. Negative effects of

human presence likely stem from fear of humans causing mammals to suppress their activity levels (Suraci, Clinchy, et al., 2019) or avoid areas of high human influence entirely (Oriol-Cotterill et al., 2015), while positive associations may reflect the shield that human presence provides for some species against predators or competitors (Berger, 2007; Hebblewhite et al., 2005; Muhly et al., 2011). Positive responses to human presence by larger bodied species with substantial space requirements (e.g., pumas, wolves, wolverines; Figure 2b) may also reflect the growing intensity of recreation and ecotourism in otherwise relatively undisturbed areas of wildlife habitat (Anton et al., 2020; Nickel et al., 2020), leaving such species with little choice but to share space with people.

Despite the loss of natural habitat associated with increasing human footprint, agricultural lands and developed areas nonetheless present opportunities for some species through resource subsidies or relaxed predation/competition (Prugh & Sivy, 2020; Sévêque et al., 2020). Increased human footprint is also associated with decreased movement and smaller home ranges for many mammal species (Doherty et al., 2021; Tucker et al., 2018), including large predators such as pumas (Nickel et al., 2021). Thus, higher intensity of use in more heavily modified habitats by species that otherwise tend to avoid human footprint (e.g., pumas and bobcats, Serieys et al., 2021; Suraci et al., 2020) may reflect restricted movement options and thus intensified use of remaining habitat fragments in moderately developed areas.

Importantly, for several mammal species that exhibited positive associations with human presence or footprint, the apparent benefits of human activity were diminished or reversed at higher disturbance levels (Figure 3). For instance, black bears, elk, and wolves were most active at sites visited by approximately one person/group every 8–12 days (Figure 3a), and several species exhibited peak intensity of use in partially cleared habitats with low density development (i.e., intermediate HFI values, Figure 3b). These results indicate that several mammal species exhibit thresholds in their tolerance for human disturbance beyond which habitat may no longer be viable. We suggest that such thresholds are critical to consider when attempting to promote "landscapes of coexistence" (i.e., ecological conditions that allow the long-term persistence of sensitive mammal species in human-dominated landscapes; Gehr et al., 2017; Oriol-Cotterill et al., 2015) and functional connectivity between populations, particularly as several large mammal species continue to recolonizing modified landscapes in North American and globally (Gantchoff & Belant, 2017; Gilbert et al., 2016; Hemmingmoore et al., 2020; Rio-Maior et al., 2019).

Larger mammal species and those with slower life histories were both less likely to occur in areas of high human footprint and exhibited lower intensity of use when present. The human footprint is associated with a multitude of threats including vehicle strikes (Grilo et al., 2020), sensory pollution (Dominoni et al., 2020), and invasive species (Shochat et al., 2010). Our results suggest that smaller mammals and those with faster life histories are better able to avoid these threats (Hill et al., 2020) or can offset heightened anthropogenic mortality through high reproductive rates (Santini et al., 2019). Additionally, species with more carnivorous diets and larger space requirements were less likely to occur in modified landscapes. Wide-ranging carnivores frequently come into conflict with humans over perceived threats to human life and livelihood (Carter & Linnell, 2016; Chapron & López-Bao, 2016; Treves & Karanth, 2003), and their large home range sizes may make them more susceptible to the impacts of habitat fragmentation in modified landscapes (Crooks, 2002; Ripple et al., 2014). Although our analyses were focused on North American mammal communities, we suggest that the patterns observed here are likely applicable to medium-to-large mammal species globally. Recent work focused on urban environments has similarly shown that both high reproductive output (large litter size) and high dietary diversity are frequently associated with mammal use of urban areas worldwide (Santini et al., 2019), highlighting the importance of these traits in allowing mammals to successfully exploit modified landscapes. Additionally, the exclusion of larger predatory mammals from areas of high human footprint is a common phenomenon in systems around the world (Ordiz et al., 2013; Oriol-Cotterill et al., 2015).

Our study provides a framework for predicting the filtering effect of human land use change on mammal communities, helping to clarify the often ambiguous relationship between human footprint and mammal community composition (Belote et al., 2020; Hill et al., 2020). Our results indicate that as human footprint increases, mammal community composition will shift toward smaller herbivorous and omnivorous species with faster reproductive strategies and smaller space requirements. The speed and extent of shifts in community composition following land conversion to agriculture or development will likely depend on local legal protections (e.g., hunting regulations; Chapron & Treves, 2016); and environmental conditions (e.g., ecosystem productivity; Belote et al., 2020). Our analysis accounted for population-level variation in these and additional factors, showing that, whereas the effects of hunting and environmental covariates varied substantially between species (Figure S2), trends toward reduced occurrence and activity of large-bodied, slow-reproducing mammals in more developed areas were robust to variation in local conditions.

Our estimates of human footprint (i.e., contemporary landscape modification) represent only a snapshot in time and do not explicitly incorporate legacies of human land use (e.g., historical management regimes; Jonason et al., 2014; Moreira & Russo, 2007) or other forms of ecological disturbance such as fire (Geary et al., 2020; Pastro et al., 2014), both of which are known to play important roles in shaping observed community structure by affecting vegetation composition and species interactions. Our objective in the present study was to detect general patterns in human disturbance impacts on mammals across a range of ecological conditions. However, we note that understanding the interaction between current human land use and other drivers of landscape pattern, both historical and contemporary, will be critical in accurately predicting mammal community responses to future landscape modification in any particular location.

Although species traits predicted responses to human footprint, they were not predictive of responses to human presence, suggesting that the benefits and costs of using habitats frequently visited by

humans (e.g., recreationists in protected areas or urban green spaces) are distributed somewhat randomly across body sizes, trophic guilds, and reproductive strategies. This finding likely reflects the fact that many species are able to mitigate the impacts of human presence on space use through increased nocturnality (Gaynor et al., 2018). Whereas landscape modification is relatively constant in space and time, human presence is largely diurnal, meaning that even species that are relatively sensitive to the immediate presence of people (e.g., many carnivores; Suraci, Clinchy, et al., 2019) may be able to use human-dominated areas at night when people are less active (Anton et al., 2020; Suraci, Frank, et al., 2019). Importantly, however, shifting temporal activity to avoid humans may be costly by constraining temporal niche space and forcing increased overlap with predators or competitors (Sévêque et al., 2020; Smith et al., 2018).

The structure and diversity of mammal communities are key determinants of ecosystem processes, with larger-bodied mammals affecting primary production and nutrient cycling through herbivory and trophic interactions (Estes et al., 2011; Schmitz et al., 2018). Here we show that the capacity of mammal species to coexist with humans in modified landscapes is predictable from suites of species traits, highlighting the types of mammal communities that are likely to persist with increased landscape conversion. Such communities will be composed of smaller, faster breeding species with limited space requirements, which may play a more muted role in driving ecosystem processes relative to larger, more mobile, and more carnivorous species (Estes et al., 2011; Ripple et al., 2014; Tucker et al., 2018). Human presence has less predictable spatial impacts on mammal communities but may nonetheless alter wildlife behavior in ways that dampen trophic interactions and the links between ecosystems (Suraci, Clinchy, et al., 2019; Tucker et al., 2018). Continued landscape modification and increased human use of remaining natural areas portend greater reliance of mammal species on human-dominated landscapes. Predicting which species are likely to thrive or perish under multiple sources of anthropogenic pressure is critical to conserving mammal communities and the ecosystem services they provide.

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AUTHOR CONTRIBUTIONS

JPS, CCW, MLA, and KMG conceived of the study. All authors contributed data to the analysis. JPS led the analysis and writing, with substantial feedback on analysis from CCW, MLA, and KMG, and with valuable input on writing from all authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on Figshare at https://doi.org/10.6084/m9.figshare.14444600.v1. All code necessary to replicate the analyses is available on GitHub at https://github.com/jsuraci/Suraci-etal-MammalLifeHistory.

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SUPPORTING INFORMATION

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

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