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9   Disturbance type and species life history predict mammal responses to humans

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67   Running head: Mammal traits predict responses to humans

68   **Abstract**

69   Human activity and land use change impact every landscape on Earth, driving declines in many

70   animal species while benefiting others. Species ecological and life history traits may predict

71   success in human-dominated landscapes such that only species with "winning" combinations of

72   traits will persist in disturbed environments. However, this link between species traits and

73   successful coexistence with humans remains obscured by the complexity of anthropogenic

74   disturbances and variability among study systems. We compiled detection data for 24 mammal

75   species from 61 populations across North America to quantify the effects of (1) the direct

76   presence of people and (2) the human footprint (landscape modification) on mammal occurrence

77   and activity levels. Thirty-three percent of mammal species exhibited a net negative response

78   (i.e., reduced occurrence or activity) to increasing human presence and/or footprint across

79   populations, while 58% of species were positively associated with increasing disturbance.

80   However, apparent benefits of human presence and footprint tended to decrease or disappear at

81   higher disturbance levels, indicative of thresholds in mammal species' capacity to tolerate

82   disturbance or exploit human-dominated landscapes. Species ecological and life history traits

83   were strong predictors of their responses to human footprint, with increasing footprint favoring

84   smaller, less carnivorous, faster-reproducing species. The positive and negative effects of human

85   presence were distributed more randomly with respect to species trait values, with apparent

86   winners and losers across a range of body sizes and dietary guilds. Differential responses by

87   some species to human presence and human footprint highlight the importance of considering

88   these two forms of human disturbance separately when estimating anthropogenic impacts on

89   wildlife. Our approach provides insights into the complex mechanisms through which human

90   activities shape mammal communities globally, revealing the drivers of the loss of larger

91   predators in human-modified landscapes.

92

Keywords

anthropogenic disturbance, carnivore, conservation, environmental filter, human footprint index,

human-wildlife coexistence, traits, ungulate, occupancy, wildlife

96

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).

114

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

123   may determine whether the immediate presence of humans induces fear responses that result in

124   reduced habitat use and suppressed activity (Clinchy et al., 2016; Ordiz et al., 2019; Suraci,

125   Clinchy, et al., 2019) or whether human presence leads to indirect benefits through relaxed

126   predation/competition (Berger, 2007; Muhly et al., 2011). Species traits may similarly determine

127   mammal responses to human footprint. Species with large space requirements may be more

128   negatively impacted by habitat loss and fragmentation (Crooks et al., 2017; Ripple et al., 2014),

129   while those with higher dietary flexibility may benefit from increased resource availability in

130   modified landscapes (Bateman & Fleming, 2012; Newsome & Van Eeden, 2017). Across

131   disturbance types, suites of traits may be strongly related to both the likelihood that a species will

132   occur in areas of high human influence (Aronson et al., 2016; Evans et al., 2011; Santini et al.,

133   2019), as well as the intensity with which a species uses such areas when present (e.g., the

134   number of individuals present and/or the frequency with which a site is visited; (Lewis et al.,

135   2015; Moll et al., 2018; Suraci, Clinchy, et al., 2019)), potentially allowing ecologists to predict

136   shifts in mammal community structure and species interactions with increasing disturbance

137   intensity.

138

139   However, variation among populations may obscure the link between species-level traits and

140   measured responses to human disturbance. Within a given mammal species, populations

141   frequently vary in the intensity or directionality of their response to a given disturbance type

142   depending on local conditions, including habitat productivity and exposure to anthropogenic

143   mortality (Belote et al., 2020; Kays et al., 2017; Moreno-Rueda & Pizarro, 2009; Sévêque et al.,

144   2020). Indeed, studies of recreation impacts in protected areas commonly report contrasting

145   responses to human presence by different populations of the same species (Bateman & Fleming,

146   2017; Patten & Burger, 2018; Reed & Merenlender, 2008; Reilly et al., 2017), and use of

147   developed areas may also vary among populations based on trade-offs between anthropogenic

148   threat and resource availability (Bateman & Fleming, 2012; Carlos et al., 2009). Therefore,

149   elucidating general patterns in mammal responses to human disturbance requires explicitly

150   accounting for variation among populations as well as across species.

151

152   Here we examine the link between mammal species traits and responses to human disturbance at

153   the continental scale, hypothesizing that species with particular combinations of trait values are

154 more negatively impacted by human influence. Specifically, we hypothesized that larger, more

155 carnivorous species and those with slower life history strategies (i.e., longer maturation periods,

156 slower reproductive rates) are more negatively affected by both human presence and human

157 footprint, given that these species are typically more likely to come into conflict with humans

158 (Oriol-Cotterill et al., 2015; Ripple et al., 2014) and may experience higher rates of

159 anthropogenic mortality (Darimont et al., 2015; Hill et al., 2020). To test our hypotheses, we

160 compiled camera trap data for 24 medium-to-large ungulate and carnivore species from 61 study

161 areas across North America (Fig. 1A), which collectively represent a substantial proportion of

162 the North American range for all mammal species in our analysis. Each camera trapping project

163 deployed cameras across gradients of both human presence (Fig. 1B) and human footprint (Fig.

164 1C), covering a broad range of both disturbance types, from undeveloped, remote landscapes to

165 well used parks and urban centers. Our analysis addresses two objectives. We first quantify

166 mammal species responses to human disturbance across North America, incorporating variation

167 among populations of the same species to determine the net effect of human presence and human

168 footprint on habitat use and activity levels for each species. We then model mammal responses to

169 anthropogenic disturbance as a function of species ecological and life history traits to discern the

170 mechanistic drivers of human influence on mammal communities.

171

172 **Materials and methods**

173 *Camera trapping projects and species*

174 We compiled data from 61 camera trapping studies (here after, "projects") from across the

175 continental United States, Canada, and Mexico, representing 3,212 unique camera locations

176 sampled for a total of 454,252 trap days. Details of each camera trapping project are presented in

177 Table S1. Projects were conducted between 2007 and 2019, ranged in spatial extent between 0.4

178 and 61,506 km^2 ($\bar{x} \pm$ SD = 3,473.1 $\pm$ 9834.9), deployed camera traps at three to 487 unique

179 camera sites ($\bar{x} \pm$ SD = 52.6 $\pm$ 87.6) and operated for between 63 and 106,480 trap days ($\bar{x} \pm$ SD

180 = 7,446.7 $\pm$ 17,488.5). While the specific locations across North America sampled in this study

181 were driven by the availability of existing camera trap data sets, we endeavored to cover a large

182 and representative proportion of the continent and to focus on areas with overlapping mammal

183 species composition. We focused our analyses on 24 medium-to-large mammal species in the

184 orders *Artiodactyla* and *Carnivora* that were reliably identifiable from camera trap images and

185 which represented three trophic guilds: herbivores, omnivores, and carnivores (Table S2). We

186 only included those species that were detected by at least three camera trapping projects and with

187 a total of at least 100 independent detections to ensure convergence of occupancy models (see

188 below). Due to data limitations, we treated eastern and western spotted skunks (*Spilogale*

189 *putorius* and *S. gracilis*) as a single species. We considered different camera trapping projects to

190 approximate separate populations of each focal species, while acknowledging that there may be

191 some overlap among adjacent projects.

192

193 We used the geographic location of each camera site to standardize the spacing between sites by

194 (i) treating groups of camera sites within 10 m of each other as a single site and (ii) subsampling

195 camera sites such that each site was at least 500 m from its nearest neighbor. For the latter step,

196 when two or more camera sites were within 500 m of each other, we retained the site with the

197 longest sampling duration. Because data on camera activity and camera failures were

198 inconsistently recorded across projects, we used detection (i.e., photograph) time stamps to

199 algorithmically identify breaks in camera activity of greater than four weeks (28 days). We

200 considered these to be likely camera failures and the durations of these activity breaks were

201 therefore subtracted from the total trap nights for the corresponding camera site. Averaged across

202 all camera sites, these breaks in activity accounted for 4.6% (± 12.3% SD) of the total time a

203 camera was deployed across the study.

204

205 *Estimating human presence and human footprint*

206 We estimated human presence as the detection rate (i.e., detections per trap day) of humans at

207 each camera site. Human detections included all people on foot, bicycles, and motorized

208 vehicles, but did not include detections of domestic animals unless a person was also present in

209 the photograph. Because the number of individuals in each photograph was inconsistently

210 reported between projects, each detection event could include one or multiple humans and thus

211 detection rates should be interpreted as groups of humans detected per trap day (Nickel et al.,

212 2020). Detections of people on camera provide a fine-scale estimate of hotspots of human

213 presence across a landscape (e.g., where recreational activity is highest).

214

215 Human footprint at each camera site was estimated from the Human Footprint Index (HFI) which

216 ranges between 0 and 50 and integrates multiple anthropogenic pressures on the landscape

217 including development, agriculture, and transportation infrastructure (Venter et al., 2016). We

218 used the most recent (i.e., 2009) HFI map and extracted the average HFI value within a 1-km

219 buffer around each camera site. This buffer size matches the resolution of the HFI layer itself and

220 is comparable to the buffer size used in previous studies examining the effects of landscape

221 context on occupancy model parameters across multiple study areas and for species with a range

222 of movement capacities (e.g., Nickel et al., 2020; Rich et al., 2017). We note that the spatial

223 resolution of the HFI (i.e., 1 km) may not match the optimal scale of effect of human footprint

224 for all species considered here (Moll et al., 2020). However, this layer is among the few available

225 at the necessary geographic extent (i.e., all of North America) and has been found to correlate

226 strongly with wildlife behavioral responses in previous large-scale studies considering a range of

227 mammal species (e.g., Tucker et al., 2018).

228

229 Across all projects human presence ranged from zero people/groups per day in remote areas to

230 more than 10 per day (max = 12.5) in heavily used protected areas and suburban neighborhoods

231 (Fig. S1a). The human footprint ranged from an HFI of zero, representing undeveloped

232 landscapes in or near protected areas, to more than 40 (max = 46.1) in urban centers such as

233 Detroit, Michigan and Albany, New York (Fig. S1b). Areas of high human footprint often also

234 have many people present (though this is not always the case, e.g., in heavily modified

235 agricultural landscapes). However, given that camera trap detections represent a fine-scale

236 estimate of human presence (i.e., in the immediate vicinity of the camera), and because cameras

237 in suburban and urban landscapes were often set in locations frequented by wildlife but not by

238 people (e.g., riparian corridors, woodlots, or private property), our measures of human presence

239 and footprint are uncorrelated at the level of individual cameras (Pearson's r = 0.003, p = 0.77)

240 and only weakly correlated at the project level (project-level means; r = 0.22, p = 0.09).

241

242 *Quantifying mammal responses to human disturbance via occupancy models*

243 We fit a series of single-species occupancy models to detection data for each of the 24 focal

244 species. Occupancy models estimate two linked parameters, occupancy probability, ψ, the

245 probability that at least one individual of a focal species "occupies" a given site, and intensity of

246   use, p, the probability of detecting the species at that site, given that the site is occupied (Burton

247   et al., 2015; MacKenzie et al., 2002). When studying wide-ranging wildlife species, individuals

248   may use multiple camera sites and may be absent from any given camera site for periods longer

249   than the survey interval (Burton et al., 2015; Efford & Dawson, 2012; Neilson et al., 2018). We

250   therefore interpret ψ as 'site use' rather than occupancy *per se* (Kays et al., 2020). We refer to p

251   as "intensity of use" (rather than simply "detection probability" (sensu MacKenzie et al., 2002))

252   to reflect the fact that the likelihood of detecting a species at a used site depends strongly on the

253   local abundance of the species at that site (Royle, 2004; Royle & Nichols, 2003) and likely also

254   varies with changes in individual behavior (e.g., increased crypsis or reduced activity levels

255   where perceived mortality risk is high (Suraci, Clinchy, et al., 2019)). We therefore use

256   covariates on p to investigate how anthropogenic disturbance affects the frequency or intensity

257   with which an occupied site is used (Lewis et al., 2015).

258

259   In addition to human presence and footprint, we estimated several covariates for each camera site

260   with the potential to affect occupancy and/or intensity of use (Table S1). We calculated percent

261   forest cover around each camera site using the 2010 Global Tree Cover database (30-m

262   resolution) (Hansen et al., 2013) and estimated net primary productivity (NPP) around each site

263   using NASA's MODIS system annual NPP layer (500-m resolution) (Running & Zhao, 2019) for

264   2016, the median year of all detection events in this study. Forest cover and NPP were estimated

265   within a 1-km buffer around each camera site, matching the spatial scale at which the human

266   footprint was estimated and capturing the landscape context experienced by animals using that

267   camera site (Nickel et al., 2020; Rich et al., 2017). We also estimated forest cover in the

268   immediate vicinity of each site (i.e., 100-m buffer) to capture the effects of local vegetation

269   cover on species detection probability. Given the large number of ecoregions represented by our

270   continental-scale data set, we elected to use forest cover and NPP as continuous proxies for

271   habitat and ecosystem type rather than expending model degrees of freedom on several discrete

272   habitat categories. Principal investigators for each camera trapping project provided data on

273   whether their project baited camera sites (with either scent lures or food rewards) as well as the

274   prevalence of legal hunting within the project area for both carnivores and ungulates. Typically,

275   hunting data were not available for each individual camera site within a project. We therefore

276   assigned each camera site to one of two hunting prevalence categories depending on hunting

277   activity across the project area: 0 = no or only limited hunting (of carnivores and/or ungulates)

278   within the project area, where limited hunting implies that only a subset of camera sites was

279   located within areas where hunting was permitted/occurring; 1 = hunting occurred across the

280   project area (i.e., at most or all camera sites, as reported by data contributors). Finally, we

281   included the geographic location of each camera site (latitude and longitude) in our occupancy

282   models to account for potential similarities between sites in occupancy and intensity of use

283   stemming from geographic proximity (Rota et al., 2016). Several other aspects of camera

284   deployment (e.g., camera height, whether cameras were set on trails) may affect the probability

285   of detecting mammal species, but data on these variables were only available for a subset of

286   camera trapping projects. We therefore included a random effect for each project in the

287   occupancy models described below to accommodate variation between projects not explicitly

288   modeled by detection covariates.

289

290   Several camera trapping projects spanned multiple seasons and years (Table S1). To satisfy the

291   occupancy model assumption of closure to changes in site-level occupancy status during a given

292   sampling period (Burton et al., 2015), data for each camera site were divided into seasonal

293   sampling periods of at most six months: summer (March to August) and winter (September to

294   February). We determined the total duration that each camera was active within each sampling

295   period using the timestamp of the first and last detection event within that period. We treated

296   each week of a given sampling period as a separate survey and modeled the number of weeks in

297   which the focal species was detected during sampling period i at camera site j in project k as

298

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

300    $z_{ijk} \sim Bernoulli(\Psi_{ijk})$

301   where S_{ijk} is the total number of weeks that camera site j (nested in project k) was active during

302   sampling period i and thus available for sampling, and ρ is the overdispersion parameter of the

303   beta-binomial distribution. We modeled y as beta-binomially distributed because preliminary

304   analyses indicated that variation between projects led to overdispersion in detection data relative

305   to the variability accommodated by the more standard binomial distribution, a situation that is

306   well handled by a beta-binomial model (Gelman & Hill, 2007). The mean of the beta-binomial

307   distribution for camera site j during sampling period i is given by the intensity of use, p,

308   multiplied by z, the latent occupancy state of the focal species at that camera site (Royle &

309   Dorazio, 2008). z_{ijk} is in turn drawn from a Bernoulli distribution with probability ψ, i.e., the

310   probability that the focal species occupies camera site j during sampling period i.

311

312   Occupancy probability and intensity of use were modeled as

313   $\quad logit(\Psi_{ijk}) = \alpha_{0jk} + \alpha_{1k}Presence_{ij} + \alpha_{2k}Footprint_j + \alpha_{3k}Presence_{ij}^2 + \alpha_{4k}Footprint_j^2$

314   $\qquad\qquad + \alpha_5 Hunt_j + \alpha_6 Forest\_1km_j + \alpha_7 NPP_j + \alpha_8 Season_i + \alpha_9 Latitude_j + \alpha_{10}$

315   $\qquad\qquad Longitude_j$

316

317   $\quad logit(p_{ijk}) = \beta_{0jk} + \beta_{1k}Presence_{ij} + \beta_{2k}Footprint_j + \beta_{3k}Presence_{ij}^2 + \beta_{4k}Footprint_j^2$

318   $\qquad\qquad + \beta_5 Hunt_j + \beta_6 Forest\_100m_j + \beta_7 Bait_j + \beta_8 Season_i$

319

320   We modeled occupancy as a function of percent forest cover in a 1-km radius around the camera

321   site to estimate the effect of local habitat type on the probability of site use, while detection

322   probability was modeled as a function of forest cover in the immediate vicinity of the camera

323   (100-m radius), as sight lines and thus the ability to detect species that are present may be

324   reduced in more heavily forested habitats relative to open areas. For both human presence and

325   human footprint, we fit linear and quadratic terms to test for potential non-linear effects of

326   increasing human disturbance on species responsiveness. Because all covariates were mean

327   centered for direct comparison (see below for details), linear terms are interpretable

328   independently of quadratic terms (Schielzeth, 2010). Different populations of a given mammal

329   species may not necessarily exhibit consistent responses to human disturbance. For both ψ and p,

330   we therefore allowed the intercept (α_0, β_0) and the coefficient estimates for human presence (α_1,

331   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

332   camera trapping project k. All project-level covariates were modeled as being drawn from a

333   common distribution, with hyperparameters μ and σ^2 describing the mean and variance across all

334   projects in the data set. For instance, α_{0k} was modeled as

335   $\alpha_{0k} \sim N(\mu_{\alpha0}, \sigma_{\alpha0}^2)$.

336   To account for the fact that many camera sites were sampled repeatedly across multiple sampling

337   periods, the intercepts were further modeled as camera site-level random effects, with camera

338   site j nested in project k, i.e.,

339    $\alpha_{0jk} \sim N(\alpha_{0k}, \sigma^2_{\alpha_k})$

340    $\beta_{0jk} \sim N(\beta_{0k}, \sigma^2_{\beta_k})$

341   where $\sigma^2_{\alpha_k}$ is an error term describing the variance between camera sites for a given project (and

342   likewise for $\sigma^2_{\beta_k}$).

343

344   Because a primary objective of this study was to model mammal responses to human disturbance

345   (estimated from occupancy model coefficients) as a function of species traits, it was essential

346   that model coefficients were comparable across species. We therefore fit identical occupancy

347   models to each species' data (using all model terms just described) rather than attempting to

348   identify the best model for each individual species through model comparison. All model

349   covariates were mean-centered, and continuous covariates were scaled by two standard

350   deviations. We centered and scaled disturbance covariates prior to subsetting the data for each

351   single-species model such that a given value of human presence/footprint received the same

352   standardized value in all models to ensure comparability across species. Pearson correlation

353   coefficients (r) between all pairs of model covariates were < 0.6, with the exception of latitude

354   and longitude (r = -0.62). For each focal species, occupancy models only included data from

355   projects that detected the species at least once.

356

357   To determine whether each human disturbance type had a net positive or negative effect on site

358   occupancy and intensity of use for a given species, we calculated the probability that each human

359   disturbance linear effect (i.e., α_1, α_2, β_1, and β_2 above) was more extreme (greater or less) than

360   zero using the Bayesian posterior distribution of the coefficient estimate (referred to as the

361   "posterior probability" of the disturbance effect). We quantified the number of species

362   exhibiting an effect of each disturbance type by counting the species for which the posterior

363   probability of a positive or negative effect was > 0.9. This value corresponds to 80% Bayesian

364   credible intervals around the disturbance coefficient that do not include zero and was chosen to

365   capture species with limited sample sizes and/or high variability between populations that

366   nonetheless exhibited a strong trend towards a positive or negative association with

367   anthropogenic influence.

368

369   *Modeling mammal responses to disturbance as a function of species traits*

370   A primary objective of this study was to examine how a species' traits affect its responsiveness

371   to human disturbance while explicitly accounting for variation between populations of the same

372   species. We therefore extracted project-level estimates for the (linear) effect of human presence

373   and human footprint on both occupancy and detection probability (i.e., α_{1k}, α_{2k}, β_{1k}, and β_{2k}

374   above) from each single-species occupancy model and modeled these values as a function of

375   species traits. We modeled each of the four disturbance-response combinations (i.e., presence

376   and footprint effects on ψ and p) separately.

377

378   For each focal species, we used the PanTHERIA database (Jones et al., 2009) to extract a suite of

379   species traits that may affect responsiveness to human disturbance. This included several traits

380   related to size and space use requirements, namely adult body mass, home range size, and

381   longevity (i.e., maximum lifespan). We also extracted traits related to species reproductive

382   strategy, including litter size, weaning age (i.e., the average age at which young become

383   independent of their mother for nutritional needs), and age at sexual maturity (Jones et al., 2009).

384   We used the EltonTraits database (Wilman et al., 2014) to extract data on the proportion of each

385   of 10 diet categories in the diet of each species and used these data to calculate two dietary

386   indices. Following Santini et al. (2019), we used the Shannon Index to estimate dietary diversity

387   for each species based on all 10 diet categories. We also calculated the proportion of the diet

388   consisting of vertebrate prey as an estimate of each species' degree of carnivory (EltonTraits diet

389   categories "vertebrate-endoderm", "vertebrate-ectoderm", "vertebrate-fish", and "vertebrate-

390   unknown"). The proportion of vertebrate prey and scavenging in the diet was used to classify

391   each species into three trophic guilds: herbivore (0%), omnivore (1-50%), and carnivore (>50%

392   vertebrate prey and scavenging). All species trait values are presented in Table S2. We

393   conducted a principal components analysis (PCA) on all trait and dietary data and extracted the

394   first two principal components (PC1 and PC2), which collectively accounted for 72.3% of the

395 variation in trait values between species. We then used PC1 and PC2 as covariates in modeling

396 species responses to human disturbance.

397

398 Our response variables in these models, i.e., the effects of presence or footprint on species

399 occupancy or detection, are themselves model estimates and are thus not perfectly observed. We

400 therefore determined the posterior variance around each project-level disturbance effect size, as

401 estimated by single-species occupancy models, and propagated this error through the multi-

402 species trait models. We treated the "true" disturbance effect on occupancy or detection, w_{is}, as

403 an unobserved latent variable for which we have an observed value, v_{is}, with an associated

404 "observation" error value, $\sigma^2_{o,is}$

405 $v_{is} \sim N(w_{is}, \sigma^2_{o,is})$

406 where i is a project-level disturbance effect size observation for species s. We then modeled the

407 true, unobserved disturbance effect, w_{is}, as a function of PC1, PC2 and their interaction using a

408 Gaussian linear model. We also included the geographic location of each project (project-level

409 mean latitude and longitude, Table S1) in all models to account for potential similarities between

410 projects in mammal responses stemming from geographic proximity. The linear models included

411 a random intercept for species to account for the fact that each species' response to disturbance

412 was estimated for several camera trapping projects. The species-level random effect was nested

413 within family to account for the influence of taxonomic relatedness in driving similar responses

414 between species. Other taxonomic levels were not included because there were either too few

415 categories (only two orders, *Artiodactyla* and *Carnivora*, were represented) or too few

416 observations per category (most genera were only represented by a single species) to estimate the

417 random effects, inhibiting model convergence.

418

419 *Model fitting and checking*

420 We analyzed all occupancy models (24, one for each focal species) and species trait models (4)

421 in a Bayesian framework using the Stan programming language called through the Rstan

422 package in R (Stan Development Team, 2020). For each model we ran three Hamiltonian Monte

423 Carlo (HMC) chains of either 2000 or 4000 iterations each (depending on ease of model

424 convergence) and retained 1,000 samples from the posterior distribution of each chain for

425 inference. Following Gelman et al. (2008) and Gabry et al. (2019), we chose vague or weakly

426 informative priors for all random variables and random starting values for each HMC chain. We

427 confirmed convergence of HMC chains by visual inspection of trace plots and via the Gelman-

428 Rubin statistic ("R-hat" values < 1.1 for all parameters) (Gelman, 2006), and verified the

429 reliability of model inference following the procedure outlined by Gabry et al. (2019). We tested

430 model fit using Bayesian p-values, which compare test statistics calculated from observed and

431 expected (i.e., model-generated) data (Hobbs & Hooten, 2015). P-values were calculated using

432 test statistics appropriate for the model distributions – for occupancy models we calculated

433 Freeman-Tukey (Conn et al., 2018) and chi-squared statistics (Royle & Dorazio, 2008), and for

434 the trait models we used the mean and coefficient of variation (Hobbs & Hooten, 2015). We

435 detected satisfactory to excellent fit between model and data for all occupancy models ($0.41 \leq p$

436 ≤ 0.92; all p-values shown in Table S5) and trait models ($0.35 \leq p \leq 0.81$; all p-values shown in

437 Table S4). All code for performing the analyses described here can be found at

438 https://github.com/jsuraci/Suraci-etal-MammalLifeHistory.

439

440 **Results**

441 Standardized occupancy model coefficients, summarizing the average response to disturbance

442 across all populations of a given species, revealed that 17% of the 24 mammal species in our

443 study (three herbivores and one carnivore) were negatively affected by human presence (i.e., the

444 posterior probability of a negative effect of human presence on occupancy and/or intensity of use

445 was > 0.9, see Methods). Elk (*Cervus elaphus*) exhibited reduced site occupancy with increasing

446 human presence, while moose (*Alces alces*), mountain goats (*Oreamnos americanus*) and

447 wolverines (*Gulo gulo*) exhibited reduced intensity of use (Fig. 2A and B). Thirty-three percent

448 of species were positively associated with human presence (two herbivores, two omnivores, four

449 carnivores). Bighorn sheep (*Ovis canadensis*), black bears (*Ursus americanus*), and wolverines

450 exhibited increased site occupancy with increasing human presence, while mule deer

451 (*Odocoileus hemionus*), bobcats (*Lynx rufus*), grey foxes (*Urocyon cinereoargenteus*), pumas

452 (*Puma concolor*), and wolves (*Canis lupus*) tended to increase intensity of use in areas of higher

453 human activity (Fig. 2A and B).

454

455 Human footprint had a negative effect on site occupancy and/or intensity of use for 25% of

456 mammal species (one herbivore, one omnivore, and four carnivores), and a positive effect for

457 38% of species (three herbivores, two omnivores, and four carnivores). Species negatively

458 associated with human footprint included grizzly bears (*Ursus arctos*), lynx (*Lynx canadensis*),

459 wolves, and wolverines, all of which were less likely to occupy sites with increasing footprint

460 and exhibited decreased intensity of use when present, while moose and martens (*Martes*

461 *americanus*) exhibited decreased intensity of use only. Raccoons (*Procyon lotor*) and white-

462 tailed deer (*O. virginianus*) were positively associated with human footprint in terms of both

463 occupancy and intensity of use, while elk, mule deer, striped skunks (*Mephitis mephitis*), red

464 foxes (*Vulpes vulpes*), bobcats, coyotes (*Canis latrans*), and pumas all tended to use occupied

465 sites more intensively at higher levels of human footprint (Fig. 2A and B).

466

467 For several species exhibiting positive responses to disturbance, intensity of use peaked at low to

468 intermediate values of human presence (six species, Fig. 3A) or footprint (eight species, Fig.

469 3B), indicative of thresholds in these species' capacity to tolerate disturbance or exploit human-

470 dominated landscapes. Red foxes were the single exception, being the only species to exhibit an

471 increasingly positive association with human presence at medium to high disturbance levels (Fig.

472 3A). Full results for all occupancy models are presented in Figure S2

473

474 The first two components of the PCA performed on species trait values (accounting for 72.3% of

475 trait variation) describe axes of increasing body size with decreasing life history speed (i.e.,

476 smaller litters, slower maturation; PC1), and increasing space use with greater carnivory (PC2;

477 Fig. 4A and Table S3). Bayesian regression models revealed that the effects of human footprint

478 on both site occupancy (Fig. 4B; β = -0.22 [95% CI = -0.48,0.01]) and intensity of use (Fig. 4C;

479 β = -0.23 [-0.57,0.04]) were increasingly negative at higher values of PC1 (posterior probability

480 of a negative slope = 0.97 and 0.95, respectively; Table S4), indicating that larger, longer-lived

481 mammal species and those with slower maturation and reproductive rates are less likely to occur

482 in modified landscapes and are less active when present. Human footprint also had an

483 increasingly negative effect on occupancy (but not intensity of use; Table S4) for species with

484 higher PC2 values (Fig. 4D; β = -0.40 [-0.76, -0.04]; probability of a negative slope = 0.99),

485 indicating that species with more carnivorous diets and larger home ranges are less likely to use a

486 given site as landscape modification increases. We did not detect a relationship between human

487 presence and species traits in their effects on site occupancy or intensity of use (Bayesian

488   regression; posterior probability of a negative slope ranged between 0.33 and 0.85 for all

489   relationships; Table S4).

490

491   **Discussion**

492   By bringing together data on activity and habitat use from mammal populations across North

493   America, our study provides a comprehensive understanding of mammal responses to human

494   disturbance. We found that species' ecological and life history traits were strong predictors of

495   their responses to human footprint on the landscape, confirming our hypothesis that larger, more

496   carnivorous, and slower reproducing species are more negatively affected by human landscape

497   modification. Contrary to our expectations, however, species traits were not strongly related to

498   their responses to human presence, highlighting the importance of considering these two forms

499   of human disturbance separately when estimating anthropogenic impacts on wildlife (Nickel et

500   al., 2020; Sévêque et al., 2020).

501

502   Our occupancy model estimates revealed relatively few overall "winners" and "losers", i.e.,

503   species that tended to respond positively or negatively across disturbance types. Instead, most

504   species exhibited differing, and frequently opposing, responses to human presence and footprint

505   (Fig. 2A and B). This pattern was previously reported for mammals in a single study area (Nickel

506   et al., 2020), and our results suggest this is a common feature of human-mammal interactions

507   across North America. Negative effects of human presence likely stem from fear of humans

508   causing mammals to suppress their activity levels (Suraci, Clinchy, et al., 2019) or avoid areas of

509   high human influence entirely (Oriol-Cotterill et al., 2015), while positive associations may

510   reflect the shield that human presence provides for some species against predators or competitors

511   (Berger, 2007; Hebblewhite et al., 2005; Muhly et al., 2011). Positive responses to human

512   presence by larger bodied species with substantial space requirements (e.g., pumas, wolves,

513   wolverines; Fig. 2B) may also reflect the growing intensity of recreation and ecotourism in

514   otherwise relatively undisturbed areas of wildlife habitat (Anton et al., 2020; Nickel et al., 2020),

515   leaving such species with little choice but to share space with people.

516

517   Despite the loss of natural habitat associated with increasing human footprint, agricultural lands

518   and developed areas nonetheless present opportunities for some species through resource

519   subsidies or relaxed predation/competition (Prugh & Sivy, 2020; Sévêque et al., 2020). Increased

520   human footprint is also associated with decreased movement and smaller home ranges for many

521   mammal species (Doherty et al., 2021; Tucker et al., 2018), including large predators such as

522   pumas (Nickel et al., 2021). Thus, higher intensity of use in more heavily modified habitats by

523   species that otherwise tend to avoid human footprint (e.g., pumas and bobcats, (Serieys et al.,

524   2021; Suraci et al., 2020)) may reflect restricted movement options and thus intensified use of

525   remaining habitat fragments in moderately developed areas.

526

527   Importantly, for several mammal species that exhibited positive associations with human

528   presence or footprint, the apparent benefits of human activity were diminished or reversed at

529   higher disturbance levels (Fig. 3). For instance, black bears, elk, and wolves were most active at

530   sites visited by approximately one person/group every 8-12 days (Fig. 3A), and several species

531   exhibited peak intensity of use in partially cleared habitats with low density development (i.e.,

532   intermediate HFI values, Fig. 3B). These results indicate that several mammal species exhibit

533   thresholds in their tolerance for human disturbance beyond which habitat may no longer be

534   viable. We suggest that such thresholds are critical to consider when attempting to promote

535   "landscapes of coexistence" (i.e., ecological conditions that allow the long-term persistence of

536   sensitive mammal species in human-dominated landscapes; (Gehr et al., 2017; Oriol-Cotterill et

537   al., 2015)) and functional connectivity between populations, particularly as several large

538   mammal species continue to recolonizing modified landscapes in North American and globally

539   (Gantchoff & Belant, 2017; Gilbert et al., 2016; Hemmingmoore et al., 2020; Rio-Maior et al.,

540   2019).

541

542   Larger mammal species and those with slower life histories were both less likely to occur in

543   areas of high human footprint and exhibited a lower intensity of use when present. The human

544   footprint is associated with a multitude of threats including vehicle strikes (Grilo et al., 2020),

545   sensory pollution (Dominoni et al., 2020), and invasive species (Shochat et al., 2010). Our results

546   suggest that smaller mammals and those with faster life histories are better able to avoid these

547   threats (Hill et al., 2020) or can offset heightened anthropogenic mortality through high

548   reproductive rates (Santini et al., 2019). Additionally, species with more carnivorous diets and

549   larger space requirements were less likely to occur in modified landscapes. Wide ranging

550   carnivores frequently come into conflict with humans over perceived threats to human life and

551   livelihood (Carter & Linnell, 2016; Chapron & López-Bao, 2016; Treves & Karanth, 2003), and

552   their large home range sizes may make them more susceptible to the impacts of habitat

553   fragmentation in modified landscapes (Crooks, 2002; Ripple et al., 2014). While our analyses

554   were focused on North American mammal communities, we suggest that the patterns observed

555   here are likely applicable to medium-to-large mammal species globally. Recent work focused on

556   urban environments has similarly shown that both high reproductive output (large litter size) and

557   high dietary diversity are frequently associated with mammal use of urban areas worldwide

558   (Santini et al., 2019), highlighting the importance of these traits in allowing mammals to

559   successfully exploit modified landscapes. Additionally, the exclusion of larger predatory

560   mammals from areas of high human footprint is a common phenomenon in systems around the

561   world (Ordiz et al., 2013; Oriol-Cotterill et al., 2015).

562

563   Our study provides a framework for predicting the filtering effect of human land use change on

564   mammal communities, helping to clarify the often ambiguous relationship between human

565   footprint and mammal community composition (Belote et al., 2020; Hill et al., 2020). Our results

566   indicate that as human footprint increases, mammal community composition will shift towards

567   smaller herbivorous and omnivorous species with faster reproductive strategies and smaller

568   space requirements. The speed and extent of shifts in community composition following land

569   conversion to agriculture or development will likely depend on local legal protections (e.g.,

570   hunting regulations; (Chapron & Treves, 2016)) and environmental conditions (e.g., ecosystem

571   productivity; (Belote et al., 2020)). Our analysis accounted for population-level variation in these

572   and additional factors, showing that, while the effects of hunting and environmental covariates

573   varied substantially between species (Fig. S2), trends towards reduced occurrence and activity of

574   large-bodied, slow-reproducing mammals in more developed areas were robust to variation in

575   local conditions.

576

577   Our estimates of human footprint (i.e., contemporary landscape modification) represent only a

578   snapshot in time and do not explicitly incorporate legacies of human land use (e.g., historical

579   management regimes; Jonason et al., 2014; Moreira & Russo, 2007) or other forms of ecological

580   disturbance such as fire (Geary et al., 2020; Pastro et al., 2014), both of which are known to play

581 important roles in shaping observed community structure by affecting vegetation composition
582 and species interactions. Our objective in the present study was to detect general patterns in
583 human disturbance impacts on mammals across a range of ecological conditions. However, we
584 note that understanding the interaction between current human land use and other drivers of
585 landscape pattern, both historical and contemporary, will be critical in accurately predicting
586 mammal community responses to future landscape modification in any particular location.
587
588 While species traits predicted responses to human footprint, they were not predictive of
589 responses to human presence, suggesting that the benefits and costs of using habitats frequently
590 visited by humans (e.g., recreationists in protected areas or urban green spaces) are distributed
591 somewhat randomly across body sizes, trophic guilds, and reproductive strategies. This finding
592 likely reflects the fact that many species are able to mitigate the impacts of human presence on
593 space use through increased nocturnality (Gaynor et al., 2018). Whereas landscape modification
594 is relatively constant in space and time, human presence is largely diurnal, meaning that even
595 species that are relatively sensitive to the immediate presence of people (e.g., many carnivores,
596 (Suraci, Clinchy, et al., 2019)) may be able to use human-dominated areas at night when people
597 are less active (Anton et al., 2020; Suraci, Frank, et al., 2019). Importantly, however, shifting
598 temporal activity to avoid humans may be costly by constraining temporal niche space and
599 forcing increased overlap with predators or competitors (Sévêque et al., 2020; Smith et al.,
600 2018).
601
602 The structure and diversity of mammal communities are key determinants of ecosystem
603 processes, with larger-bodied mammals affecting primary production and nutrient cycling
604 through herbivory and trophic interactions (Estes et al., 2011; Schmitz et al., 2018). Here we
605 show that the capacity of mammal species to coexist with humans in modified landscapes is
606 predictable from suites of species traits, highlighting the types of mammal communities that are
607 likely to persist with increased landscape conversion. Such communities will be composed of
608 smaller, faster breeding species with limited space requirements, which may play a more muted
609 role in driving ecosystem processes relative to larger, more mobile, and more carnivorous
610 species (Estes et al., 2011; Ripple et al., 2014; Tucker et al., 2018). Human presence has less
611 predictable spatial impacts on mammal communities but may nonetheless alter wildlife behavior

612   in ways that dampen trophic interactions and the links between ecosystems (Suraci, Clinchy, et

613   al., 2019; Tucker et al., 2018). Continued landscape modification and increased human use of

614   remaining natural areas portend greater reliance of mammal species on human-dominated

615   landscapes. Predicting which species are likely to thrive or perish under multiple sources of

616   anthropogenic pressure is critical to conserving mammal communities and the ecosystem

617   services they provide.

618

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623   **Author contributions:** JPS, CCW, MLA and KMG conceived of the study. All authors

624   contributed data to the analysis. JPS led the analysis and writing, with substantial feedback on

625   analysis from CCW, MLA, and KMG, and with valuable input on writing from all authors.

626   **Data and code availability:** The data that support the findings of this study are openly available

627   on figshare at https://doi.org/10.6084/m9.figshare.14444600.v1. All code necessary to replicate

628   the analyses is available on GitHub at https://github.com/jsuraci/Suraci-etal-

629   MammalLifeHistory.

630

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932

933   **Figure legends:**
934   **Figure 1.** Continental-scale assessment of mammal responses to human disturbance.
935   (**a**) Locations of 61 camera trap projects across North America are shown. Projects ranged from
936   undeveloped but heavily used protected areas (i.) through mosaics of developed and undeveloped
937   land (ii.) to urban centers (iii.). Within each project, camera sites spanned a gradient of both (**b**)
938   human presence and (**c**) human footprint. The color of each camera site (point) in **b** and **c**
939   represents human detections per day and the Human Footprint Index value, respectively, at that
940   location (both color gradients on the log scale). Mean ± SD disturbance levels are shown for the
941   three example projects.

942

943   **Figure 2.** Human presence and footprint have contrasting impacts within and among mammal
944   species. Occupancy model coefficient estimates for the effects of human presence (square) and
945   human footprint (diamond) on (**a**) site occupancy and (**b**) intensity of site use. Error bars are 95%
946   (thin) and 80% (thick) Bayesian credible intervals. Coefficient estimates are grouped by trophic
947   guild (based on percent of vertebrate prey and scavenging in the diet, see Table S2).

948

949 **Figure 3.** Non-linear effects of human disturbance. Occupancy model predictions for the change

950 in intensity of site use with increasing (**a**) human presence and (**b**) human footprint. Results are

951 shown for species for which models estimated a > 0.9 probability of a quadratic effect. Lines are

952 color coded by trophic guild, as defined in Figure 2.

953

954 **Figure 4.** Species traits predict responses to human footprint. (**a**) Biplot of the principal

955 components analysis performed on species trait data, with each mammal species plotted based on

956 its values of the first two principal components (PC1 – larger body size and slower life history

957 and PC2 – greater space use and more carnivorous). Factor loadings for each trait are shown in

958 grey (see also Table S3). Mammal responses to human footprint were increasingly negative with

959 increasing values of PC1 for both (**b**) site occupancy and (**c**) intensity of use. Occupancy

960 responses to footprint (**d**) were also negatively associated with PC2. Data points in **b-d** are

961 population-level estimates of each species' response to human footprint, where values above

962 zero (dashed line) indicate a positive response (i.e., increased occupancy or intensity of use with

963 increasing footprint) and those below zero a negative response. Solid lines and shaded areas are

964 the estimated slope and 95% Credible Intervals from hierarchical linear models (see also Table

965 S4). Data in all plots are color-coded by trophic guild, as defined in Figure 2.
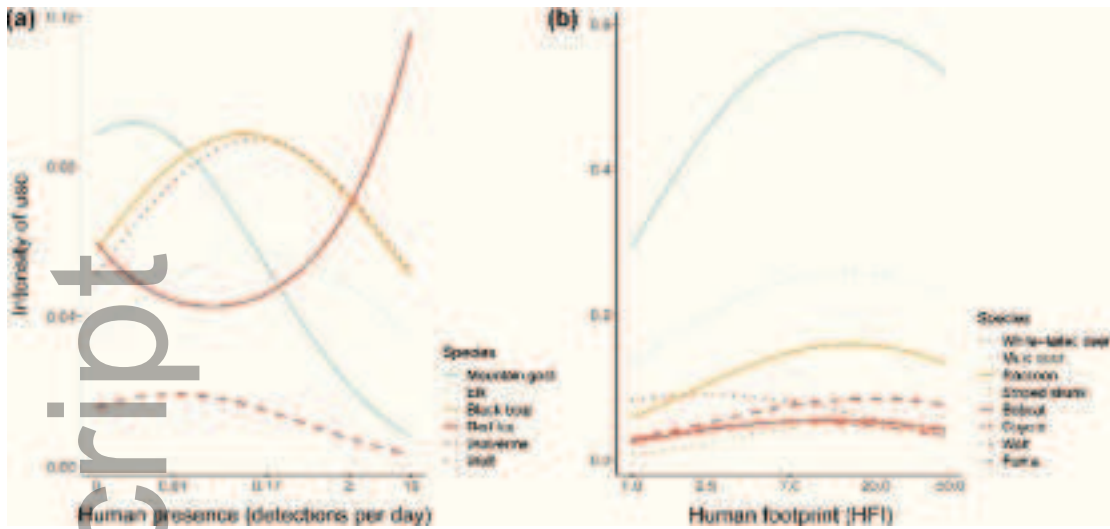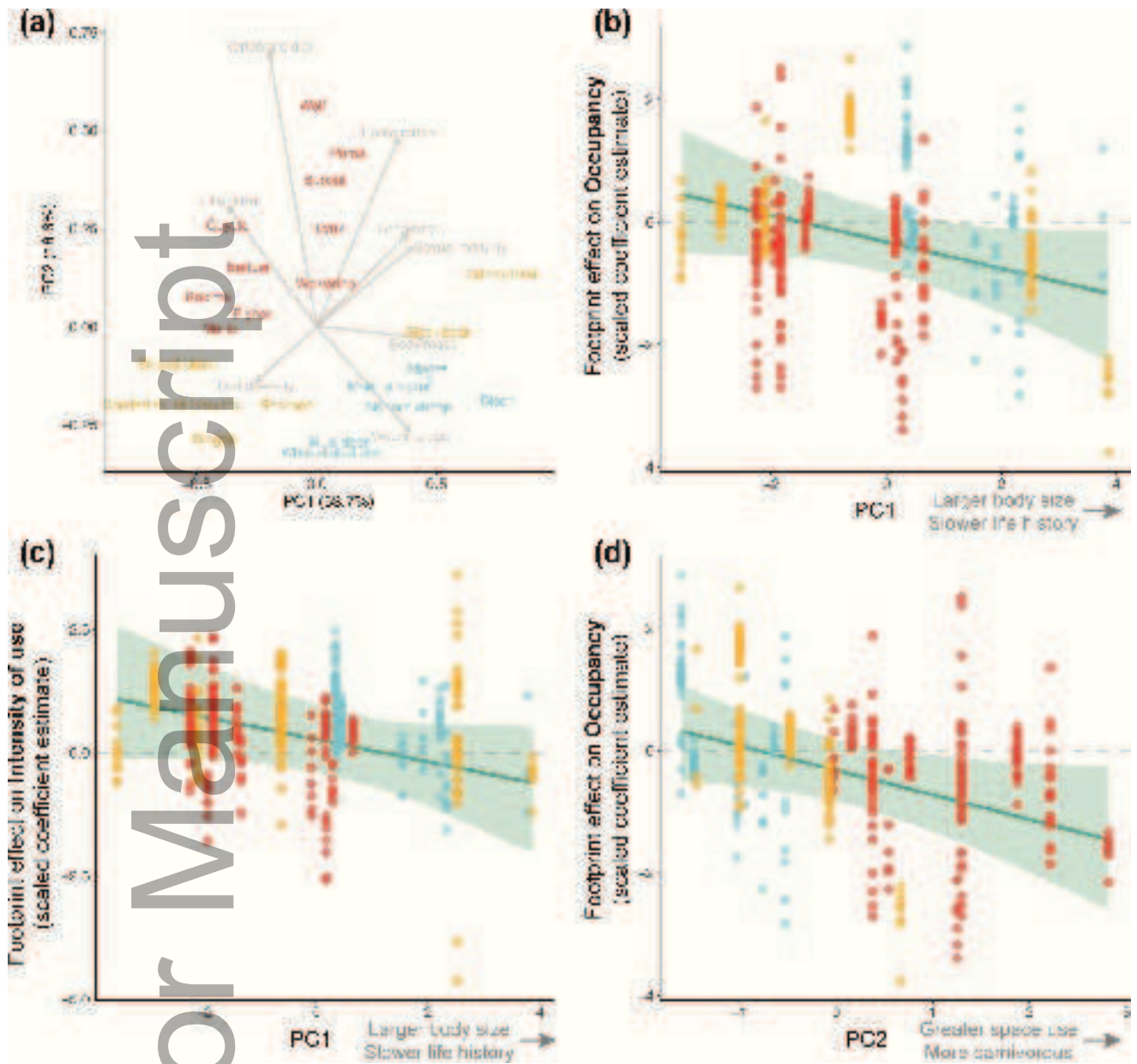
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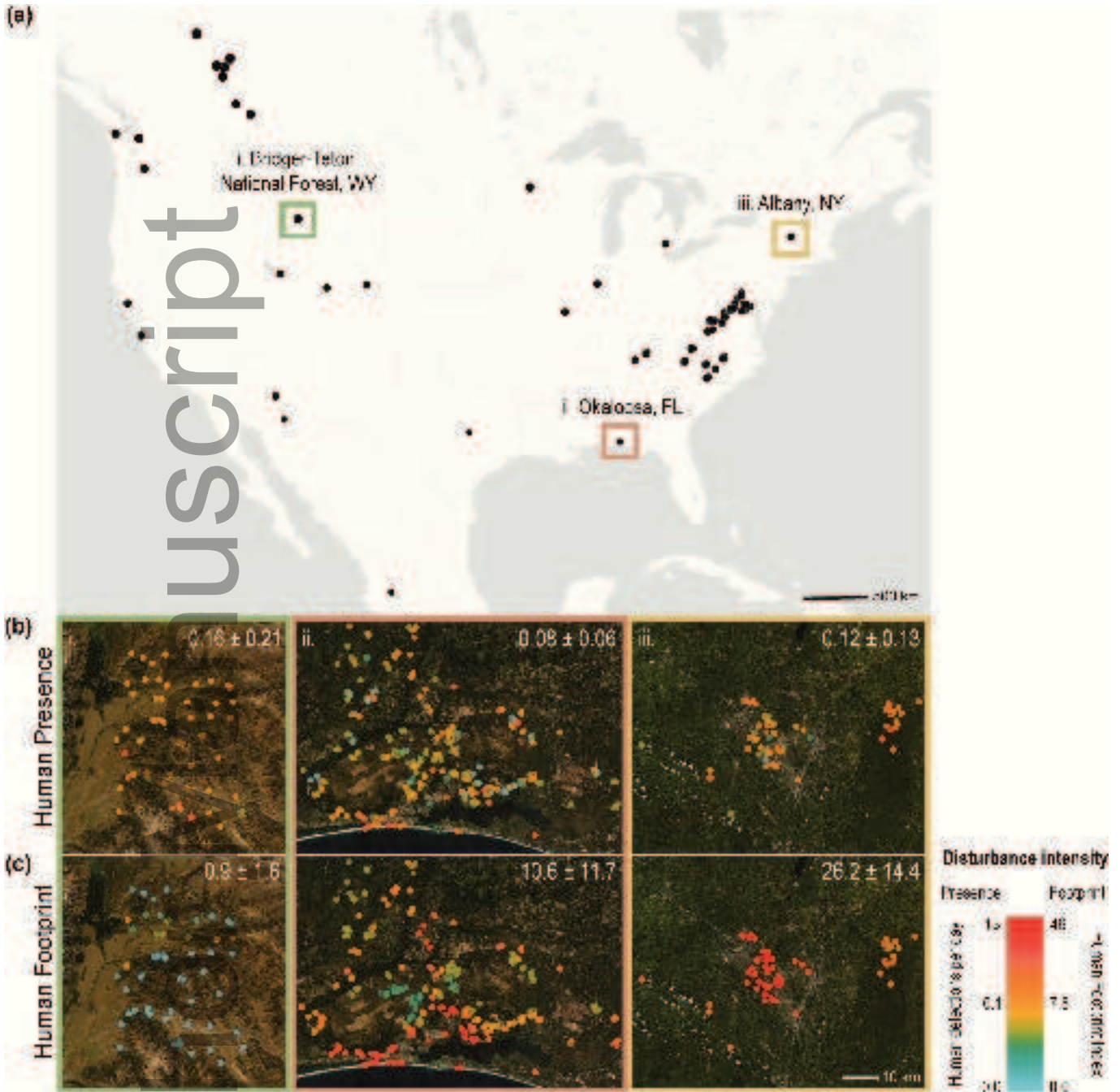
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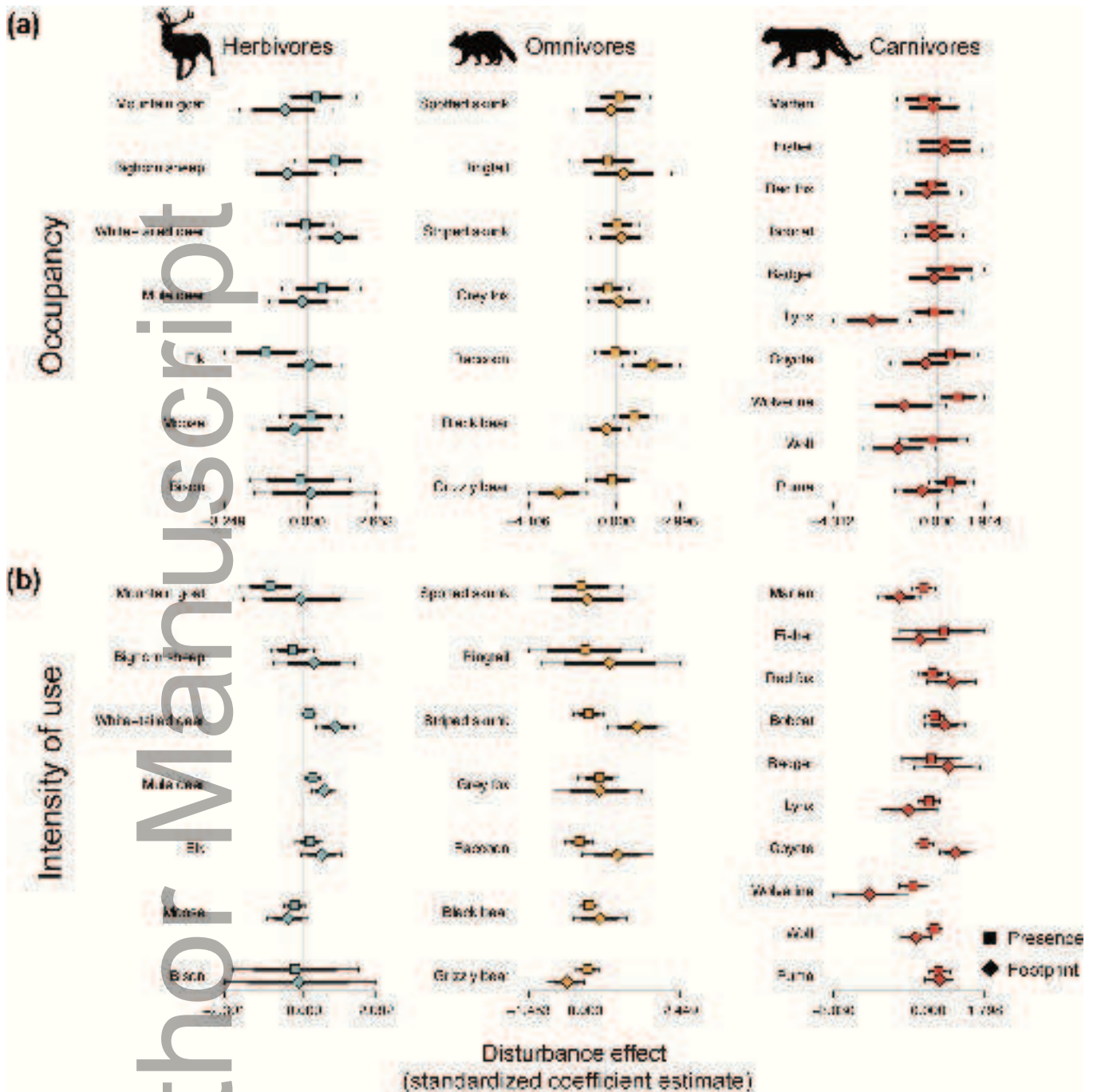
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