Urbanization alters sandy beach scavenging assemblages but not ecosystem function

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Open Research Statement: This manuscript uses novel data and code that are publicly accessible in GitHub at the following link, and will be permanently archived in a Zenodo repository upon publication acceptance: https://github.com/fgerraty/Urban_Scavengers

2. Abstract

Urbanization is rapidly transforming coastal landscapes around the world, altering the structure and function of marine, intertidal, and terrestrial ecosystems. In this study, we explore the impact of urbanization on the structure of vertebrate scavenging assemblages and the ecosystem functions they provide in sandy beach ecosystems across 40km of the central California coast, USA. We surveyed vertebrate scavenging assemblages using baited camera traps on 17 beaches spanning a gradient of coastal urbanization. We found that urbanization extent within small spatial scales (i.e., 1km or 3km radii of each site) and the rate of beach visitation by humans or domestic dogs were the best additive predictors of assemblage structure. We identified pronounced urbanization-associated shifts in the composition of vertebrate scavenger guilds but found that that these differences did not lead to subsequent changes in ecosystem functions performed by shoreline scavengers. Rates of carrion processing did not differ across the urbanization gradient, with synanthropic and non-native species compensating for the absence of the predominate native scavengers documented in rural areas. Our results underscore the pervasive and nuanced effects of urbanization on the dynamics of land-sea connectivity and demonstrate that urban ecosystems can sometimes sustain critical ecosystem functions in the face of landscape transformation. Recognizing the intricate interplay between urbanization and shoreline ecosystem dynamics, we suggest comprehensive consideration of cross-realm impacts in ongoing conservation and development efforts to ensure the sustainability and resilience of urban land- and seascapes.

3. Main Text

Introduction

Urbanization is one of the fastest and most transformative forms of landscape modification on the planet (Grimm et al., 2008, Angel et al., 2005). Coastal areas in particular are associated with large and growing urban centers, leading to pronounced changes in the structure and function of both terrestrial and adjacent marine ecosystems (Small & Nicholls 2003, Todd et al., 2019). Urbanization often generates complex environmental gradients, from highly developed urban areas to agricultural or undeveloped landscapes in nearby rural regions (McDonnell & Pickett 1990). These urbanization gradients provide unique experimental settings for exploring biotic responses to anthropogenic development and associated shifts in ecosystem function (Des Roches et al., 2021, Gilby et al., 2022).

Scavenging is a crucial yet frequently undervalued ecological process that impacts ecosystem structure, function, and stability (Wilson and Wolkovich 2011). Scavengers play pivotal roles in maintaining ecosystem health and function by consuming carrion, recycling and redistributing nutrients within and across ecosystem borders, regulating disease, and stabilizing food web dynamics (Moleón et al., 2014; Beasley et al., 2015). Scavenging is a particularly important ecological process in sandy beach ecosystems, which have little *in situ* primary production and therefore depend on spatial subsidies—often in the form of macroalgal wrack and marine animal carrion—as an organic matter resource base (Hyndes et al., 2022; Moleón et al., 2019). Sandy beaches are also attractive for adjacent urban development, such that understanding how urbanization influences sandy beach scavenging dynamics and carrion processing is central to effective coastal zone management, shoreline habitat conservation and restoration, and urban planning (Huijbers et al., 2013, Gilby et al., 2022).

Anthropogenic development has been associated with changes in sandy beach scavenging communities and depressed carrion processing rates in other parts of the world (Huijbers et al., 2013, Huijbers et al., 2015, Gilby et al., 2022). However, such investigations have been geographically limited to Australian coastlines and have all included sites with red foxes (*Vulpes vulpes)*, a widespread and abundant invasive scavenger that substantially changes the rate of beach-cast marine carrion processing (Brown et al., 2015, Kimber et al., 2020). Examining urbanization-driven changes to scavenging dynamics in other ecoregions is crucial to assess whether observed patterns and processes are consistent across diverse ecological contexts. Such inquiry can provide a more holistic perspective on how urbanization influences sandy beach ecosystems to better inform place-based management and development strategies.

In this study, we investigate the influence of urbanization and human disturbances (i.e., human visitation, domestic dog visitation, and agricultural cultivation) on the composition of vertebrate scavenging assemblages and rates of carrion processing at beaches along 40km of coastline in central California, USA. The California coast is a biodiversity hotspot with an extensive footprint of urbanized coastal landscapes, yet the consequences of urbanization for sandy beach vertebrate scavengers remains unknown in the region (Dobson et al., 1997, Myers 1990). We hypothesized that scavenging assemblages vary systematically across the urbanization gradient, with scavenging guilds in highly urbanized areas composed of synanthropic species such as gulls (*Larus spp.*), American crows (*Corvus brachyrhynchos*), and non-native rats (*Rattus spp.*). In lesser urbanized areas, we hypothesized that scavenging guilds are be composed of “urban avoider” species such as deer mice (*Peromyscus* spp.) in addition to species considered highly abundant in nearby coastal grassland ecosystems such as coyotes (*Canis latrans*) and ravens (*Corvus corax*) (Fischer et al., 2014, Ellington and Gehrt 2019, Kelly et al., 2002). Based on findings in other regions (e.g., Huijbers et al., 2013, Huijbers et al., 2015, Gilby et al., 2022), we hypothesized that rates of carrion processing are lower in urban than rural areas, with urban beaches having insufficient functional redundancy of the vertebrate scavenger guild to compensate for the absence of scavengers associated with rural beaches. By investigating the environmental drivers of sandy beach vertebrate scavenger assemblages and the ecosystem functions these scavengers confer, we intend to inform ongoing shoreline conservation and urban development initiatives along the California coast.

Methods

Vertebrate Scavenger Surveys

We used baited wildlife cameras to assess vertebrate scavenger assemblages on beaches across a diverse coastal landscape spanning 40km of shoreline in Santa Cruz County, central California, USA. Our study region contains dozens of sandy beaches and encompasses a prominent urbanization gradient, providing an excellent opportunity to test the influence of urbanization on carrion processing in sandy beach ecosystems (Fig. 1). We surveyed 17 sandy beaches managed by California State Parks and the University of California Younger Lagoon Reserve distributed across this urbanization gradient from February-May 2023. Within each beach, survey locations were established above the high tide line at the interface between sandy beach and foredunes, rocky cliffs, or concrete embankments bordering each beach.

To survey coastal vertebrate scavengers and measure carrion consumption rates, at each site we placed a motion-triggered camera trap (Browning Strike Force HD Pro X) baited with a single Pacific herring (*Clupea pallasii*) carcass weighing an average of 134g ± 30g (SE). Cameras were positioned 1-2m from the fish carrion and programmed to record 20 second HD videos when triggered, with a 30 second "quiet period" following video capture before another video could be triggered. We deployed baited cameras within two hours of sunset or sunrise and replaced bait three times at approximately 12-hour intervals (at sunrise or sunset), resulting in a 48-hour sampling window encompassing two "night" and two "day" surveys (Gilby et al., 2022). We conducted 2-3 of these 48-hour surveys at each site, resulting in 8 or 12 carcasses deployed at each site across the four-month study period. At any given time, we surveyed approximately the same number of high and low urbanization sites (>50% and <50% urbanization extent within 1km radius, respectively; see "Quantifying Land Cover" for further details) to prevent confounding with weather or season effects. All herring were weighed prior to each 12-hour deployment, and those that showed evidence of scavenging activity but were not removed by scavengers were also weighed following deployment. All baited camera trapping protocols were approved by University of California, Santa Cruz, Institutional Animal Care and Use Committee (#Raimp_2207_a1).

While processing the videos, individual scavengers were identified to species or genus (in the case of rodents) and were classified as scavenging when contact was made between the scavenger's mouth and the carcass. We determined the maximum number of individuals of each vertebrate species observed scavenging the carcass in a single video clip (MaxN)(Gilby et al., 2017, Bingham et al., 2018). To provide the most conservative relative abundance estimates, we pooled data across all carcasses deployed at each site and used the largest MaxN value for each scavenger species for site-level analyses of scavenging assemblages. While processing videos, we also flagged video clips when the first scavenger arrived at each carcass as well as videos in which carcasses were removed from the camera field of view (i.e. carcass removal). From these videos, we were able to determine the time from carcass deployment to the first scavenging event and to carcass removal—two of four metrics of carrion processing that were used as a proxy for ecosystem function. We also identified video clips documenting humans or domestic dogs visiting the carcass or in the video background, and the mean number of videos of humans and/or dogs per day of camera deployment were used to approximate the rate of beach visitation.

Quantifying Land Cover

We used the U.S. Geological Survey 2019 National Land Cover Database (NLCD) to quantify the spatial extent of urbanization (i.e., anthropogenic development) and agricultural land within three buffers of each study site. Buffer radii of 1km, 3km, and 5km were selected to reflect the approximate home ranges of our focal scavenger species and to identify the spatial scales at which urbanization and agriculture most strongly influence ecological responses (Riley et al., 2003, Linz et al., 1992, Neatherlin and Marzluff, 2004). We performed all land cover quantification and statistical analyses in R Statistical Software (v4.3.1, R Core Team 2023), and all data and code associated with manuscript is publicly available at https://github.com/fgerraty/Urban_Scavengers. To generate metrics of urbanization extent, we created an urbanized land class that included the following NLCD classes: developed open space, low-intensity development, medium-intensity development, and high-intensity development (Kreling et al., 2019). We used the *extract* function from the *raster* package to determine the percentage of land cover (excluding Open Water NLCD class) categorized as urbanized within the three buffer radii of each site (Hijmans 2023). We used the same procedure to develop and quantify the spatial extent of an agricultural land class (NLCD classes: pasture/hay, cultivated crops) within the same buffer radii. These categorical groupings allowed us to distinguish the relative influence of anthropogenic development, agricultural cultivation, and undeveloped lands in aggregate.

Scavenging Assemblage Analyses

We utilized two complimentary methods of multivariate community analysis to examine environmental drivers of scavenging assemblages at each beach: (1) permutational multivariate analysis of variance (PERMANOVA) and (2) multivariate generalized linear models (MvGLMs). Eight environmental predictors at each site were considered in assemblage analyses. These were urbanization extent at 1km, 3km, and 5km scales, agricultural extent at 1km, 3km, and 5km scales, and the mean daily count of video captures of humans and domestic dogs at each site. No scavengers were documented interacting with carcasses at one rural beach (Strawberry) despite observations of common ravens and coyote tracks at the beach during carcass deployments, so we removed this site from all subsequent analyses.

Using the *vegan* and *AICcPermanova* packages, we generated all possible models using our eight predictor variables and then filtered out models that have a high degree of collinearity among predictors (maximum VIF>5) (Oksanen et al., 2022, Corcoran 2023). This resulted in sixty-four combinations of non-collinear predictors (including a null model), which never included multiple scales of urbanization or agricultural cultivation due to high collinearity. We used the combinations of non-collinear predictors to fit sixty-four linear models to Bray-Curtis dissimilarity matrices calculated from scavenger species MaxN values using PERMANOVA (Table S4). We filtered the fitted models to include only those with delta AICc less than 2, resulting in seven top models (Table S2). We calculated the adjusted R-squared for each predictor using AIC and model averaging to further explore the best predictors of scavenging assemblages (Table S3). Using an information theoretic approach to perform model selection on a suite of non-collinear models allowed us to account for high levels collinearity among urbanization and agricultural measures without excluding potentially important predictor variables.

Because violations of mean-variance assumptions may confound dispersion and location effects when using ordination-based approaches, we supplemented PERMANOVA analyses with MvGLMs using the *manyglm* function in the *mvabund* package (Warton et al., 2012, Wang et al., 2022, Jupke and Schäfer, 2020). We fit MvGLM models with negative binomial distributions, log link functions, and an offset term of sampling effort (number of fish deployed per site) using the same modeling suite of predictor combinations from PERMANOVA analyses. This resulted in sixty-four MvGLM models total and, after filtering to only include those with delta AIC less than 2, four top models (Tables S5, S6). MvGLM also identifies species whose abundance and prevalence correlate significantly with the multivariate model; following Gilby et al., (2022), those species that significantly correlated with the best fit model were considered indicator species in this study. Results of the best-fit MvGLM were visualized using a non-metric multidimensional scaling ordination, with vectors representing significant predictor terms and indicator species. Relationships between urbanization and indicator species were visualized using univariate GLMs with the same distributions, link functions, and offsets as the multivariate models.

Carrion Processing Analyses

Both community-level multivariate analysis approaches identified urbanization at the 1km scale as one of the best single-term predictors of scavenging assemblages (see results), so we used the 1km scale to explore the impact of urbanization extent on four metrics of carrion processing for each carcass: (1) the probability of any vertebrate scavenging activity, (2) the probability of complete carcass removal, (3) the time from carcass deployment to the first vertebrate scavenging event and (4) the time from carcass deployment to complete carcass removal. Our four metrics of carrion processing rates were modelled using generalized linear mixed effects models. We used the *glmer* function in the *lme4* package for analyses with binomial distribution (1 and 2) and the *glmmTMB* function in the *glmmTMB* package for analyses with gamma distribution (3 and 4), and model assumptions were evaluated using the *DHARMa* package (Bates et al., 2015, Brooks et al., 2017, Hartig 2022). For each fish carcass deployed, the binary probabilities of (1) any vertebrate scavenging activity and (2) complete carcass removal were modelled using mixed-effects logistic regression (generalized linear mixed-effects models with binomial distribution and a logit link) with site as a random effect. The elapsed time (in hours) from carcass deployment to (3) the first scavenging event and (4) complete carcass removal were modelled using generalized linear mixed-effects models with gamma distributions and log links with site as a random effect.

Results

Across the 189 carcasses deployed at 17 sites, we recorded 1,231 scavenging events by 12 vertebrate scavenger species. No data were collected from 22 carcass deployments due to camera failure or human interference (i.e., carcass removal by humans). The most abundant scavenger species we documented were deer mice, common ravens, and American crows. We recorded the most unique scavenging events (969 events at 25 carcasses) by deer mice, which was largely due to the tendency of deer mice to return repeatedly to carcasses and scavenge carrion in place. Common ravens were recorded scavenging the most individual carcasses (42 carcasses) at the most sites (11 sites) and were also responsible for the most instances of carcass removal (40 carcasses) (Figure 3, Table S1). We documented several non-native scavenger species—rats, Virginia opossums (*Didelphis virginiana)*, domestic cats (*Felis catus*) and domestic dogs (*Canis lupus familiaris*)—and several native mammalian mesocarnivore: coyotes, gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*). While sample size of scavenging events by many of these species was limited, several species exhibited distinct temporal patterns of scavenging activity (Fig. 3, Fig. 6).

Urbanization substantially influenced the structure of vertebrate scavenging assemblages on sandy beaches, and beach visitation by humans and domestic dogs were significant additive predictors of assemblage structure. Urbanization extent was highly correlated at all scales, but both analytical approaches identified urbanization at smaller spatial scales (1km and 3km) as the best single-term predictors of scavenging assemblages (Tables S2, S3, S5). The best fitting PERMANOVA model identified urbanization at the 3km scale as the best predictor of scavenging assemblages ($p<0.001$), with next-best fitting models identifying urbanization at the

1km scale (PERMANOVA $p<0.001$, $\Delta AICc = 0.026$), and urbanization at the 5km scale (PERMANOVA $p<0.001$, $\Delta AICc = 0.531$) as the best predictors (Table S2). MvGLM modeling identified urbanization at the 1km scale as the best singular predictor of scavenging assemblages, with human visitation or domestic dog visitation as significant additive predictors (Table S5). The best fit MvGLM model included the additive effects of urbanization at the 1km scale (χ^2=43.99, p=.001) and the rate of beach visitation by humans (χ^2=25.32, p=.022). Testing for scavenger species with univariate GLMs that correlated significantly with the multivariate model revealed that the large differences in scavenging assemblages were best explained by variation in the distribution and abundance of two indicator species: American crows (*Corvus brachyrhynchos*) and deer mice (*Peromyscus spp.*) (Figs. 4, 5).

In contrast to urbanization-associated shifts in community structure, urbanization did not significantly alter any of the four measures of carrion processing rates (Fig. S2). While individual beaches had somewhat variable rates of carrion processing (i.e., proportion of carcasses with any scavenging ranged from 0.4-1; proportion of carcasses completely removed by scavengers ranged from 0.16-1), this variability was not correlated with urbanization extent; all generalized linear mixed effects models investigating carrion processing rates yielded non-significant urbanization effects (Fig. S2).

Discussion

Our findings show that urbanization can lead to pronounced changes in the composition of shoreline scavenger guilds, but that these differences in scavenging assemblages do not necessarily lead to subsequent changes in ecosystem functions performed by shoreline scavengers. Urban environments tended to support synanthropic and non-native scavengers such as American crows, rats, raccoons, and domestic cats and dogs, while scavenging guilds in rural areas were dominated by common ravens, deer mice, and coyotes. The retention of function across urbanization levels suggests that there is some level of functional redundancy in California's urbanized shorelines, with synanthropic and non-native species compensating for the loss of the predominate scavengers documented in rural areas. This functional redundancy underscores the adaptability of urban scavengers to diverse food sources such as beach-cast carrion, while also providing insight into the often-overlooked ecosystem services provided by scavengers in urban settings (Inger et al., 2016, Luna et al., 2021).

Both scavenging community analysis techniques yielded similar results, enhancing our confidence in the findings that urbanization at smaller spatial scales (1km and 3km) was more predictive of scavenging assemblages than larger scales (5km) and that human and domestic dog visitation rates were important additive predictors. This finding contrasts with that of Gilby et al., (2022), which found that urbanization extent at larger scales predicted shoreline scavenging assemblages better than urbanization extent at smaller scales along the Sunshine Coast, Australia. Our contrasting results likely reflect ecological differences between regions, such as variation in the home range size and urbanization response of predominate scavengers, and highlight the need for comparable investigations in additional locales. Our results suggest that restoring and conserving small (1-3km radius) patches of undeveloped habitats along urban shorelines may prove effective in sustaining scavenging assemblages that resemble those in less urbanized areas along the California coast.

If ecosystem function is the target of shoreline management efforts rather than the presence of the species themselves, then synanthropic species that occupy highly urbanized areas will be able to provide equivalent carrion processing ecosystem functions on sandy beaches in the absence of conservation or restoration efforts. While several studies have documented urbanization-associated reductions in scavenger species richness and carrion processing rates (Sebastián-González et al., 2019, Huijbers et al., 2013, Gilby et al., 2022), in some cases urbanization may produce spatial refugia (i.e., “human shield”) for generalist mesocarnivore scavengers and lead to an increased rate of carrion processing relative to adjacent rural areas (Moll et al., 2018, Patterson et al., 2023). Our findings signal that the consequences of urbanization for carrion processing can differ across ecosystem types and ecological contexts. While we found that synanthropic and non-native species associated with urban shorelines can provide carrion processing rates equivalent to those conferred by scavengers on rural beaches, it is doubtful that these differences do not lead to other ecological consequences such as altered pathways of marine-to-terrestrial nutrient redistribution. Incorporating additional measures of ecosystem function that reflect the impact of beach scavengers on nutrient cycling and terrestrial food webs could provide a more comprehensive understanding of the true ecological consequences of modified scavenging assemblages along urban coastlines.

While our primary objectives were to examine urbanization-associated shifts in scavenging community structure and ecosystem function, we noticed several temporal trends of shoreline vertebrate scavenging activity worthy of further investigation. While the sample size of scavenging events was low for most species, many species exhibited distinct diel patterns of scavenging activity (Fig. 3, Fig. 6, Fig. S3). Apart from domestic dogs, mammals were typically documented scavenging during nighttime hours and birds were most often documented during daytime and crepuscular hours (Fig. 3, Fig. S3). Among the three species with the most documented scavenging events—deer mice, common ravens, and American crows—deer mice were only documented during nighttime hours and exhibited a peak of carcass visitation between the hours 20:00-22:00, while common ravens and American crows were primarily documented during daytime hours with notable peaks in scavenging activity between 7:00-9:00 (Fig. 6). These peaks for avian scavengers likely reflect the first scavenging event after morning carcass deployment (mean deployment time = 8:03), suggesting that these species rapidly identify and scavenge shoreline carrion during early daytime hours. For deer mice, the peak in visitation in the early evening may indicate that the animals engage in opportunistic feeding until satiation, with scavenging activity tapering off throughout the nighttime hours. Deer mice were also recorded burying the herring carcasses in sand on several occasions, which may serve to hide the carrion from diurnal avian scavengers, act as a food cache for future deer mouse exploitation, and/or retain marine nutrients in sandy beach food webs. Lastly, exploring the interaction between urbanization and diel patterns of shoreline scavenging activity could elucidate the ecological consequences of shifts in urban animal behavior associated with human disturbances (Gallo et al., 2023). We suggest that future research should incorporate temporal processes into urban scavenging studies to provide additional complexity to our understanding of human-modified ecosystem dynamics.

With more than half of the world’s population now living in cities, contemporary urbanization is driving extreme and widespread landscape transformation while also presenting opportunities for sustainability (Grimm et al., 2008). Mitigating negative ecological consequences of urban development in coastal cities requires understanding the impacts of urbanization on landscapes and biodiversity, and how these modifications propagate to influence ecosystem functions in both marine and terrestrial realms (Threlfall et al., 2021). Given the consequential role of scavengers in human-wildlife interactions and public health initiatives, understanding anthropogenic impacts to scavenging dynamics remains a critical knowledge gap in urban ecological studies and an important trajectory of future research (Markandya et al., 2008, Ogada et al., 2012, Luna et al., 2021). Our findings—that urbanization alters vertebrate scavenging assemblages but not carrion processing rates—highlight the need for a nuanced approach to coastal urban conservation and management that identifies whether individual species or the ecosystem functions they perform are the target of ecological interventions. Incorporating such careful considerations of shoreline scavenging dynamics will be central to effective cross-ecosystem management and the planning of sustainable and resilient urban land- and seascapes.

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5. Conflict of Interest Statement

All authors declare that they have no conflicts of interests to disclose.

6. Ethics Statement

All methods were approved by the University of California, Santa Cruz, Institutional Animal Care and Use Committee (IACUC number Raimp_2207_a1). Access to and baited camera placement on beaches was approved by a CA State Parks district permit and direct approval by the UCSC Younger Lagoon natural reserve director.

7. References

Angel, S., Sheppard, S. C., and Civco, D. L. (2005). The dynamics of global urban expansion, Transport and Urban Development Department. Washington, DC: The World Bank. Available at: https://nyuscholars.nyu.edu/en/publications/the-dynamics-of-global-urban-expansion.

Bates D., Maechler M., Bolker B., Walker S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Beasley, J.C., Olson, Z.H., DeVault T.L. (2015). Ecological Role of Vertebrate Scavengers. https://doi.org/10.1201/b18819-9

Bingham, E. L., Gilby, B. L., Olds, A. D., Weston, M. A., Connolly, R. M., Henderson, C. J., Maslo, B., Peterson, C. F., Voss, C. M., & Schlacher, T. A. (2018). Functional plasticity in vertebrate scavenger assemblages in the presence of introduced competitors. *Oecologia*, *188*(2), 583–593. https://doi.org/10.1007/s00442-018-4217-0

Brooks M.E., Kristensen K., van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Maechler M., and Bolker B.M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400. https://doi.org/10.32614/RJ-2017-066.

Brown, M. B., Schlacher, T. A., Schoeman, D. S., Weston, M. A., Huijbers, C. M., Olds, A. D., & Connolly, R. M. (2015). Invasive carnivores alter ecological function and enhance complementarity in scavenger assemblages on ocean beaches. *Ecology*, *96*(10), 2715–2725. https://doi.org/10.1890/15-0027.1

Corcoran D. (2023). AICcPermanova: Model Selection of PERMANOVA Models Using AICc. R package version 0.0.2, https://CRAN.R-project.org/package=AICcPermanova.

Des Roches, S., Brans, K. I., Lambert, M. R., Rivkin, L. R., Savage, A. M., Schell, C. J., Correa, C., De Meester, L., Diamond, S. E., Grimm, N. B., Harris, N. C., Govaert, L., Hendry, A. P., Johnson, M. T. J., Munshi-South, J., Palkovacs, E. P., Szulkin, M., Urban, M. C., Verrelli, B. C., & Alberti, M. (2021). Socio-eco-evolutionary dynamics in cities. *Evolutionary Applications*, *14*(1), 248–267. https://doi.org/10.1111/eva.13065

Dobson, A. P., Rodriguez, J. P., Roberts, W. M., & Wilcove, D. S. (1997). Geographic Distribution of Endangered Species in the United States. *Science*, *275*(5299), 550–553. https://doi.org/10.1126/science.275.5299.550

Ellington, E. H., & Gehrt, S. D. (2019). Behavioral responses by an apex predator to urbanization. *Behavioral Ecology*, *30*(3), 821–829. https://doi.org/10.1093/beheco/arz019

Fischer, J. D., Schneider, S. C., Ahlers, A. A., & Miller, J. R. (2015). Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, *29*(4), 1246–1248. https://doi.org/10.1111/cobi.12451

Gallo, T., Fidino, M., Gerber, B., Ahlers, A. A., Angstmann, J. L., Amaya, M., Concilio, A. L., Drake, D., Gay, D., Lehrer, E. W., Murray, M. H., Ryan, T. J., St Clair, C. C., Salsbury, C. M., Sander, H. A., Stankowich, T., Williamson, J., Belaire, J. A., Simon, K., & Magle, S. B. (2022). Mammals adjust diel activity across gradients of urbanization. *eLife*, *11*, e74756. https://doi.org/10.7554/eLife.74756

Gilby, B. L., Olds, A. D., Yabsley, N. A., Connolly, R. M., Maxwell, P. S., & Schlacher, T. A. (2017). Enhancing the performance of marine reserves in estuaries: Just add water. *Biological Conservation*, *210*, 1–7. https://doi.org/10.1016/j.biocon.2017.03.027

Gilby, B. L., Henderson, C. J., Olds, A. D., Ballantyne, J. A., Cooper, T. K. A., & Schlacher, T. A. (2022). Cross-ecosystem effects of coastal urbanisation on vertebrate assemblages and ecological function. *Animal Conservation*, acv.12807. https://doi.org/10.1111/acv.12807

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global Change and the Ecology of Cities. *Science*, *319*(5864), 756–760. https://doi.org/10.1126/science.1150195

Hartig F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.6, <https://CRAN.R-project.org/package=DHARMa>.

Hijmans R. (2023). raster: Geographic Data Analysis and Modeling. R package version 3.6-23, <https://CRAN.R-project.org/package=raster>.

Huijbers, C. M., Schlacher, T. A., Schoeman, D. S., Olds, A. D., Weston, M. A., & Connolly, R. M. (2015). Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. *Diversity and Distributions*, *21*(1), 55–63. https://doi.org/10.1111/ddi.12282

Huijbers, C. M., Schlacher, T. A., Schoeman, D. S., Weston, M. A., & Connolly, R. M. (2013). Urbanisation alters processing of marine carrion on sandy beaches. *Landscape and Urban Planning*, *119*, 1–8. https://doi.org/10.1016/j.landurbplan.2013.06.004

Hyndes, G. A., Berdan, E. L., Duarte, C., Dugan, J. E., Emery, K. A., Hambäck, P. A., Henderson, C. J., Hubbard, D. M., Lastra, M., Mateo, M. A., Olds, A., & Schlacher, T. A. (2022). The role of inputs of marine wrack and carrion in sandy-beach ecosystems: A global review. *Biological Reviews*, brv.12886. https://doi.org/10.1111/brv.12886

Inger, R., Cox, D. T. C., Per, E., Norton, B. A., & Gaston, K. J. (2016). Ecological role of vertebrate scavengers in urban ecosystems in the UK. *Ecology and Evolution*, *6*(19), 7015–7023. https://doi.org/10.1002/ece3.2414

Jupke, J. F., & Schäfer, R. B. (2020). Should ecologists prefer model- over distance-based multivariate methods? *Ecology and Evolution*, *10*(5), 2417–2435. https://doi.org/10.1002/ece3.6059

Kelly, J. P., K. L. Etienne, and J. E. Roth. 2002. Abundance and distribution of the common raven and American crow in the San Francisco Bay Area, California. Western Birds 33:202–217.

Kimber, O., Gilby, B. L., Henderson, C. J., Olds, A. D., Connolly, R. M., Maslo, B., Weston, M. A., Rowden, A., Kelaher, B., & Schlacher, T. A. (2020). The fox and the beach: Coastal landscape topography and urbanisation predict the distribution of carnivores at the edge of the sea. *Global Ecology and Conservation*, *23*, e01071. https://doi.org/10.1016/j.gecco.2020.e01071

Kreling, S. E. S., Gaynor, K. M., & Coon, C. A. C. (2019). Roadkill distribution at the wildland-urban interface. *The Journal of Wildlife Management*, *83*(6), 1427–1436. https://doi.org/10.1002/jwmg.21692

Linz, G. M., Knittle, C. E., & Johnson, R. E. (1992). Home Range of Breeding Common Ravens in Coastal Southern California. *The Southwestern Naturalist*, *37*(2), 199. https://doi.org/10.2307/3671670

Luna, Á., Romero-Vidal, P., & Arrondo, E. (2021). Predation and Scavenging in the City: A Review of Spatio-Temporal Trends in Research. *Diversity*, *13*(2), 46. https://doi.org/10.3390/d13020046

Markandya, A., Taylor, T., Longo, A., Murty, M. N., Murty, S., & Dhavala, K. (2008). Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. *Ecological Economics*, *67*(2), 194–204. https://doi.org/10.1016/j.ecolecon.2008.04.020

McDonnell, M. J., & Pickett, S. T. A. (1990). Ecosystem Structure and Function along Urban-Rural Gradients: An Unexploited Opportunity for Ecology. *Ecology*, *71*(4), 1232–1237. https://doi.org/10.2307/1938259

Moleón, M., Sánchez-Zapata, J. A., Margalida, A., Carrete, M., Owen-Smith, N., & Donázar, J. A. (2014). Humans and Scavengers: The Evolution of Interactions and Ecosystem Services. *BioScience*, *64*(5), 394–403. https://doi.org/10.1093/biosci/biu034

Moleón, M., Selva, N., Quaggiotto, M. M., Bailey, D. M., Cortés-Avizanda, A., & DeVault, T. L. (2019). Carrion Availability in Space and Time. In P. P. Olea, P. Mateo-Tomás, & J. A. Sánchez-Zapata (Eds.), *Carrion Ecology and Management* (Vol. 2, pp. 23–44). Springer International Publishing. https://doi.org/10.1007/978-3-030-16501-7_2

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Robison, T., Millspaugh, J. J., & Montgomery, R. A. (2018). Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems*, *21*(4), 765–778. https://doi.org/10.1007/s11252-018-0758-6

Myers, N. (1990). The biodiversity challenge: Expanded hot-spots analysis. *The Environmentalist*, *10*(4), 243–256. https://doi.org/10.1007/BF02239720

Neatherlin, E. A., & Marzluff, J. M. (2004). Responses of American crow populations to campgrounds in remote native forest landscapes. *Journal of Wildlife Management*, *68*(3), 708–718. https://doi.org/10.2193/0022-541X(2004)068[0708:ROACPT]2.0.CO;2

Ogada, D. L., Torchin, M. E., Kinnaird, M. F., & Ezenwa, V. O. (2012). Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission: *Vulture Declines, Facultative Scavengers, and Disease Transmission*. *Conservation Biology*, *26*(3), 453–460. https://doi.org/10.1111/j.1523-1739.2012.01827.x

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). vegan: Community Ecology Package. R package version 2.6-4, https://CRAN.R-project.org/package=vegan.

Patterson, J. R., Szabo, N., & Beasley, J. C. (2023). Effects of urbanization on the efficiency and composition of vertebrate scavengers. *Food Webs*, *37*, e00317. https://doi.org/10.1016/j.fooweb.2023.e00317

R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Riley, S. P. D., Sauvajot, R. M., Fuller, T. K., York, E. C., Kamradt, D. A., Bromley, C., & Wayne, R. K. (2003). Effects of Urbanization and Habitat Fragmentation on Bobcats and Coyotes in Southern California. *Conservation Biology*, *17*(2), 566–576. https://doi.org/10.1046/j.1523-1739.2003.01458.x

Sebastián-González, E., Barbosa, J. M., Pérez-García, J. M., Morales-Reyes, Z., Botella, F., Olea, P. P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar, J. A., Cortés-Avizanda, A., Selva, N., Lambertucci, S. A., Bhattacharjee, A., Brewer, A., Anadón, J. D., Abernethy, E., Rhodes, O. E., … Sánchez-Zapata, J. A. (2019). Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. *Global Change Biology*, *25*(9), 3005–3017. https://doi.org/10.1111/gcb.14708

Small, C., & Nicholls, R. J. (2003). A Global Analysis of Human Settlement in Coastal Zones. *Journal of Coastal Research*, *19*(3), 584–599. http://www.jstor.org/stable/4299200

Todd, P. A., Heery, E. C., Loke, L. H. L., Thurstan, R. H., Kotze, D. J., & Swan, C. (2019). Towards an urban marine ecology: Characterizing the drivers, patterns and processes of marine ecosystems in coastal cities. *Oikos*, *128*(9), 1215–1242. https://doi.org/10.1111/oik.05946

Threlfall, C. G., Marzinelli, E. M., Ossola, A., Bugnot, A. B., Bishop, M. J., Lowe, E. C., Imberger, S. J., Myers, S., Steinberg, P. D., & Dafforn, K. A. (2021). Toward cross-realm management of coastal urban ecosystems. *Frontiers in Ecology and the Environment*, *19*(4), 225–233. https://doi.org/10.1002/fee.2323

Wang Y., Naumann U., Eddelbuettel D., Wilshire J., Warton D. (2022). mvabund: Statistical Methods for Analysing Multivariate Abundance Data_. R package version 4.2.1, https://CRAN.R-project.org/package=mvabund.

Warton, D. I., Wright, S. T., & Wang, Y. (2012). Distance-based multivariate analyses confound location and dispersion effects: *Mean-variance confounding in multivariate analysis*. *Methods in Ecology and Evolution*, *3*(1), 89–101. https://doi.org/10.1111/j.2041-210X.2011.00127.x

Wilson, E. E., & Wolkovich, E. M. (2011). Scavenging: How carnivores and carrion structure communities. *Trends in Ecology & Evolution*, *26*(3), 129–135. https://doi.org/10.1016/j.tree.2010.12.011

8. Figures

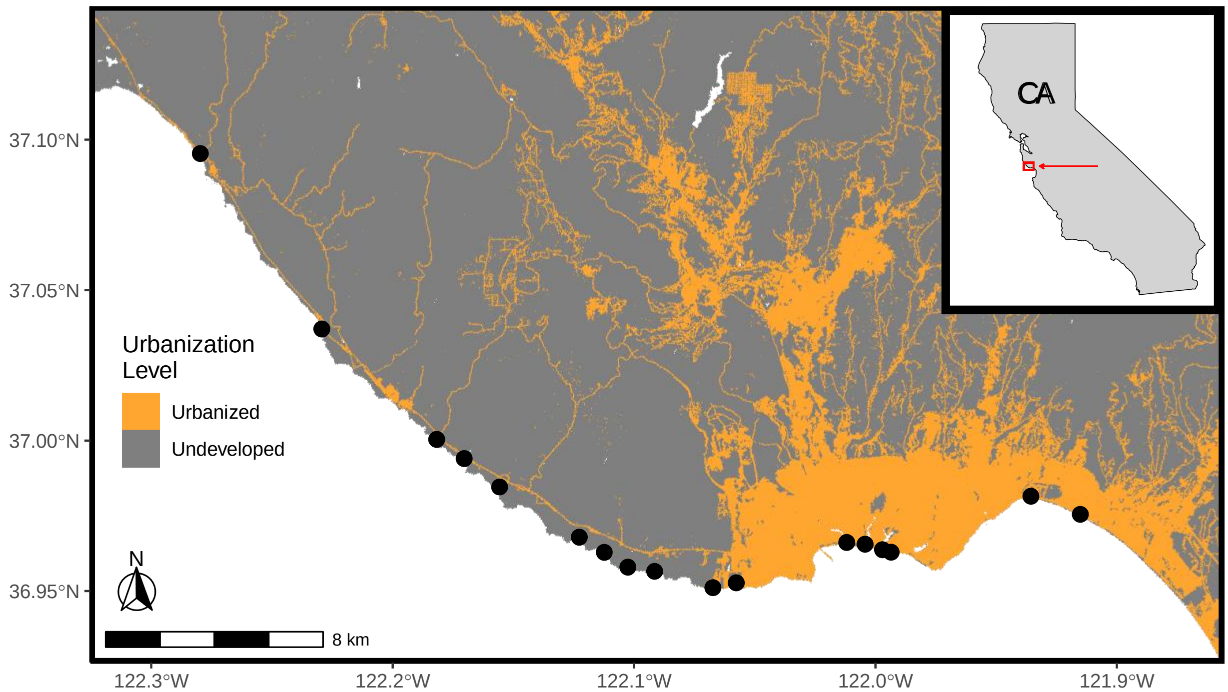

Figure 1. Map of urbanized areas and survey sites along the central coast of California (CA).

Figure 2. Examples of detected scavenger species: (A) coyote (*Canis latrans*), (B) gray fox (*Urocyon cinereoargenteus*), (C) common raven (*Corvus corax*), (D) striped skunk (Mephitis mephitis), (E) western gull (*Larus occidentalis*), (F) Virginia opossum (*Didelphis virginiana*)

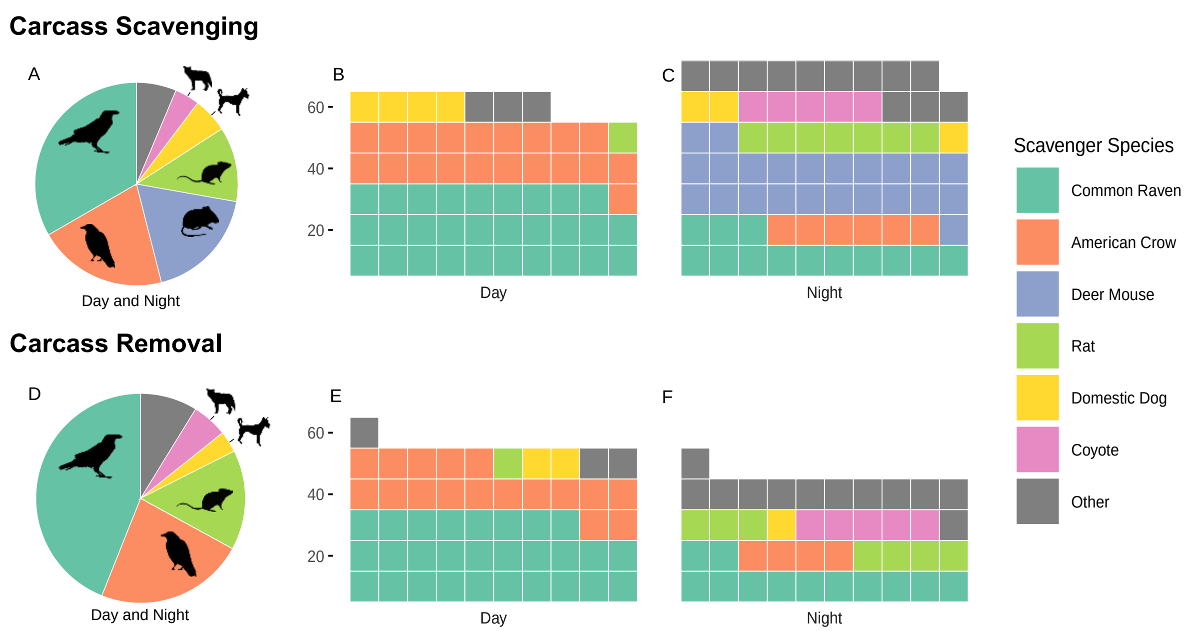

Figure 3. Partitioning of scavenging events among primary scavenger species for all scavenging events (A-C) and events of carcass removal (D-F). Panels show the proportion of scavenging and carcass removal events attributable to each species (A,D) and the actual number of carcasses scavenged and removed by each species during diurnal (B,E) and nocturnal (C,F) carrion deployments.

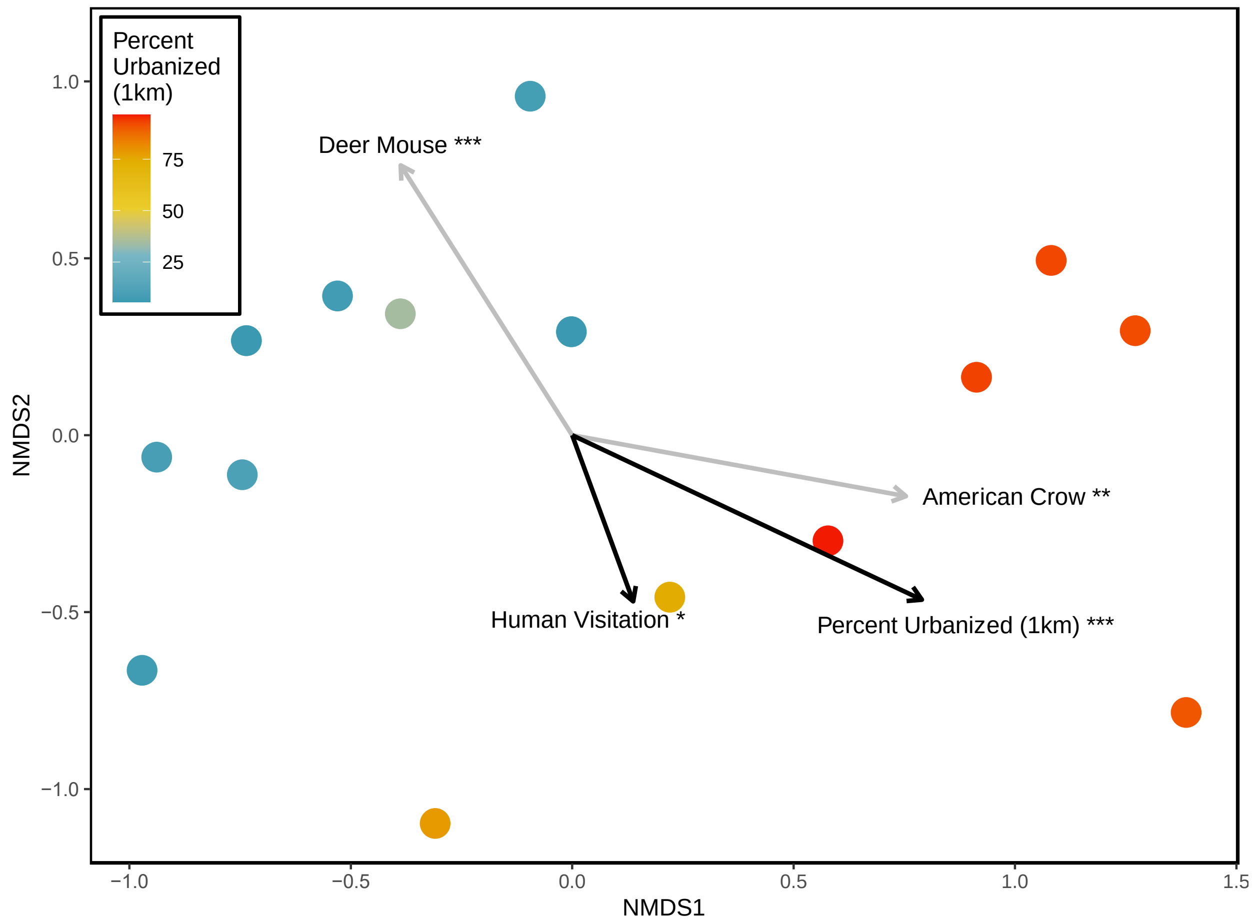

Figure 4. Non-metric multidimensional scaling (NMDS) plot illustrating scavenging assemblages at each site, as well as vectors representing predictor variables and indicator species from the best-fitting MvGLM model. The overall stress of the two-dimensional NMDS is 0.08.

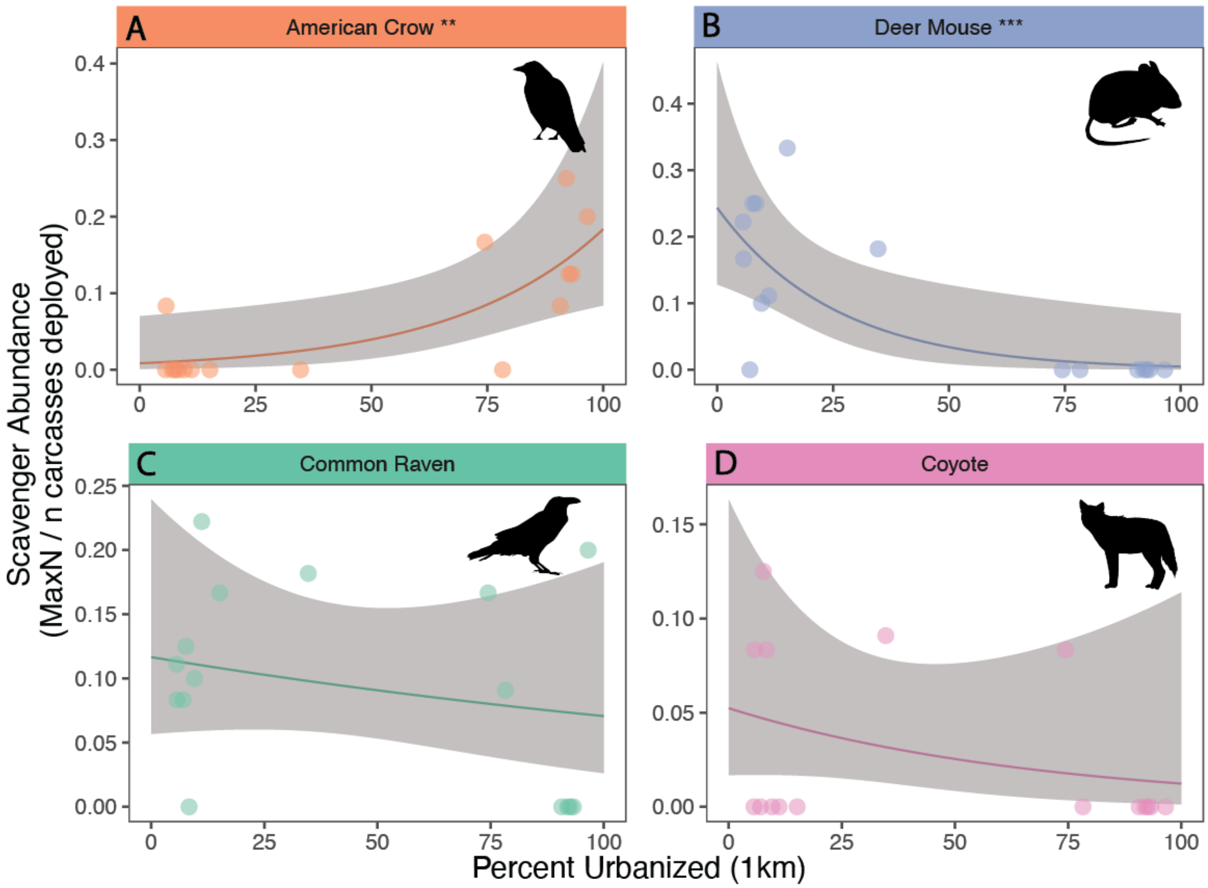

Figure 5. Generalized linear models illustrating relationships between urbanization extent and our two indicator species whose abundance and prevalence correlate significantly with the best fit MvGLM model—(A) American crows and (B) deer mice—as well as two widely-documented scavenger species whose abundance and prevalence are not significantly correlated with the multivariate model: (C) common ravens and (D) coyotes. Fitted GLMs have negative binomial distributions and log links and are offset by sampling effort (# carcasses deployed per site), with shaded regions representing ± SE.

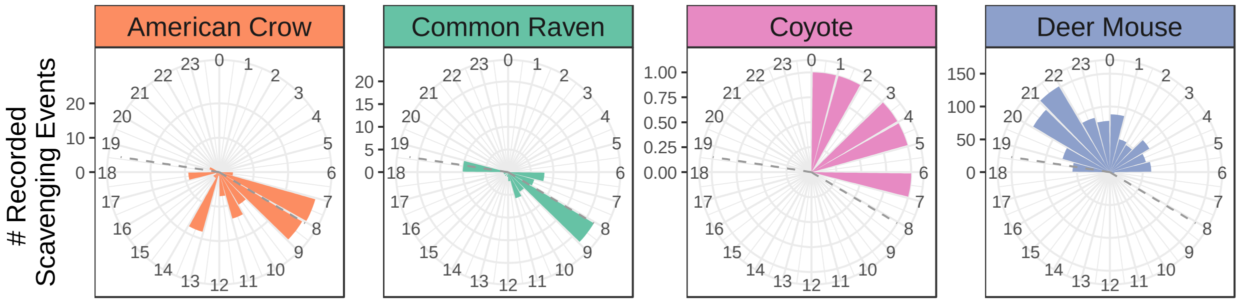

Figure 6. Temporal dynamics of scavenging by four widely documented vertebrate scavenging species. The length of each radiating bar representing the number of documented scavenging events between each hour marker throughout the 24-hour diel cycle. Dashed lines depict the average deployment time of morning and evening carcasses throughout our study.

9. Supplemental Information

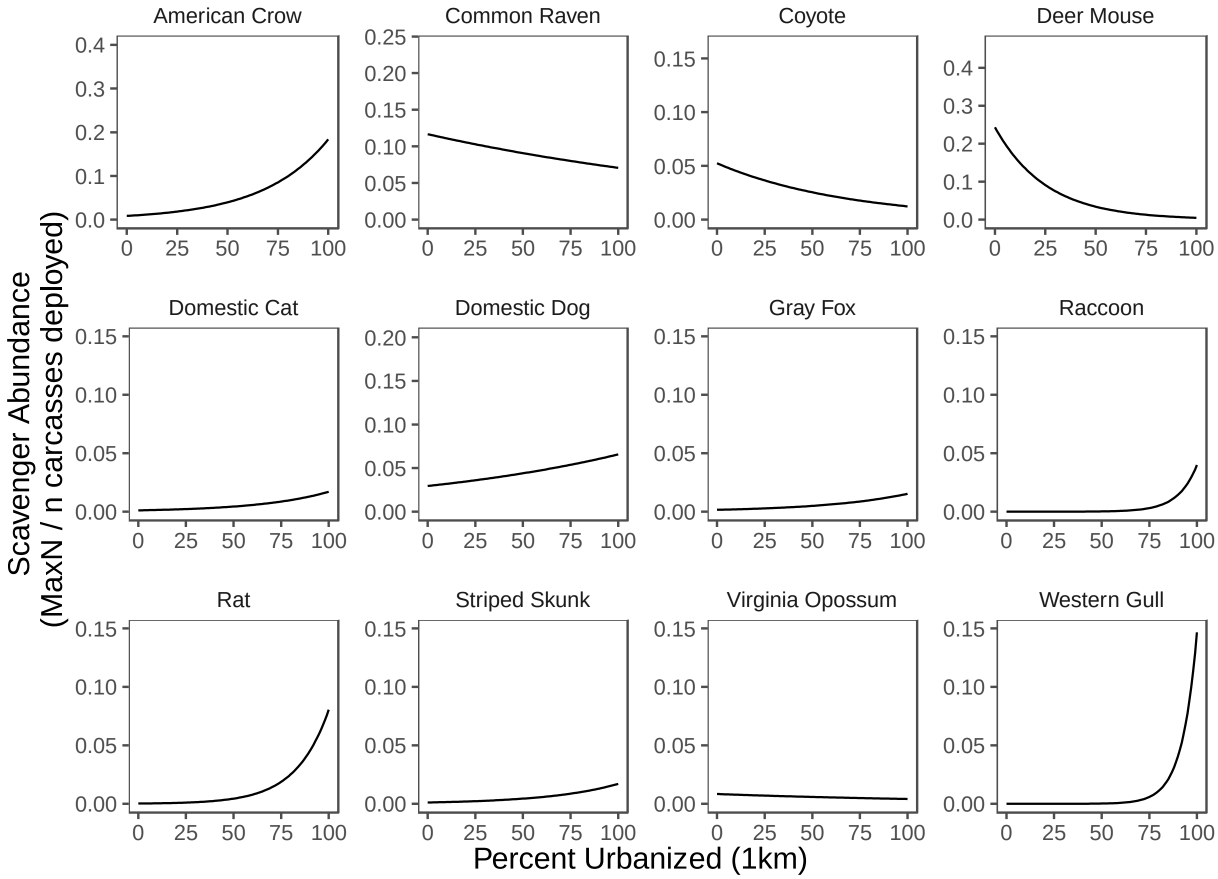

Figure S1. Single-species univariate models illustrating relationships between urbanization extent and abundance all scavenger species documented in this study. All fitted univariate models have negative binomial distributions and log links and are offset by sampling effort (# carcasses deployed per site), with shaded regions representing ± SE.

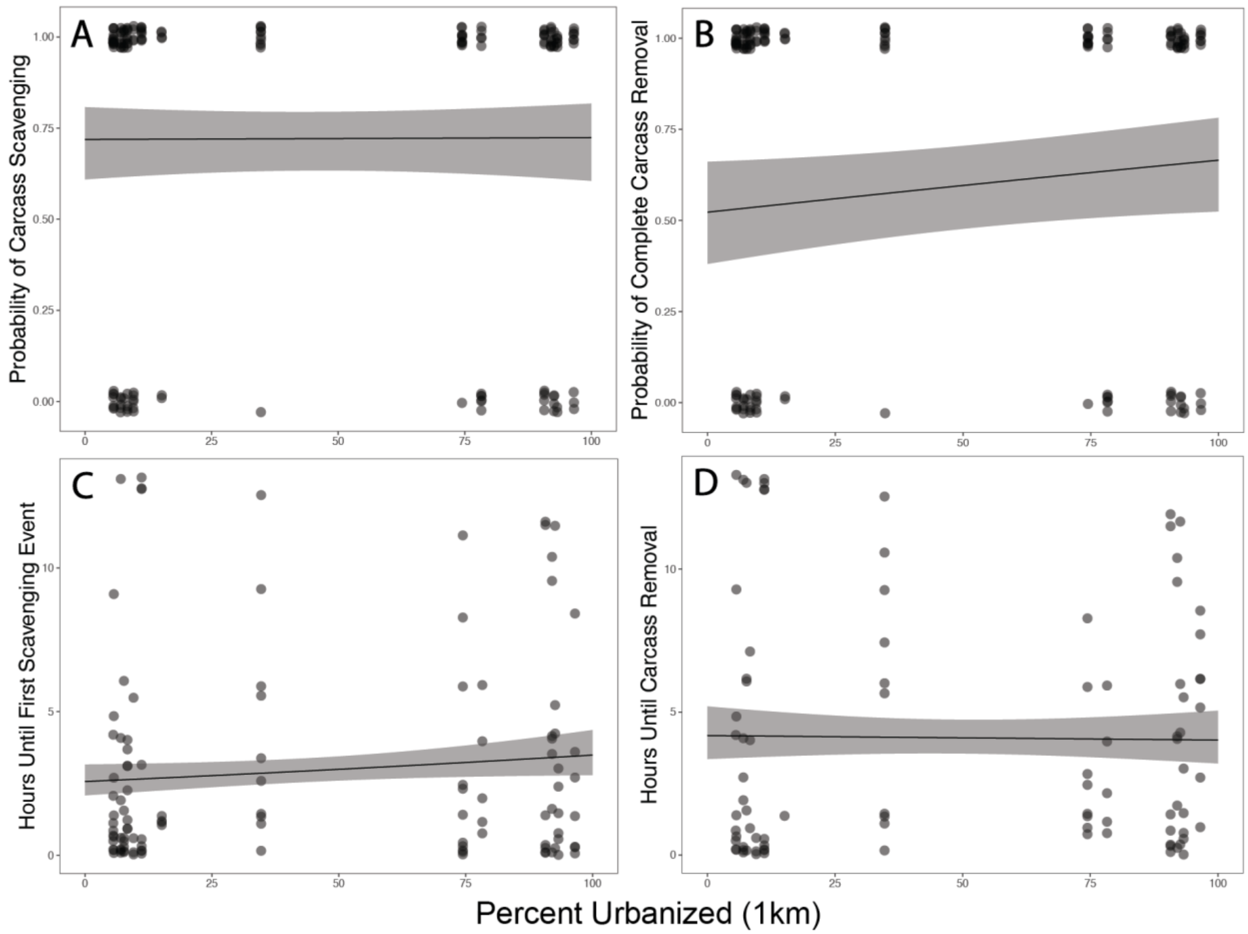

Figure S2. Generalized linear mixed-effects models, with site as a random effect, illustrating the relationship between urbanization extent and four metrics of carrion processing: (A) the probability of a carcass being scavenged, (B) the probability of a carcass being removed by scavengers, (C) the time until the first scavenging event on a carcass, and (D) the time until carcass removal by scavengers. Fitted GLMMs have (A,B) binomial distribution and logit links or (C,D) gamma distribution and log links, with shaded regions representing ± SE. We applied a vertical jitter to points in panels A and B to increase readability.

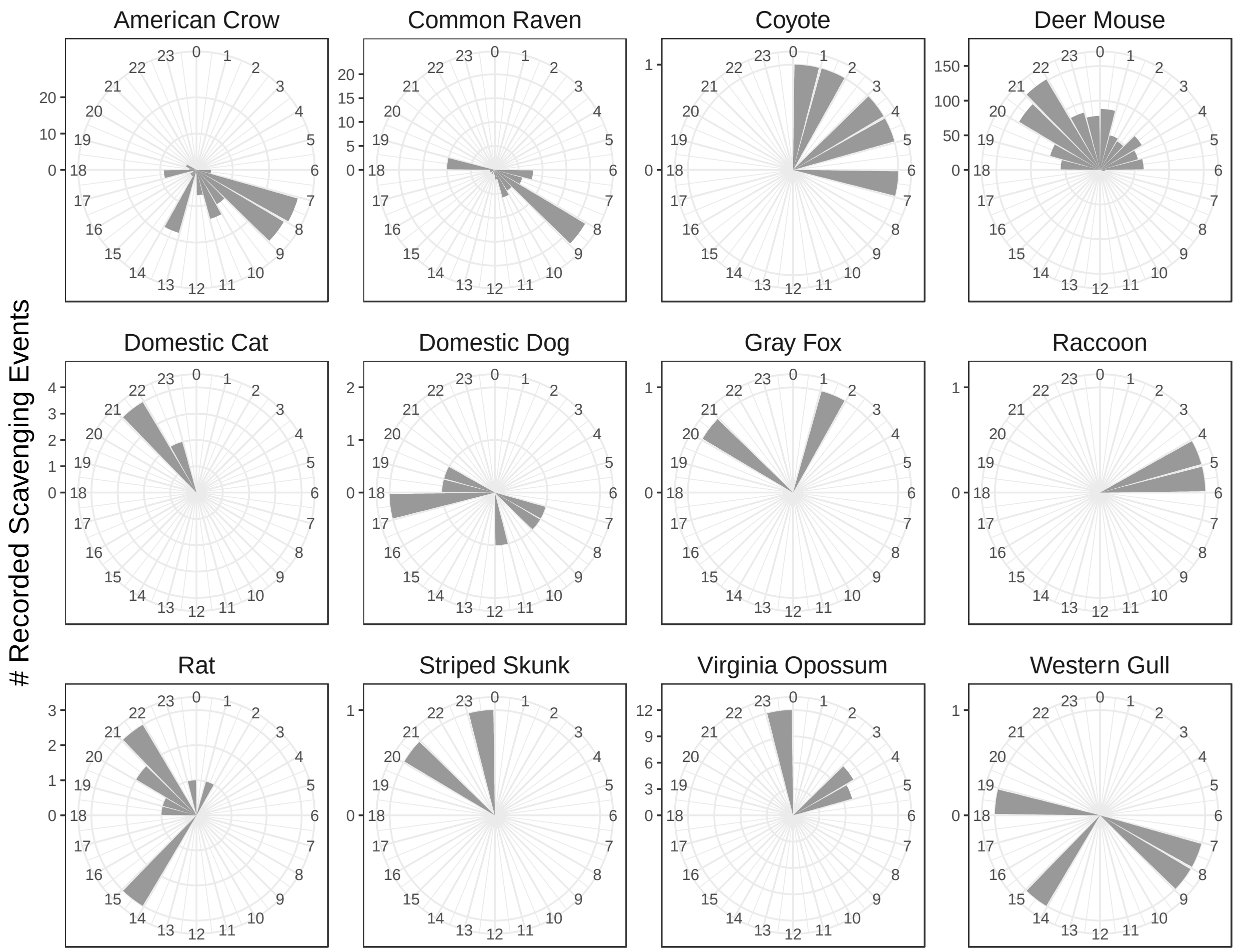

Figure S3. Temporal dynamics of scavenging by all vertebrate scavenging species documented in this study. The length of each radiating bar representing the number of documented scavenging events between each hour marker throughout the 24-hour diel cycle. Dashed lines depict the average deployment time of morning and evening carcasses throughout our study.

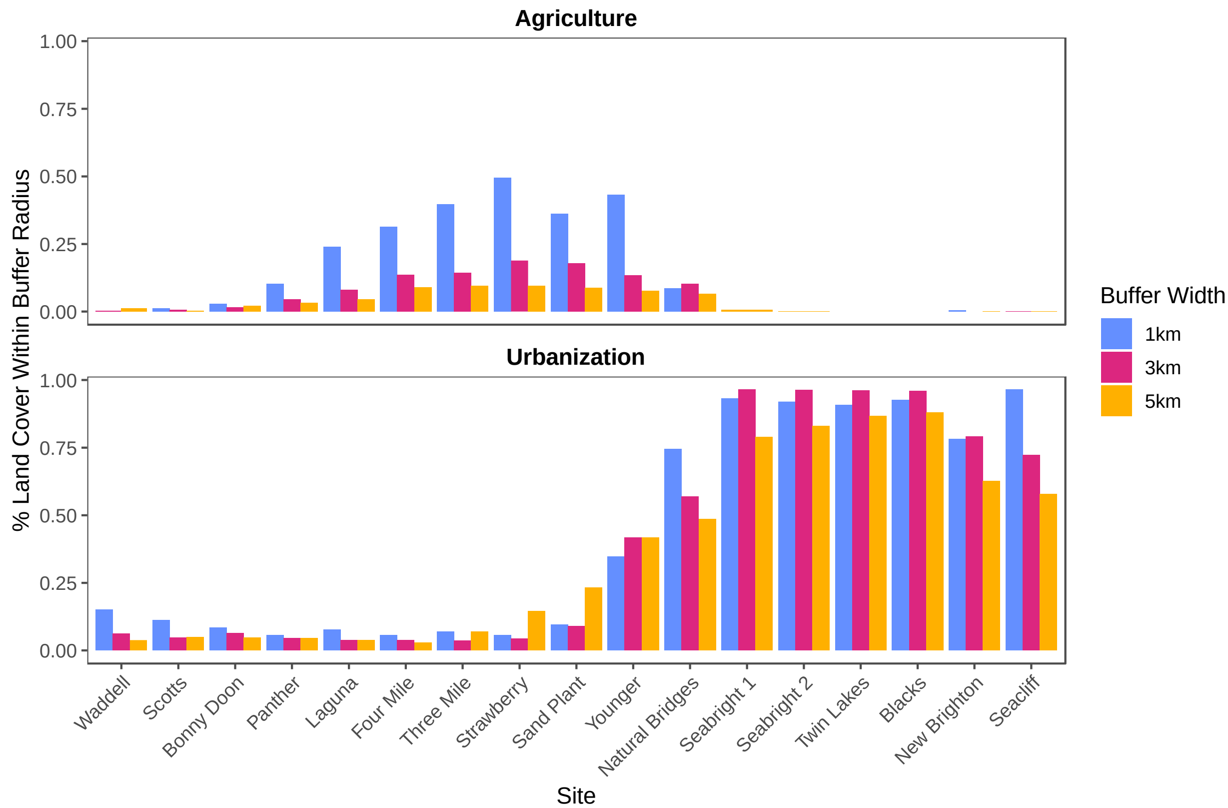

Figure S4. Values of agricultural extent and urbanization extent at 1km, 3km, 5km scales for each study site.

Table S1. Vertebrate scavenger species documented in this study, whether they are considered non-native in the region, and several metrics of scavenger abundance.

Common Name	Scientific Name	Considered Invasive in Region?	# Documented Scavenging Events	# Unique Carcasses Scavenged	# Sites Recorded	Sum of MaxN for All Sites
American Crow	*Corvus brachyrhynchos*		131	27	7	10
Common Raven	*Corvus corax*		63	43	11	15
Coyote	*Canis latrans*		5	5	5	5
Deer Mouse	*Peromyscus spp.*		969	25	8	15
Domestic Cat	*Felis catus*	Yes	6	1	1	1
Domestic Dog	*Canis lupus familiaris*	Yes	7	7	6	7
Gray Fox	*Urocyon cinereoargenteus*		2	2	1	1
Rat	*Rattus spp.*	Yes	12	8	3	3
Raccoon	*Procyon lotor*		2	2	1	1
Striped Skunk	*Mephitis mephitis*		2	2	1	1
Virginia Opossum	*Didelphis virginiana*	Yes	27	4	1	1
Western Gull	*Larus occidentalis*		4	4	2	3

Table S2. Table of top PERMANOVA models (ΔAICc < 2).

PERMANOVA Top Models Summary (ΔAICc <2)			
Model terms	**AICc**	**ΔAICc**	**AIC Weight**
Urbanization Extent 3km	-26.86358	0.00000000	0.22897755
Urbanization Extent 1km	-26.83722	0.02636014	0.22597941
Urbanization Extent 5km	-26.33244	0.53114315	0.17557256
Urbanization Extent 3km + Domestic Dog Visitation	-25.15868	1.70490332	0.09762878
Urbanization Extent 1km + Domestic Dog Visitation	-25.09082	1.77276216	0.09437186
Urbanization Extent 1km + Human Visitation	-25.02332	1.84026233	0.09123995
Urbanization Extent 3km + Human Visitation	-24.91036	1.95321404	0.08622990

Table S3. Table of top PERMANOVA predictors after model averaging.

PERMANOVA Top Predictors Summary

Predictor	Aikake Adjusted Rsq	Number of Top Models
Urbanization Extent 3km	0.173593196	3
Urbanization Extent 1km	0.173047067	3
Domestic Dog Visitation	0.008550503	2
Human Visitation	0.007023153	2
Urbanization Extent 5km	0.075871554	1

Table S4. Table of all fitted PERMANOVA models.

All Fitted PERMANOVA Models

Model terms	AICc	ΔAICc	AIC Weight
Urbanization Extent 3km	-26.86358	0.00000000	0.1035336551
Urbanization Extent 1km	-26.83722	0.02636014	0.1021780277
Urbanization Extent 5km	-26.33244	0.53114315	0.0793862480
Urbanization Extent 3km + Domestic Dog Visitation	-25.15868	1.70490332	0.0441434725
Urbanization Extent 1km + Domestic Dog Visitation	-25.09082	1.77276216	0.0426708344
Urbanization Extent 1km + Human Visitation	-25.02332	1.84026233	0.0412547215
Urbanization Extent 3km + Human Visitation	-24.91036	1.95321404	0.0389893959
Urbanization Extent 1km + Agricultural Extent 3km	-24.60041	2.26316538	0.0333919229
Urbanization Extent 5km + Domestic Dog Visitation	-24.54521	2.31836952	0.0324828406
Urbanization Extent 1km + Agricultural Extent 5km	-24.52484	2.33873653	0.0321537300
Urbanization Extent 3km + Agricultural Extent 3km	-24.41956	2.44402234	0.0305048461
Urbanization Extent 3km + Agricultural Extent 5km	-24.34001	2.52356891	0.0293153795
Urbanization Extent 5km + Human Visitation	-24.31543	2.54815191	0.0289572550
Urbanization Extent 1km + Agricultural Extent 1km	-24.18180	2.68177695	0.0270857634
Urbanization Extent 3km + Agricultural Extent 1km	-24.09265	2.77092943	0.0259048967
Urbanization Extent 5km + Agricultural Extent 3km	-24.07902	2.78455434	0.0257290206
Urbanization Extent 5km + Agricultural Extent 1km	-23.86426	2.99931827	0.0231093568
Urbanization Extent 5km + Agricultural Extent 5km	-23.85969	3.00388815	0.0230566137
Urbanization Extent 1km + Human Visitation + Domestic Dog Visitation	-23.03463	3.82894448	0.0152628915
Urbanization Extent 3km + Human Visitation + Domestic Dog Visitation	-22.98090	3.88267380	0.0148583178
Urbanization Extent 1km + Agricultural Extent 3km + Domestic Dog Visitation	-22.37583	4.48775348	0.0109793912
Urbanization Extent 5km + Human Visitation +	-22.30807	4.55550598	0.0106136800

All Fitted PERMANOVA Models

Model terms	AICc	ΔAICc	AIC Weight
Domestic Dog Visitation			
Urbanization Extent 3km + Agricultural Extent 3km + Domestic Dog Visitation	-22.27730	4.58628134	0.0104516103
Urbanization Extent 1km + Agricultural Extent 5km + Domestic Dog Visitation	-22.25013	4.61344940	0.0103105952
Urbanization Extent 3km + Agricultural Extent 5km + Domestic Dog Visitation	-22.13709	4.72649067	0.0097439969
Urbanization Extent 5km + Agricultural Extent 3km + Domestic Dog Visitation	-21.94495	4.91862709	0.0088514668
Urbanization Extent 1km + Agricultural Extent 1km + Domestic Dog Visitation	-21.93704	4.92654315	0.0088165017
Urbanization Extent 3km + Agricultural Extent 1km + Domestic Dog Visitation	-21.92708	4.93650022	0.0087727175
Urbanization Extent 1km + Agricultural Extent 1km + Human Visitation	-21.73190	5.13168215	0.0079570287
Urbanization Extent 1km + Agricultural Extent 3km + Human Visitation	-21.71537	5.14820540	0.0078915615
Urbanization Extent 5km + Agricultural Extent 1km + Domestic Dog Visitation	-21.71198	5.15160224	0.0078781697
Urbanization Extent 1km + Agricultural Extent 5km + Human Visitation	-21.71170	5.15188246	0.0078770660
Urbanization Extent 3km + Agricultural Extent 1km + Human Visitation	-21.66857	5.19501089	0.0077090216
Urbanization Extent 5km + Agricultural Extent 5km + Domestic Dog Visitation	-21.62481	5.23877120	0.0075421790
Urbanization Extent 3km + Agricultural Extent 3km + Human Visitation	-21.53743	5.32614597	0.0072197747
Urbanization Extent 3km + Agricultural Extent 5km + Human Visitation	-21.47718	5.38639555	0.0070055238
Urbanization Extent 5km + Agricultural Extent 1km + Human Visitation	-21.46617	5.39741088	0.0069670458
Urbanization Extent 5km + Agricultural Extent 3km + Human Visitation	-21.26519	5.59839201	0.0063009519

All Fitted PERMANOVA Models

Model terms	AICc	ΔAICc	AIC Weight
Urbanization Extent 5km + Agricultural Extent 5km + Human Visitation	-21.02558	5.83800135	0.0055895347
Agricultural Extent 1km	-20.25336	6.61021998	0.0037991856
Agricultural Extent 5km	-20.04341	6.82016903	0.0034205871
Agricultural Extent 3km	-20.04017	6.82340545	0.0034150564
Null Model	-19.91577	6.94780688	0.0032091089
Domestic Dog Visitation	-19.62992	7.23365816	0.0027817150
Urbanization Extent 3km + Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	-19.08917	7.77441315	0.0021227027
Urbanization Extent 1km + Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	-19.04755	7.81602406	0.0020789952
Urbanization Extent 1km + Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	-19.01852	7.84505894	0.0020490315
Urbanization Extent 1km + Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	-18.97686	7.88671970	0.0020067909
Urbanization Extent 3km + Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	-18.96611	7.89747093	0.0019960321
Urbanization Extent 5km + Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	-18.89473	7.96884884	0.0019260520
Urbanization Extent 3km + Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	-18.83546	8.02811545	0.0018698141
Urbanization Extent 5km + Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	-18.73905	8.12452609	0.0017818171
Agricultural Extent 1km + Domestic Dog Visitation	-18.72191	8.14166656	0.0017666118
Human Visitation	-18.58049	8.28308479	0.0016460103
Agricultural Extent 5km + Human Visitation	-18.54671	8.31687087	0.0016184377
Agricultural Extent 3km + Human Visitation	-18.53394	8.32963439	0.0016081421
Agricultural Extent 3km + Domestic Dog Visitation	-18.42946	8.43412024	0.0015262849
Agricultural Extent 1km + Human Visitation	-18.38578	8.47779425	0.0014933167

All Fitted PERMANOVA Models

Model terms	AICc	ΔAICc	AIC Weight
Urbanization Extent 5km + Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	-18.38504	8.47853827	0.0014927613
Agricultural Extent 5km + Domestic Dog Visitation	-18.31188	8.55170314	0.0014391392
Human Visitation + Domestic Dog Visitation	-17.61905	9.24452397	0.0010177912
Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	-16.28682	10.57675470	0.0005228396
Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	-16.16088	10.70270249	0.0004909296
Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	-16.09002	10.77356370	0.0004738402

Table S5. Table of top MvGLM models (ΔAIC < 2).

MvGLM Top Models Summary (ΔAIC <2)

Model terms	df	AIC
Urbanization Extent 1km + Human Visitation	13	260.4491
Urbanization Extent 1km + Domestic Dog Visitation	13	261.1986
Agricultural Extent 5km + Human Visitation	13	262.0895
Urbanization Extent 1km	14	262.1853

911 **Table S6.** Table of all fitted MvGLM models.

All MvGLM Models		
Model terms	**df**	**AIC**
Urbanization Extent 1km + Human Visitation	13	260.4491
Urbanization Extent 1km + Domestic Dog Visitation	13	261.1986
Agricultural Extent 5km + Human Visitation	13	262.0895
Urbanization Extent 1km	14	262.1853
Agricultural Extent 1km + Human Visitation	13	263.7093
Agricultural Extent 3km + Human Visitation	13	264.0475
Urbanization Extent 3km + Human Visitation	13	264.4773
Urbanization Extent 1km + Human Visitation + Domestic Dog Visitation	12	266.9031
Urbanization Extent 5km + Human Visitation	13	266.9189
Urbanization Extent 3km	14	266.9910
Urbanization Extent 1km + Agricultural Extent 5km + Human Visitation	12	267.4801
Urbanization Extent 3km + Domestic Dog Visitation	13	268.3273
Urbanization Extent 5km + Domestic Dog Visitation	13	269.5914
Urbanization Extent 5km	14	269.8151
Urbanization Extent 1km + Agricultural Extent 5km	13	269.9977
Urbanization Extent 1km + Agricultural Extent 3km	13	270.9724
Human Visitation	14	271.5862
Urbanization Extent 3km + Agricultural Extent 5km	13	271.6423
Urbanization Extent 1km + Agricultural Extent 3km + Human Visitation	12	272.2057
Domestic Dog Visitation	14	272.3701
Urbanization Extent 1km + Agricultural Extent 1km + Human Visitation	12	272.8191
Urbanization Extent 3km + Agricultural Extent 3km	13	272.9447
Urbanization Extent 5km + Agricultural Extent 5km	13	272.9639
Agricultural Extent 1km + Domestic Dog Visitation	13	273.7047
Agricultural Extent 1km	14	274.1322

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All MvGLM Models

Model terms	df	AIC
Urbanization Extent 3km + Agricultural Extent 5km + Human Visitation	12	274.4584
Urbanization Extent 3km + Human Visitation + Domestic Dog Visitation	12	274.9716
Human Visitation + Domestic Dog Visitation	13	275.0108
Urbanization Extent 1km + Agricultural Extent 5km + Domestic Dog Visitation	12	275.1098
Urbanization Extent 5km + Agricultural Extent 1km + Human Visitation	12	275.2664
Urbanization Extent 5km + Agricultural Extent 5km + Human Visitation	12	275.2791
Urbanization Extent 1km + Agricultural Extent 1km	13	275.5768
Urbanization Extent 3km + Agricultural Extent 1km + Human Visitation	12	275.7097
Urbanization Extent 5km + Agricultural Extent 3km + Human Visitation	12	276.6337
Urbanization Extent 5km + Agricultural Extent 3km	13	276.7654
Agricultural Extent 5km + Domestic Dog Visitation	13	276.7709
Urbanization Extent 3km + Agricultural Extent 3km + Human Visitation	12	276.8291
Urbanization Extent 5km + Human Visitation + Domestic Dog Visitation	12	276.8751
Urbanization Extent 1km + Agricultural Extent 3km + Domestic Dog Visitation	12	277.6490
Urbanization Extent 1km + Agricultural Extent 1km + Domestic Dog Visitation	12	277.9824
Null Model	15	278.4332
Urbanization Extent 3km + Agricultural Extent 5km + Domestic Dog Visitation	12	278.5873
Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	12	278.6015
Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	12	278.6922
Agricultural Extent 3km	14	278.8957
Agricultural Extent 3km + Domestic Dog Visitation	13	278.9896
Agricultural Extent 5km	14	279.0450
Urbanization Extent 5km + Agricultural Extent 5km + Domestic Dog Visitation	12	279.3764
Urbanization Extent 3km + Agricultural Extent 1km	13	279.4531
Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	12	279.7839

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All MvGLM Models

Model terms	df	AIC
Urbanization Extent 5km + Agricultural Extent 1km	13	280.4272
Urbanization Extent 3km + Agricultural Extent 3km + Domestic Dog Visitation	12	280.6248
Urbanization Extent 5km + Agricultural Extent 1km + Domestic Dog Visitation	12	282.7655
Urbanization Extent 3km + Agricultural Extent 1km + Domestic Dog Visitation	12	282.8540
Urbanization Extent 5km + Agricultural Extent 3km + Domestic Dog Visitation	12	283.3892
Urbanization Extent 1km + Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	11	286.7540
Urbanization Extent 1km + Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	11	287.0228
Urbanization Extent 1km + Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	11	288.2137
Urbanization Extent 5km + Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	11	291.4385
Urbanization Extent 3km + Agricultural Extent 1km + Human Visitation + Domestic Dog Visitation	11	291.7624
Urbanization Extent 5km + Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	11	292.2339
Urbanization Extent 3km + Agricultural Extent 3km + Human Visitation + Domestic Dog Visitation	11	292.7097
Urbanization Extent 3km + Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	11	293.5100
Urbanization Extent 5km + Agricultural Extent 5km + Human Visitation + Domestic Dog Visitation	11	293.6249