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*Research article*

# People or predators? Comparing habitat-dependent effects of hunting and large carnivores on the abundance of North America’s top mesocarnivore

**Remington J. Moll[1], Austin M. Green[2], Maximilian L. Allen[3] and Roland Kays[4]**

[1]Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH, USA
[2]Science Research Initiative, University of Utah, Salt Lake City, UT, USA
[3]Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, IL, USA
[4]Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA

**Correspondence: Roland Kays (rwkays@ncsu.edu)**

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Variation in animal abundance is shaped by scale-dependent habitat, competition, and anthropogenic influences. Coyotes *Canis latrans* have dramatically increased in abundance while expanding their range over the past 100 years. Management goals typically seek to lower coyote populations to reduce their threats to humans, pets, livestock and sensitive prey. Despite their outsized ecological and social roles in the Americas, the factors affecting coyote abundance across their range remain unclear. We fit Royle–Nichols abundance models at two spatial scales in a Bayesian hierarchical framework to three years of data from 4587 camera trap sites arranged in 254 arrays across the contiguous USA to assess how habitat, large carnivores, anthropogenic development and hunting regulations affect coyote abundance. Coyote abundance was highest in southwestern USA and lowest in the northeast. Abundance responded to some factors as expected, including positive (soft mast, agriculture, grass/shrub habitat, urban–natural edge) and negative (latitude and forest cover) relationships. Colonization date had a negative relationship, suggesting coyote populations have not reached carrying capacity in recently colonized regions. Several relationships were scale-dependent, including urban development, which was negative at local (100-m) scales but positive at larger (5-km) scales. Large carnivore effects were habitat-dependent, with sometimes opposing relationships manifesting across variation in forest cover and urban development. Coyote abundance was higher where human hunting was permitted, and this relationship was strongest at local scales. These results, including a national map of coyote abundance, update ecological understanding of coyotes and can inform coyote management at local and landscape scales. These findings expand results from local studies suggesting that directly hunting coyotes does not decrease their abundance and may actually increase it. Ongoing large carnivore recoveries globally will likely affect subordinate carnivore abundance, but not in universally negative ways, and our work demonstrates how such effects can be habitat and scale dependent.

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Keywords: camera traps, *Canis latrans*, competition, coyote, distribution, intraguild, trapping

## Introduction

The spatial variation in abundance across a species' range is governed by a suite of biotic and abiotic factors, including resource availability, climatic conditions, competition, predation and anthropogenic influence (Elton 1927). Understanding how these factors interact for a given species is not only interesting from an ecological point of view, but also important for wildlife management, which is typically directed to increase or decrease the abundance of a population. For terrestrial carnivores, the most important of these factors are often positive effects of preferred habitat and prey availability, and negative effects of interference competition from sympatric carnivores and humans (Levi and Wilmers 2012, Ripple et al. 2014). Anthropogenic influence has tended to trigger declines in larger, or specialist carnivores while some smaller, more generalist carnivores have persisted or even flourished in human-modified landscapes (Gompper 2002, Prugh et al. 2009). Humans can also directly reduce carnivore abundance through hunting, which is often a leading cause of carnivore mortality (Collins and Kays 2011). Given such large impacts and the charismatic nature of terrestrial carnivores, hunting regulations for these species are often scrutinized and debated by scientists, managers, policy makers and the public alike (Treves 2009).

Over the past 100 years, coyotes *Canis latrans* have benefited from anthropogenic landscape changes across North America and dramatically expanded their pre-European colonization range (Hody and Kays 2018). As anthropogenic development fragmented landscapes, coyotes' habitat generalism and flexible diet facilitated their colonization into new biomes, including heavily forested regions of the eastern USA. Concurrently, coyotes faced reduced competition with larger carnivores, as pumas *Puma concolor* and wolves *Canis* spp. were extirpated from many areas during the 20th century (Hody and Kays 2018). Coyotes are now one of the most abundant mesocarnivores in North America and frequently ascend to the position of an apex carnivore in ecosystems that lack larger carnivores (Gompper 2002, Prugh et al. 2009, Avrin et al. 2023).

Coyotes have widespread ecological and social effects, and the strength of these often depends on coyote abundance. Coyotes can negatively influence populations of endangered prey species (Witczuk et al. 2013) and smaller carnivores (Levi and Wilmers 2012, Gompper et al. 2016, Moll et al. 2021). Coyotes can also alter rodent and other prey populations (Henke and Bryant 1999), leading to cascading effects on ecosystems and influencing complex, large-scale phenomena such as Lyme disease occurrence (Levi et al. 2012). Beyond these ecological effects, coyotes come into conflict with humans due to real and perceived threats of harm to livestock, pets and humans themselves (Berger 2006). For example, White and Gehrt (2009) reported 142 attacks on humans and Alexander and Quinn (2011) reported 91 attacks on dogs *Canis familiaris* including 38 mortalities. One strategy to reduce these conflicts has been to enact liberal hunting and trapping regulations aimed at reducing coyote abundance (Berger 2006). This approach has been challenged by experiments showing limited effectiveness (Gulsby et al. 2015, Margenau et al. 2023), positive correlations between hunting and coyote abundance (Kays et al. 2017), and continued coyote range expansion into Central America (Hody et al. 2019). Given the expansion of coyotes and their ecological and social impacts, it is critical to understand the relative importance of factors affecting their abundance.

While it is generally accepted that large carnivore extirpation and landscape change facilitated coyote range expansion (Gompper 2002, Prugh et al. 2009, Hody and Kays 2018), the factors affecting local coyote abundance across their range are less clear. For example, local and regional studies have often failed to find strong predictors of coyotes' distribution or abundance (Cherry et al. 2016, Moll et al. 2021). Occupancy modeling has often yielded lackluster insights because coyotes frequently occur at nearly all sites in a study area (Lesmeister et al. 2015, Kays et al. 2017, Moll et al. 2018). While coyote abundance has been positively linked to grassland and forest habitat (Kays et al. 2008, Lesmeister et al. 2015, Cherry et al. 2016) and prey availability (O'Donoghue et al. 1997), there is conflicting evidence regarding other factors, such as urban land cover (Gehrt et al. 2011, Moll et al. 2018, Gámez and Harris 2021). Likewise, although interference competition with larger carnivores can reduce coyote abundance (Berger and Gese 2007, Levi and Wilmers 2012), the strength of this effect likely varies with local contexts and large carnivore densities (Crimmins and Van Deelen 2019). Human hunting has had surprising effects on coyote abundance, as the local removal of animals seems to be quickly compensated for by increased immigration and breeding, resulting in neutral or even positive effects on local populations (Henke and Bryant 1999, Gulsby et al. 2015, Kays et al. 2017). Finally, these factors vary across spatial scales (Kays et al. 2008, Moll et al. 2021), suggesting that some equivocal relationships in the literature might be clarified via a multi-scale framework.

Here, we use a continent-scale, multi-year camera trap survey to clarify how habitat, large carnivores, hunting, anthropogenic development, and their interactions affect variation in coyote abundance at multiple spatial scales. Specifically, we evaluated a suite of hypotheses related to these factors (Table 1) using coyote abundance models. Compared to local studies of coyote abundance, our continental-scale data encompass a larger range of variability and contexts that helps clarify the relative importance of these factors in shaping coyote abundance across their range, with implications for coyote management and coyotes' effects on other species and ecosystem processes.

Table 1. Covariates evaluated in models of coyote *Canis latrans* abundance. Each covariate represents a hypothesis supported by theory and/or previous studies. Detection covariates are in italics. The data source is SNAPSHOT USA unless indicated by the reference in the Description and data source column. Covariates in bold text indicate those that were statistically significant (95% credible intervals not overlapping zero) in at least one final model. See the Supporting information for additional covariate details.*Covariate evaluated at circular buffers with radii of 100 m and 5 km.

| Covariate | Description and data source | Effect | Hypothesis/reason |
|---|---|---|---|
| **Urban development*** | Proportion medium/high intensity urban (Dewitz and USGS 2021) | – | Urban development fragments habitat, and increases anthropogenic mortality and disturbance (Kays et al. 2008, Wang et al. 2015, Moll et al. 2018) |
| Forest* | Proportion forest (deciduous, coniferous, or mixed) (Dewitz et al. 2021) | +/– | Forest habitat provides cover, prey, and denning sites (Kays et al. 2008) but could reduce hunting efficiency (Richer et al. 2002) |
| Grassland* | Proportion grassland (Dewitz et al. 2021) | + | Natural grasslands provide small mammal prey and cover for resting and denning sites (Cherry et al. 2016, Jensen et al. 2022) |
| Shrub/scrub* | Proportion shrub/scrub (Dewitz et al. 2021) | + | Shrub/scrub supports small mammal prey (Jensen et al. 2022) |
| **Grassland/shrubland*** | Proportion of combined grassland and shrub/scrub (Dewitz et al. 2021) | + | As above |
| **Agriculture*** | Proportion agricultural (Dewitz et al. 2021) | + | Agriculture supports small mammal prey and prey accessibility (Richer et al. 2002) |
| **Urban–natural edge*** | Edge habitat between natural and low-intensity urban development (Dewitz et al. 2021) | + | Urban–natural edges provide movement corridors and access to natural and anthropogenic food sources (Fedriani et al. 2001) |
| Forest–grassland edge* | Edge habitat between forest and grassland (Dewitz et al. 2021) | + | Forest–open edge provides a mix of small mammal prey and cover (Theberge and Wedeles 1989, Randa and Yunger 2006, Kays et al. 2008) |
| Forest–shrub edge* | Edge habitat between forest and shrub/scrub (Dewitz et al. 2021) | + | Forest–open edge provides a mix of small mammal prey and cover (Theberge and Wedeles 1989, Randa and Yunger 2006, Kays et al. 2008) |
| Forest–grass/shrub edge* | Edge habitat between forest and combined grassland and shrub scrub (Dewitz et al. 2021) | + | Forest–open edge provides a mix of small mammal prey and cover (Theberge and Wedeles 1989, Randa and Yunger 2006, Kays et al. 2008) |
| Smaller prey | Number of detections of squirrels (Family Sciuridae) and lagomorphs per camera trap day | + | These prey species are important food sources (Jensen et al. 2022) |
| Deer | White-tailed *Odocoileus virginianus* and mule deer *O. hemionus* detections per camera trap day | + | Ungulates are an important food source (Jensen et al. 2022) |
| **Soft mast** | Mean abundance of soft mast between years 1991 and 2011 as predicted by the MASTIF network (Clark et al. 2019) multiplied by local (1-km) forest cover | + | Soft mast is a key fall food source (Jensen et al. 2022) |
| Black bear | Detection of black bear *Ursus americanus* at the camera array | – | Black bears limit coyotes via interference competition (Moll et al. 2021) |
| Wolves | Whether the camera trap array was within gray wolf *Canis lupus* or red wolf *C. rufus* range (https://ecos.fws.gov) | –/+ | Gray wolves limit coyotes via interference competition and intraguild predation (Berger and Gese 2007, Levi and Wilmers 2012) but might also increase scavenging opportunities (Jensen et al. 2022) |
| Puma | Whether the camera trap array was within puma *Puma concolor* range (https://ecos.fws.gov) | –/+ | Pumas limit coyotes via interference competition and intraguild predation (Wang et al. 2015, Elbroch and Kusler 2018) but might also increase scavenging opportunity (Sivy et al. 2017) |
| Total large carnivores | Number of large carnivores (black bear, gray wolf, puma) whose range overlapped camera trap arrays (https://ecos.fws.gov/) | – | Large carnivores limit coyotes via interference competition and intraguild predation |
| **Colonization decade** | Year coyotes colonized an area (1900 used for historic range; Hody and Kays 2018) | – | Areas colonized earlier will have higher abundances due to higher reproduction and dispersal rates from more established populations |
| Site location | Site latitude and longitude | –/+ | Control for potential spatial autocorrelation from unmodeled geographic factors |

*(Continued)*

Table 1. Continued.

| Covariate | Description and data source | Effect | Hypothesis/reason |
|---|---|---|---|
| **Hunting** | Whether coyote hunting was permitted for a given camera array | −/+ | Hunting could reduce (Henke and Bryant 1999) or increase abundance through compensatory effects (Kays et al. 2017) |
| Vegetation greenness | Normalized difference vegetation index in 16-day window of June each year (Didan and Huete 2015) | − | Denser vegetation reduces camera trap detection rates for mammals (Allen et al. 2022a) |
| Effort | Total survey days per camera | −/+ | Accounts for temporal heterogeneity in the detection process due to unmodeled factors |

## Material and methods

### Study area

We used a camera trap network deployed across the contiguous USA from the SNAPSHOT USA project (Cove et al. 2021, Kays et al. 2022, Shamon et al. 2024). The camera traps were deployed over three years as part of a coordinated survey, resulting in 4587 sites (1492 in 2019, 1467 in 2020, and 1628 in 2021) arranged in 254 arrays (Fig. 1). The network was active from late August to early November each year, spanned 25°10′12″ to 48°24′36″ latitude and −124°12′36″ to −68°39′36″ longitude, and covered the major biomes present throughout the contiguous USA.

### Field methods

Participants in the SNAPSHOT USA project established camera traps in arrays following standardized protocols detailed elsewhere (Cove et al. 2021). Briefly, cameras were placed > 200 m apart at approximately 30–50 cm above ground and each array had a minimum active period of 400 camera trap nights. We used cameras as the spatial unit for analyses. Cameras per array varied from one to 112 (average = 18.1, SD = 12.4). Camera models varied, but all employed fast trigger speeds and captured images of sufficient resolution for species identification. These images were processed via the eMammal (https://emammal.si.edu) and Wildlife Insights (https://www.wildlifeinsights.org) online platforms and identifications were reviewed by at least one expert.

### Covariate development

We developed a suite of 22 covariates that we hypothesized a priori could influence coyote abundance and detection rate. We detail these covariates and their expected relationship with coyote abundance in Table 1 and the Supporting information. We developed habitat covariates using the 2019 National Land Cover Database (Dewitz and USGS 2021) and the R packages 'landscapemetrics' (Hesselbarth et al. 2019), 'sf' (Pebesma 2018), and 'terra' (Hijmans 2023), using R ver. 4.1.3 (www.r-project.org). We created habitat and the soft mast covariates at two spatial scales using circular buffers around each site with radii of 100-m and 5-km. We chose the 100-m scale to capture local camera site characteristics (as noted above, all cameras were placed > 200 m from the next nearest camera). We chose the 5-km scale based on work demonstrating that coyotes responded to urban development most strongly at this scale (Kays et al. 2008, Moll et al. 2020).

### Statistical analyses

We used data from continental SNAPSHOT USA collected from late August to early November. We prepared weekly (seven consecutive days) coyote detection histories and used a Royle–Nichols model (Royle and Nichols 2003) to estimate site-level coyote abundance and modeled it against the covariates. Some covariates were correlated (Pearson's $r > |0.7|$), so we first ran univariate models on the full dataset while holding detection probability constant and retained uncorrelated predictors that produced a 'significant' signal (i.e. 95% credible interval did not overlap 0; Zuur et al. 2010, Dormann et al. 2013). If two correlated predictors produced significant signals, we retained that with the largest effect under the assumption that it would more biologically meaningful (Zuur et al. 2010). We repeated this process for the detection covariates (Allen et al. 2022a, b). We ran two models, one for each scale (100-m and 5-km). We kept final model structure equivalent across spatial scales and standardized continuous covariates (mean = 0, SD = 1) to facilitate model convergence and comparison of effect sizes.

Our model estimated coyote abundance, $N_i$, as:

$$N_i \sim \text{Poisson}(\lambda_i)$$

where $\lambda_i$ describes the expected abundance of coyotes at site i. We modeled the effects of covariates on $\lambda$ using a log-link. Following the modeling procedure described above, these final covariates included latitude, time since coyote colonization, urban development, grass and shrubland habitat, agricultural habitat, forest cover, forest soft mast cover, urban–natural edge, large carnivores, and hunting regulations, as well as interactions between three habitat covariates (urban development, forest cover, and grass and shrubland habitat) with large carnivores and hunting. We included these interactions because other work on carnivores has suggested that the effects of hunting and interspecific competition could depend on habitat (Creel 2001, Hunter and Caro 2008, Dyck et al. 2022) but investigations into such interactions for coyotes and large carnivores are lacking. We modeled interactions with these three habitat types because they varied strongly across study sites and were among those hypothesized to most strongly influence coyote

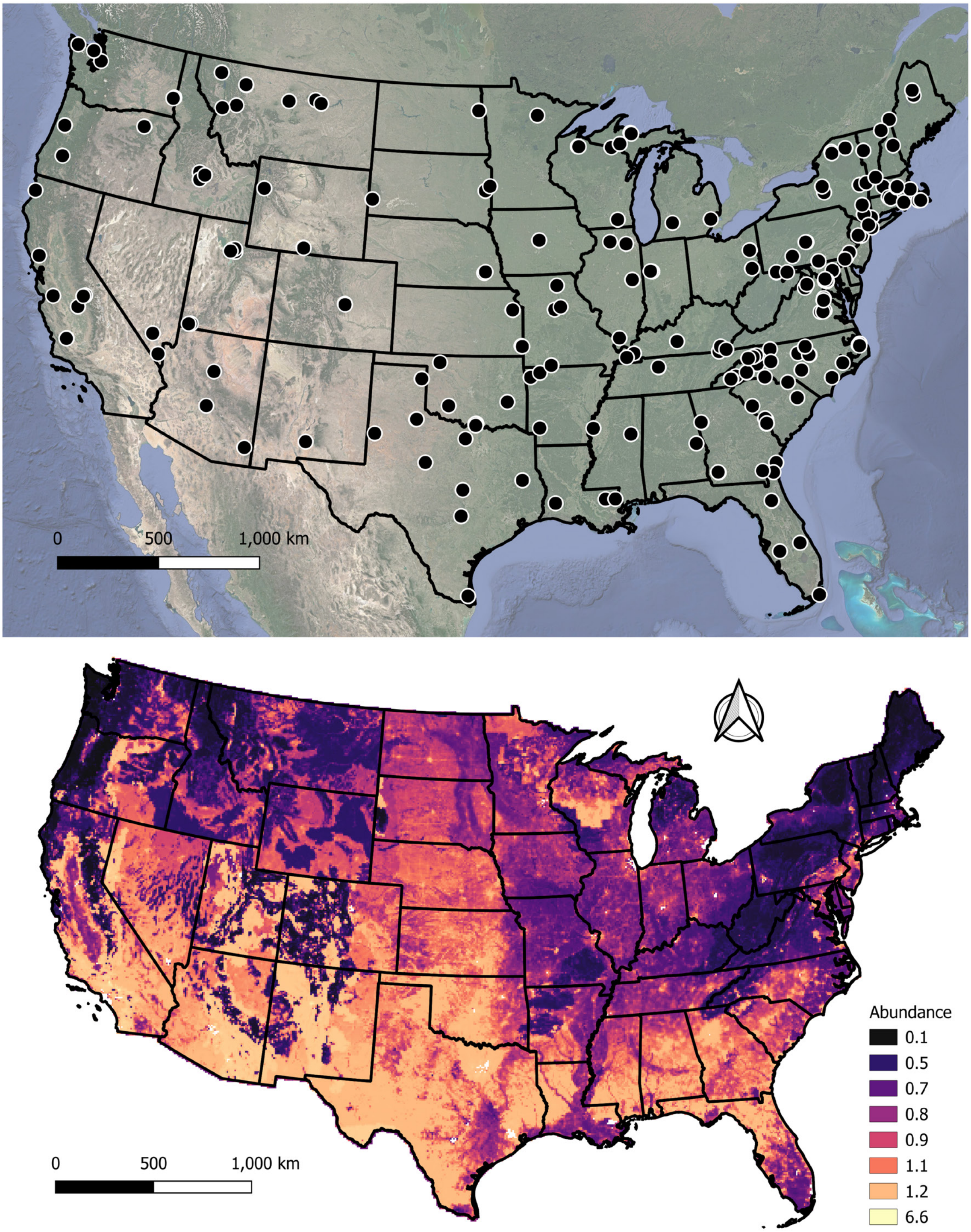

Figure 1. Top: camera trap array locations from SNAPSHOT USA sites 2019–2021. Bottom: model-predicted relative abundance of coyotes across the contiguous USA. Coloration based on quantile classification. Note that coloration is based on quantiles, but model predictions were not limited to quantile values. White areas indicate urban development raster values that exceeded those collected in the dataset.

abundance (Kays et al. 2008, Cherry et al. 2016, Moll et al. 2018, Jensen et al. 2022, Table 1). We included a year-specific intercept and a random effect of camera array to control for spatial autocorrelation and/or array-level heterogeneity not captured by the covariates. We estimated abundance $N_i$ using the Royle–Nichols model formulation. The detection sub-model was:

$$y_{i,k} \sim \text{Bernoulli}\left(p_{i,k}\right)$$

$$p_{i,k} = 1 - \left(1 - r_{i,k}\right)^{N,i}$$

where $y_{i,k}$ describes the detection/non-detection of coyote at site $i$ during weekly sampling occasion $k$; $p_{i,k}$ is the site-specific probability of detection of one or more coyote based on both the site and sampling occasion-specific detection probability of a particular individual, $r_{i,k}$, and site-specific local abundance. We modeled covariate effects (effort and vegetation greenness; Table 1) on individual detection probability $r$ using a logit link function (Royle and Nichols 2003). Finally, we included an overdispersion term in the detection model that was normally distributed with a mean of zero and a model-estimated variance.

We ran the models including hunting regulations on a truncated dataset (n = 1587 sites across 68 arrays), as we could not obtain hunting data from all arrays. Because we only had range-wide data for puma and wolf covariates, these covariates were only included in the 5-km model. Thus, we ran a total of four models: two at the 100-m scale (one full model and one truncated to hunting regulation sites; neither including puma or wolf covariates), and two at the 5-km scale (one full model and one truncated to hunting regulation sites; both including puma and wolf covariates). We report the probability of effect (PoE) for each covariate as the probability density contained on one side of 0. The PoE quantifies the probability that a covariate positively or negatively affects coyote abundance, given the model and data.

We ran models within a Bayesian framework using Markov chain Monte Carlo simulations via package R 'jagsUI' (Kellner and Meredith 2021). We ran three unthinned chains of 20 000 iterations, with the first 10 000 iterations discarded following an adaptation phase of 10 000 iterations (Link and Eaton 2012). After testing the sensitivity of prior distributions on parameter estimates, we used diffuse, normal distributions (mean = 0, variance = 1000) for all coefficient priors and a uniform (0,10) prior distribution for the standard deviation of the overdispersion parameter. We assessed model convergence using the Gelman–Rubin statistic, where values $< 1.1$ indicated successful convergence (Gelman et al. 2004). We assessed model fit by calculating Bayesian p-values using chi-squared discrepancy statistics (Kéry and Royle 2015). We visualized model results across the contiguous USA in QGIS 3.30.0 (QGIS Development Team 2022) by creating rasters for each covariate except soft mast and hunting (omitted due to insufficient spatial data availability) and multiplying raster cells by the posterior mean of associated coefficients from the 5-km model.

## Results

There were 3166 detections of coyote at 1526 sites during 169 157 survey days. Models for each scale had acceptable fit (Bayesian p-values 0.90–0.92), with excellent convergence (Gelman–Rubin statistics $< 1.04$).

Predicted mean local coyote abundance ranged from 0.01 to 12.01 in the 100-m model (mean = 0.89) and from 0.01 to 9.28 in the 5-km model (mean = 0.89). Coyote abundance did not change across years or scales (Supporting information). Coyote abundance was highest in southwestern USA and lowest in the northeast, with substantial variation between these areas, including low abundance in western mountainous areas and high abundance in the central agricultural regions (Fig. 1). Below we report significant covariate relationships (those where the 95% credible interval did not overlap zero), and present all relationships in Fig. 2 and the Supporting information.

### 100-m scale model

At the 100-m scale, coyote abundance was positively, significantly associated with (ordered from strongest to weakest effect size) hunting ($\alpha_{hunt} = 1.09$, PoE = 0.97), grass and shrubland cover ($\alpha_{grsh} = 0.21$, PoE = 1.00), agricultural cover ($\alpha_{agr} = 0.17$, PoE = 1.00), and soft mast forest cover ($\alpha_{sftmst} = 0.04$, PoE = 0.95; Fig. 2). Coyote abundance was negatively, significantly affected by urban development ($\alpha_{urb} = -0.73$, PoE = 1.00), latitude ($\alpha_{lat} = -0.25$, PoE = 1.00; Fig. 2), and colonization decade ($\alpha_{col} = -0.05$, PoE = 1.00).

There were significant negative interactions between bear detection and grass and shrubland cover ($\alpha_{grsh \times bear} = -0.31$, PoE = 0.99) and bear detection and forest cover ($\alpha_{frt \times bear} = -0.25$. PoE = 0.99), and there was a significant, positive interaction with beat detection and urban development ($\alpha_{urb \times bear} = 0.48$, PoE = 0.97). Finally, there were significant, positive interactions between areas where hunting was permitted and both grass and shrubland cover ($\alpha_{grsh \times hunt} = 2.21$, PoE = 1.00) and forest cover ($\alpha_{frt \times hunt} = 0.52$, PoE = 1.00; Fig. 3).

### 5-km model

At the 5-km scale, coyote abundance was positively, significantly affected by urban–natural edge ($\alpha_{URN} = 0.13$, PoE = 0.97; Fig. 2). Abundance was negatively, significantly affected by latitude ($\alpha_{lat} = -0.22$, PoE = 0.99) and colonization decade ($\alpha_{col} = -0.05$, PoE = 0.98; Fig. 2).

There were significant, negative interactions between forest cover and latitude ($\alpha_{frt \times lat} = -0.31$, PoE = 1.00), and there was also a strongly significant negative interaction between urban development and colonization decade ($\alpha_{urb \times col} = -0.08$, PoE = 1.00), where abundance was more negatively affected by urban habitats with more recent colonization (Fig. 2). There were significant, negative interactions between urban development and puma presence ($\alpha_{urb \times puma} = -1.15$, PoE = 1.00) and forest cover and puma presence ($\alpha_{frt \times puma} = -0.29$, PoE = 0.96; Fig. 3), and a significant, positive interaction between forest cover and wolf presence ($\alpha_{frt \times wolf} = 0.45$, PoE = 0.98; Fig. 3).

## Discussion

We used a three-year dataset to evaluate factors shaping large-scale variation in the abundance of one of the most successful mesocarnivores in the Anthropocene, the coyote. This

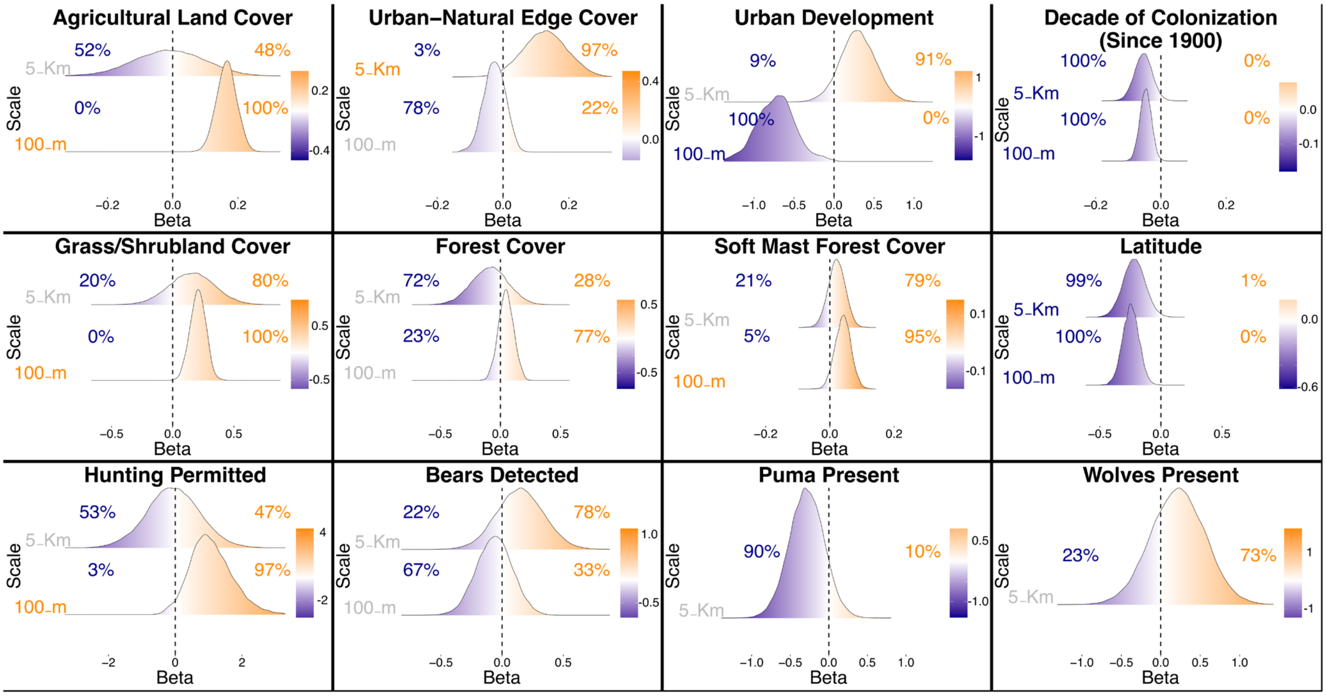

Figure 2. Coefficient posterior distributions from coyote abundance models fit to data across the contiguous USA collected by the SNAPSHOT USA project. Colored scale labels on the y-axis denote significant effects (> 95% of posterior probability density on one side of 0). Note: y-axis scale varies across panels.

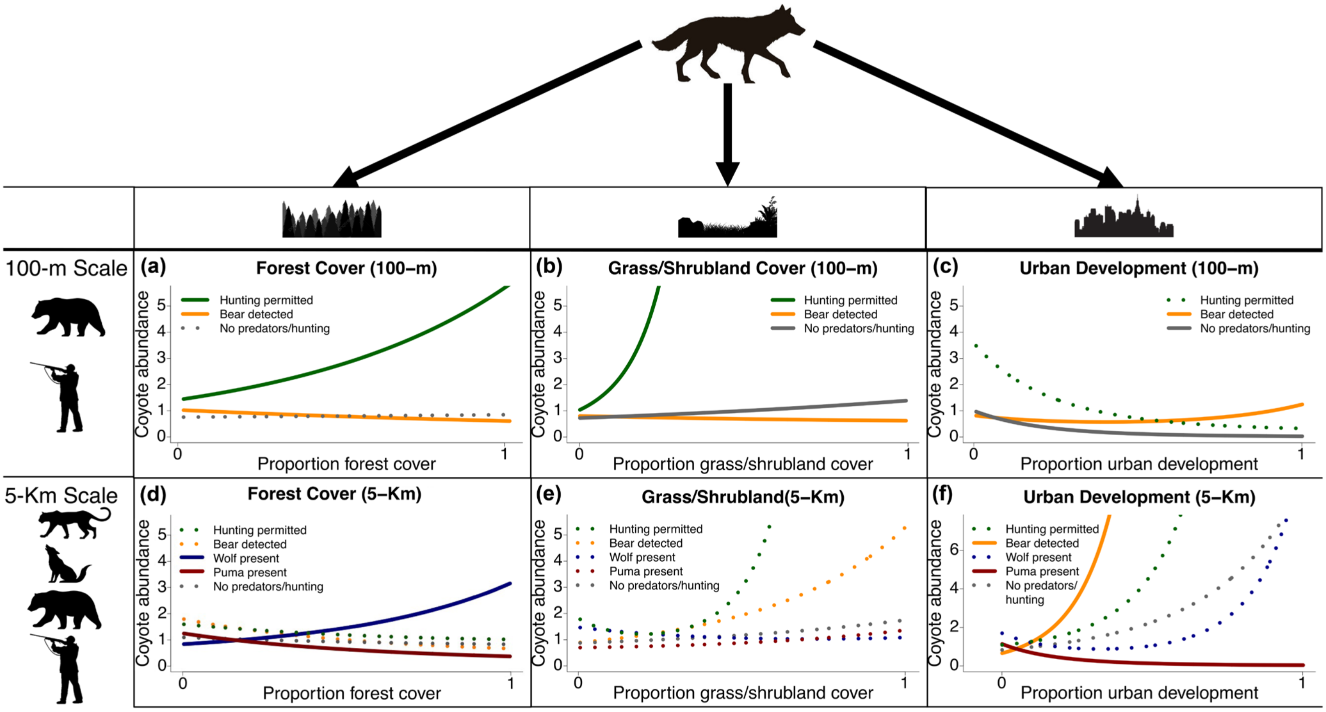

Figure 3. Interactive effects of hunting and apex predators (black bears, wolves, and pumas) on coyote habitat associations across scales based on models fit to data across the contiguous USA collected by the SNAPSHOT USA project. Significant interactions are represented as solid lines and non-significant interactions are dashed lines. Significant, positive interactions include hunting with forest cover and grass/shrubland cover at the 100-m scale (a–b), wolf with forest cover at the 5-km scale (d), and bear with urban development at both scales (c–f). Significant, negative interactions include bear with forest cover and grass/shrubland cover at the 100-m scale (a–b), and puma with forest cover and urban development at the 5-km scale (d–f).

analysis revealed several trends that clarify the sometimes-equivocal coyote ecology literature. While some relationships were as expected (e.g. positive effects of grassland and agriculture, and negative effects of latitude), our model uncovered important interactions between large carnivores and habitat, which implies that coyote response to dominant competitors strongly depends on habitat, and vice versa. Indeed, the effects of large carnivore covariates by themselves were not significant (Fig. 2) but each large carnivore species had at least one significant interaction with a habitat variable (Fig. 3), thereby highlighting the context dependency of large carnivore effects on coyotes. We also found a positive association between hunting regulations and abundance, providing the largest-scale evidence that this frequent management tool is ineffective at reducing coyote abundance. Relatedly, we found that the effects of large carnivores and habitat changed across spatial scales, particularly with factors related to urban development and the interactive effect of black bears and forest cover.

Other studies have examined how large carnivores affect coyotes (Wang et al. 2015, Gompper et al. 2016, Moll et al. 2021, Avrin et al. 2023) but have not considered potential interactions between predators and habitat. We found that the negative effect of black bears and pumas on coyote abundance intensified with increasing forest cover, although for black bears this was only true at the local scale and for pumas at the landscape scale (Supporting information). Black bears and coyotes are competitors for food and space, and since our data all come from the fall season, the results suggest that this competition might be locally intense during the fall when bears are hyperphagic prior to hibernation and when coyote diet includes more fruit species that bears also consume (Jensen et al. 2022). Coyotes and pumas have a more complicated relationship since pumas regularly kill coyotes but also provision coyotes with carcasses to scavenge (Allen et al. 2014, Ruprecht et al. 2021). The overall negative impact suggests the balance of these factors reduces coyote local abundance where they overlap with puma, especially in forests that are more often used by pumas.

In contrast to bears and pumas, coyote abundance was more positively associated with wolf distribution, and this had a positive interaction with forest cover. The wolf–forest interaction was unexpected given that wolves are a forest-dwelling species that have been shown to limit coyote abundance (Berger and Gese 2007, Levi and Wilmers 2012). However, recent work suggests that this effect could be reduced or absent if wolf densities are low (Crimmins and Van Deelen 2019) and that carcass provisioning can result in positive wolf–coyote associations at local scales (Sivy et al. 2017). Additionally, snow tracking work suggests that, in winter, coyotes frequent trails and travel corridors used by wolves in forests with little spatial or temporal avoidance, likely due to scavenging opportunities that compensate for lower coyote hunting efficiency in forests (Richer et al. 2002). Moreover, few wolf–coyote studies have occurred in fall, with many efforts aggregating data over years or occurring in summer or winter. Given that coyote fall diets are more vegetative, another possibility is that direct wolf–coyote resource competition is lower in forested areas during that season. More broadly, coyote abundance might fluctuate seasonally due to life history characteristics. For example, birthing season (late spring and summer) is associated with both new individuals entering the population and reduced home range and territory size during pup-rearing (Parker 1995). Juveniles tend to disperse during fall and early winter, which could impact local abundance positively or negatively, depending on site characteristics (Berger and Gese (2007) documented higher dispersal out of areas with wolves than those without wolves).

Large carnivore effects also varied by urban development, with bear effects becoming more positive and puma effects more negative as development increased. Bears tended to make urban effects more positive at every scale, even though the overall effect of urban development changed from negative at small scales to positive at large scales (Fig. 3). This pattern could be the result of coyotes tolerating greater development when in the presence of a larger, dominant competitor, perhaps to exploit smaller habitat patches more effectively than black bears. The overall change in urban development's effect across scales implies that at a broad spatial scale, such development and concomitant fragmentation tends to increase coyote abundance, which aligns with previous work and the general notion that forest fragmentation facilitated eastward coyote expansion (Gompper 2002, Hody and Kays 2018). At local scales, however, urban development reduced coyote abundance, a finding corroborated in several localized studies and perhaps related to coyote space requirements (Kays et al. 2008, Wang et al. 2015, Moll et al. 2018). The reasons behind the puma–urban interaction are less clear. Recent work has revealed complex risk–reward tradeoffs between pumas and coyotes, where the benefits of scavenging puma kills are counterbalanced by mortality risk due to direct killing (Ruprecht et al. 2021). Pumas might abandon carcasses more quickly in more urbanized areas (Smith et al. 2017), which would imply that scavenging opportunity might be greater in such locations. However, more urbanized areas could provide alternative food sources for coyotes (Fedriani et al. 2001), thus the putative benefit of puma-provisioned food might be reduced and thereby result in a net negative effect of pumas on coyotes through direct mortality risk.

Hunting can cause substantial mortality in carnivore populations and coyote hunting regulations tend to be liberal, often lacking seasonal restrictions or bag limits (Knowlton et al. 1999, Collins and Kays 2011). Yet, we found that hunting regulations had positive local effects. Other work has shown that high levels of removal can reduce coyote abundance (Henke and Bryant 1999), but that abundance rebounds quickly if hunting pressure decreases (Berger 2006, Gulsby et al. 2015, Margenau et al. 2023). Hunting can result in a younger coyote age structure and might temporarily reduce intraspecific competition for food, leading to larger litter sizes (Knowlton et al. 1999). In turn, these changes could result in compensatory rebound (Connolly 1995). In our study, this compensatory effect appears particularly probable in coyotes' native grassland habitat (Fig. 3), likely reflecting coyotes' ability to exploit plentiful food resources. Kays et al. (2017) also found a positive effect of hunting on coyote occupancy and site visitation, and hypothesized that removal of resident individuals might increase immigration by transients, which could explain the pattern found here, given that this study coincided with the fall dispersal period. Overall, our results imply that hunting does not negatively impact coyote abundance, but it often actually increases local abundance Thus hunting is not only an ineffective control strategy, but can have the opposite intended management effect.

Our results confirmed several other hypothesized relationships related to habitat and environmental effects, as well as time since colonization. Agriculture and grassland/shrub habitat had positive effects on coyote abundance, as has been found elsewhere (Richer et al. 2002, Cherry et al. 2016). Urban–natural edge also had a positive effect on coyotes, probably due to increased prey availability and foraging efficiency, and because edges facilitate travel between patches (Fedriani et al. 2001). Latitude had a negative effect on coyote abundance, as did the year of colonization. Coyote abundance has been qualitatively observed to decrease with latitude due to less favorable climatic and prey conditions, but this is the first study to directly quantify this relationship, although a meta-analysis found a positive effect of latitude on coyote home range size, which could correspond to lower densities (Ellington and Murray 2015). Given that the model controlled for the effects of latitude, habitat, and food resources, we surmise the effect of colonization decade could be due to the generational time required to effectively adapt to new conditions and prey sources. This suggests that coyote populations may not have reached carrying capacity in these new areas and will continue growing in the future. An additional explanation for lower abundance in the northeast is that hybridization with wolves and domestic dogs in eastern coyote populations has resulted in larger body masses and home ranges due to increased prey and space requirements, thereby leading to lower local abundances (Ellington and Murray 2015). While we did not explicitly evaluate genetic introgression or hybridization effects in this analysis, we did include an array-level random effect to control for unmodeled heterogeneity in coyote abundance. Thus, we suspect that such genetic effects could be present but do not preclude the relationships reported here; future work would help clarify this possibility. Finally, we found no support for an effect of squirrel, lagomorph, or deer prey on coyote abundance. It is possible that these prey could influence local coyote abundance more strongly in other seasons due to diet preferences (lagomorphs in spring and winter and ungulates in winter; Jensen et al. 2022). However, we did find a positive effect of soft mast (which is likely due to coyotes' vegetative diet during the fall), emphasizing the importance of soft mast resources for coyote populations (Jensen et al. 2022).

## Conclusions

Coyote management is typically focused on lowering their abundance to reduce potential harmful impacts on species they threaten (e.g. humans, White and Gehrt 2009), pets (Alexander and Quinn 2011), prey upon (endangered marmots, Witczuk et al. 2013), or hybridize with (e.g. red wolf, Bohling and Waits 2015). Coyotes can also influence subordinate species like foxes and thus have cascading effects on other ecosystem-level processes like rodent populations and disease dynamics (Levi et al. 2012). Given the outsized role of coyotes on ecosystems, and that many of these effects are likely density dependent, our results have important applied implications. First, our analysis confirms that hunting regulations do not limit coyote abundance and are more likely to increase it. Direct killing of coyotes has historically been the first management response through liberal hunting regulations, bounty programs, and targeted removal (Berger 2006). Our large-scale model results support other correlational (Kays et al. 2017) and experimental (Gulsby et al. 2015) studies showing this relationship.

Second, our results show that large carnivores have strong but complex effects on coyotes, which is important since all three large predators are increasing their populations and geographic range in North America. Pumas have the strongest and most consistent negative effects on coyotes, suggesting that their expansions into parts of their historic range in eastern USA (Larue et al. 2019) could reduce coyote populations, especially in more developed or less forested areas. Wolf populations are also reclaiming parts of their historic range in the USA (e.g. Colorado and California), and our results suggest that the impact of wolves on coyote abundance is overall positive, and that they are likely to continue to coexist, especially in forests. Black bears are the most abundant large carnivore in the world (Ripple et al. 2014) and our results suggest they are likely to compete with coyotes for food and reduce their abundance in wild areas, but have less of an impact in developed areas.

Finally, our results underscore the importance of spatial scale for several of these relationships, which suggests that management actions aimed at coyote populations or human–coyote conflict should consider a multi-scale approach. For example, given hunting's stronger effects at local scales (i.e. the 100-m scale model), managers should consider local hunting restrictions where human, livestock, or pet conflict is expected, particularly those adjacent to grassland or forest habitat, while still allowing for the selective removal of problem individual coyotes (Baker and Timm 2017). Given the contrasting effects of urban development across scales, managers should also expect highest conflict to occur in local, natural habitat patches – particularly agricultural and grassland patches – embedded within a broader urbanized matrix.

Beyond these applied and coyote-specific considerations, our work sheds light on interspecific competition in carnivore communities and the role of scale in wildlife ecology. Previous work has emphasized the potential of large carnivores to suppress smaller, subordinate carnivores (Palomares and Caro 1999, Berger and Gese 2007, Levi and Wilmers 2012, Prugh and Sivy 2020, Moll et al. 2021). Such work relates to the mesopredator release hypothesis (Soulé et al. 1988), which predicts that loss of large carnivores releases smaller carnivore populations from competition, thereby enabling these species to ascend to higher trophic positions, with implications for prey populations (Elmhagen and Rushton 2007, Ritchie and Johnson 2009). Our study adds to these concepts by suggesting such patterns are habitat dependent. This habitat-contingency in interspecific carnivore dynamics has been suggested previously (Creel 2001), but this study is one of the few to show it on a continental scale. Our work also builds upon the long history of research on ecological scale (Weins 1989, Levin 1992) in at least two ways. First, this work demonstrates the utility of broad-scale, continental evaluations of species–habitat relationships by demonstrating that such evaluations can contextualize local studies reporting conflicting or equivocal relationships. Large-scale studies can also clarify a species' realized, range-wide Grinnellian niche and thereby better classify species on the generalist–specialist continuum (Devictor et al. 2008, 2010, Moll et al. 2016) and inform species distribution modeling and broad-scale ecological predictions, such as forecasts of species range dynamics across climate scenarios (Fletcher et al. 2016, Briscoe et al. 2019, Sirén et al. 2022). Second, while our models generally produced similar results across scales, it was striking that human-related landscape effects on coyotes via urban development reversed across these scales (Fig. 2). Scale-dependent responses to human landscape development have been reported in other taxa (e.g. bats Gallo et al. 2018; and birds Paton et al. 2019). This concept reinforces the general idea that evaluations of human impacts on wildlife populations should be conducted in a multi-scale framework, with implications for management and conservation approaches across scales (Fletcher and Hutto 2008).

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## Author contributions

**Remington J. Moll**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (lead); Writing – review and editing (lead). **Austin M. Green**: Conceptualization (equal); Formal analysis (lead); Writing – original draft (equal); Writing – review and editing (equal). **Maximilian L. Allen**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Roland Kays**: Conceptualization (equal); Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal).

## Transparent peer review

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## Data availability statement

The data from this manuscript are available from the SNAPSHOT USA project, available from Cove et al. (2021), Kays et al. (2022) and Shamon et al. (2024). A digital raster of the map of coyote abundance is available at Moll (2024).

## Supporting information

The Supporting information associated with this article is available with the online version.

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