

REVIEW

Coyote diet in North America: geographic and ecological patterns during range expansion

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ABSTRACT

1. Coyotes *Canis latrans* have expanded their geographic range by 40% in the last 120 years, raising questions about their ecological impacts in the newly colonised areas. Despite a wealth of local knowledge on coyote diet in North America, we have little information about how and why diet might vary throughout the species' range.
2. We conducted the first rangewide meta-analysis of coyote diet by investigating how ecoregion, coyote mass, environmental conditions, presence of top predators and alternative food items are related to coyote dietary diversity, as well as consumption of small mammals, lagomorphs, vegetation and ungulates.
3. Using data from 93 studies, we used generalised linear mixed models to determine which variables best explained coyote dietary patterns.
4. Coyotes were generally more carnivorous in temperate forests than in other ecoregions, primarily due to greater ungulate consumption. Dietary diversity was most influenced via a negative effect of mammal consumption; coyote diet was more diverse in the spring and where human footprint was greater. There was minor variation in small mammal consumption, but lagomorph consumption was greater in spring and winter and when coyotes were larger. Vegetation consumption was greatest in summer and autumn. Ungulate consumption was positively related to coyote mass, snow cover and the presence of grey wolves *Canis lupus*.
5. Both intrinsic and extrinsic factors were related to coyote diet. Larger coyotes ate larger foods, which parallels the relationship between mass and prey size across the carnivore guild. Wolves and humans have opposing effects on coyote diet. Coyotes seem to prioritise eating wild mammals, though more work is needed to quantify scavenging. Collectively, our findings emphasise the need for continued local or regional studies to understand the highly variable ecological effects of coyotes within the diverse ecosystems they currently inhabit and are poised to inhabit.

INTRODUCTION

In a world where populations of most terrestrial carnivore species are declining (52%), a small number of species are increasing (4%; Marneweck et al. 2021). Several of the species with increasing populations are not simply recovering from past decline, but have also colonised new areas. Golden jackals *Canis aureus* and raccoons *Procyon lotor* are expanding throughout Europe (Arnold et al. 2012, Salgado 2018), and coyote *Canis latrans* geographic range has expanded by 40% throughout North America (Hody & Kays 2018). The arrival of these carnivores has raised concerns about their ecological impact in the new areas, particularly on prey species.

For most of the last 10000 years, coyotes were restricted to the western two-thirds of North America (Hody & Kays 2018). However, from around 1900, they began to expand north into Alaska, south into Central America and east to the Atlantic Ocean. Several mechanisms likely facilitated coyote range expansion, including widespread conversion of forest to agriculture (Macdonald & Sillero-Zubiri 2004), and hybridisation with grey wolves *Canis lupus* and domestic dogs *Canis familiaris* (VonHoldt et al. 2011). Hybridisation with wolves in the northeast makes coyotes larger, increasing their colonisation rate and ability to kill adult white-tailed deer *Odocoileus virginianus* (Kays et al. 2010, Thornton & Murray 2014). Indeed, a central line of inquiry in the last 20 years has been understanding the conditions under which coyotes act as ecological surrogates to wolves, now that coyotes are the largest carnivore (hereafter ‘carnivore’ in the taxonomic sense) across much of the eastern USA (Gompper 2002, Benson et al. 2017). The absence of wolves and pumas *Puma concolor* in most of eastern North America is also thought to have facilitated coyote range expansion (Berger & Gese 2007); thus, wolf presence is likely to have both catalysed and limited coyote expansion, depending on the context.

Coyotes are intrinsically adaptable, with diverse diets that tend to reflect seasonal changes in food availability (Hidalgo-Mihart et al. 2001, Schrecengost et al. 2008). Some coyotes eat a greater variety of foods in human-dominated areas (Fedriani et al. 2001), while others in relatively undisturbed areas exhibit selectivity for small mammals or lagomorphs (Hernández et al. 2002, Prugh 2005). Coyotes can also be capable predators of wild ungulate adults and neonates (Benson et al. 2017, Gingery et al. 2018). On average, coyotes are responsible for 44% of white-tailed deer fawn mortalities in the south-eastern USA (Kilgo et al. 2019), which, when combined with adult deer mortality from hunting by humans, can contribute to deer population declines (Kilgo et al. 2012).

At the continental scale, coyote diet could be influenced by multiple intrinsic and extrinsic factors (Table 1). First, coyote size could influence dietary composition. Carnivores weighing more than ~20 kg tend to kill prey as large as themselves, while carnivores weighing less than ~20 kg tend to kill prey smaller than themselves (Carbone et al. 1999). In most of their range, coyotes average 12–15 kg in body mass, though they can weigh more than 20 kg in the northeast (Hinton et al. 2019). Thus, larger coyotes may eat larger food items. Environmental factors could also influence coyote diet. Grey wolf and dingo *Canis lupus dingo* diets were both shown to have substantial regional variability (Newsome et al. 2016, Doherty et al. 2018), which could also be true for coyotes given the diversity of habitats they live in. Snow cover reduces the availability of small mammals and vegetation (Korslund & Steen 2006), while increasing both ungulate vulnerability to predation and the availability of ungulate carcasses (Coulson et al. 2001, Hebblewhite 2005). Primary productivity might also be related to food availability (e.g. fruit abundance; Fernández-Martínez et al. 2016). Humans can influence coyote diet through provisioning food subsidies (Fedriani et al. 2001, Newsome et al. 2015) or by influencing food availability. Lastly, in areas of co-occurrence, large carnivores can provision ungulate carcasses to coyotes (Prugh & Sivy 2020), and the presence of wolves can change coyote behaviour and diets (Miller et al. 2012, Colborn et al. 2020).

Given their recent range expansion and apparent trophic flexibility, quantifying the geographic variation in coyote diet can help us understand their ecological role in different contexts. It can also help us make predictions about their potential impact in new areas, such as South America (Méndez-Carvajal & Moreno 2014, Hody & Kays 2018). Accordingly, the goal of this study was to conduct the first review of coyote diet throughout their range. Our objectives were to: 1) investigate ecoregional patterns in coyote diet, focusing on consumption of the six most frequently eaten food items (small mammals, lagomorphs, vegetation, ungulates, invertebrates and birds), and 2) evaluate support for various hypotheses (Table 1) relating to dietary diversity and the consumption of the four core food items (small mammals, lagomorphs, vegetation and ungulates).

METHODS

Literature search

In April 2020, we searched Web of Science, Google Scholar and ProQuest for literature on coyote diets (Appendices S1 and S2). We also searched Google Scholar

Table 1. Factors hypothesised to influence coyote *Canis latrans* dietary diversity and consumption of small mammals, lagomorphs, ungulates and vegetation by coyotes in North America. 'NA' (not applicable) indicates that the factor was not used in that analysis. Our seasonal predictions were abbreviated as 'Sp' = spring, 'Su' = summer and 'W' = winter. We bolded and enlarged predictions that matched our results

Factor	Description	Predicted association (+ = positive, – = negative, ~ = no effect)				
		Diversity	Ungulate	Lagomorph	Small mammals	Vegetation
Season	The season the samples represented: spring, summer, autumn (reference), winter	Sp (+), Su (+), W (–)	NA	Sp (+), Su (+), W (–)	Sp (–), Su (+), W (+)	Sp (–), Su (–), W (–)
Coyote mass	The mean mass of coyotes from Hinton et al. (2019). Scale = kg	(–)	(+)	(–)	(–)	(–)
Snow cover	Mean snow cover (Normalised Differential Snow Index) within a 50-km buffer. Scale = 0–100	(–)	(+)	(–)	(–)	(–)
Productivity	Mean Normalised Difference Vegetation Index (NDVI) within a 50-km buffer. Scale = –1 to 1	(+)	(~)	(+)	(~)	NA
Human footprint	Mean measure of human modification within a 50-km buffer. Scale = 0–1	(~)	(~)	(+)	(~)	(+)
Wolves	Whether wolves <i>Canis lupus</i> occurred in the study area when the samples were collected	(~)	(+)	(~)	(~)	(~)
Puma	Whether pumas <i>Puma concolor</i> occurred in the study area when the samples were collected	(~)	(+)	(–)	(~)	(~)
Ungulate %FO	Percent frequency of occurrence of ungulates from the diet dataset.	(–)	NA	(–)	(–)	(–)
Lagomorph %FO	Percent frequency of occurrence of lagomorphs from the diet dataset	(–)	(~)	NA	(–)	(–)
Small mammal %FO	Percent frequency of occurrence of small mammals from the diet dataset	(–)	(~)	(–)	NA	(–)

and ProQuest in Spanish and French (this was not possible on Web of Science), because the coyote's range extends into Central America and Canada and studies may have been published in those languages (Appendix S2). These searches resulted in ≥2066 potentially appropriate results (see Appendix S1 for why '≥'). We scanned titles and abstracts for evidence of quantified coyote diet results and downloaded 221 publications for further review. We also used a 'snowball' approach to identify additional articles missed during our above searches, wherein we reviewed the literature cited sections of the first 100 of the 221 screened studies (sorted alphabetically). We stopped at 100 because our rate of new article discovery had slowed dramatically by articles 80–100. This snowball search resulted in an additional 29 studies. In total, we downloaded 250 studies subject to additional screening through eight criteria designed to standardise our analyses (Appendix S3):

1. Samples were scat and not intestinal tracts.
2. Dietary data were assessed using morphometric methods and recorded as the percentage frequency of occurrence (%FO; the number of scat samples found to contain a given prey category divided by the total number of samples). Note that %FO can total >100% for a given dataset because each scat can contain more than one prey category.

3. Dietary data were reported by season (i.e. not just an annual average).
4. Seasonal sample sizes were ≥20.
5. If sample sizes for each season were not reported, then the total sample size divided by number of seasons was ≥50.
6. Samples were unique (i.e. we generally used the peer-reviewed article if the same results were published in a thesis or dissertation).
7. Authors reported all contents in samples (i.e. we excluded studies that were not comprehensive in their description of diet and only focused on certain food categories).
8. At least four of the six most consumed food categories (ungulates, lagomorphs, small mammals, vegetation, birds and invertebrates) were reported.

Data collection

We retained 93 studies after implementing our criteria for inclusion, which contained 294 seasonal records. For each study, we recorded the location, the sample size for each season and the median year it occurred. We recorded the latitude and longitude when provided, but often had to estimate the coordinates by visually selecting a centroid using figures provided by the authors or searching for the study site on Google Maps. Some studies reported data from multiple study sites, in which

case we recorded information from each study site separately. We recorded which seasons were reported and, unless specified by the authors, classified spring as March–May, summer as June–August, autumn as September–November and winter as December–February. Some studies only reported a wet and dry season, which we entered as either summer or winter depending on which climate the study took place in (e.g. southern México's wet season is in summer, while California's wet season is in winter).

We recorded %FO of 12 food categories: 1) small mammals (e.g. small rodents); 2) lagomorphs; 3) wild ungulates (hereafter 'ungulates'); 4) wild pigs *Sus scrofa*; 5) livestock (including poultry); 6) Carnivora (including opossums *Didelphis virginiana*, domestic cats *Felis catus* and domestic dogs); 7) birds; 8) reptiles and amphibians (hereafter, 'reptiles' because amphibians were very rarely reported); 9) invertebrates (e.g. Arthropoda); 10) vegetation (e.g. fruit); 11) anthropogenic foods; and 12) other foods (e.g. beavers *Castor canadensis* and fish). For most prey categories, we summed %FO values for different species within a single category. However, small prey item values are potentially artificially inflated when using %FO because multiple species can be in a single sample (Reynolds & Aebischer 1991). Therefore, for small mammals, vegetation and invertebrates, we recorded the largest %FO value for a species in those categories (Doherty et al. 2018). For studies that reported grass or pine needles as the greatest vegetation %FO ($n = 5$), we chose the next highest %FO value to represent vegetation for that dataset because these items are sometimes inadvertently collected with scat samples. Each of the 12 food categories except wild pigs received a value for each season in a study (i.e. we entered a zero if the category was not reported; Lange et al. 2021). We chose this approach because we assumed that, unless we had reason to believe otherwise (and had excluded the study; see criteria seven and eight above), authors reported coyote diets comprehensively. For wild pigs, we only included studies that reported them ($n = 48$), given that their range has been limited to the southern USA and parts of California (Bevins et al. 2014), and so they did not co-occur with coyotes in most of the studies. Therefore, our summary statistics for wild pigs represent their consumption by coyotes where the two species co-occur.

Ecoregional patterns

In order to quantify geographic differences in coyote diet, we calculated the mean %FO for each of the 12 food categories within eight Level I North American ecoregions (United States Environmental Protection Agency 2020). This layer had 15 initial categories, but we combined North

American deserts and southern semi-arid highlands (as 'North American deserts') because they are both arid and border each other. We also combined Temperate sierras, Tropical dry forests and Tropical wet forests (as 'southern forests') due to small sample sizes for the latter two ($n = 1, 2$, respectively), proximity to each other and sharing tree cover as a common attribute.

We tested for differences among ecoregions using generalised linear mixed models with a negative binomial distribution and site as a random effect using the R package glmmTMB (Brooks et al. 2017). Site was a random effect because most (79/93) of the studies reported data from multiple seasons collected from the same study site. There were also four pairs of studies that occurred in the same study area but during different years. Our response variables were %FO of the six most consumed food items (small mammals, lagomorphs, vegetation, ungulates, invertebrates and birds – those that collectively comprised ~90 %FO; Fig. 1). We set the Great Plains ecoregion as the reference category, assessed model fit (dispersion parameter ~1) and only reported effects from ecoregions whose 95% confidence intervals did not overlap zero.

Assessing continental patterns

We evaluated support for the hypothesised influence of season, coyote body mass, environmental conditions (snow cover, human footprint, productivity), presence of large carnivores and consumption of alternative food items on coyote dietary diversity and consumption of the four core food items (Table 1). For the dietary diversity analysis, we used small mammals, lagomorphs, vegetation, ungulates, invertebrates and birds in our calculations because of their prevalence in coyote diet. We then conducted separate analyses on small mammals, lagomorphs, vegetation and ungulates because they all occurred in at least 20% of scats on average (Fig. 1) and they were the most consistently reported by authors (Appendix S4).

COYOTE MASS

We estimated the body mass (kg) of coyotes for each of our datasets using a compilation of 65 studies that weighed coyotes (Hinton et al. 2019; Appendix S5). We used the mean mass from the nearest mass study to represent each diet study.

ENVIRONMENTAL CONDITIONS

We used the rgee package (Aybar et al. 2020) in R to interface with Google Earth Engine (Gorelick et al. 2017) and calculate the mean value of snow cover, human footprint and productivity within a 50-km radius buffer of

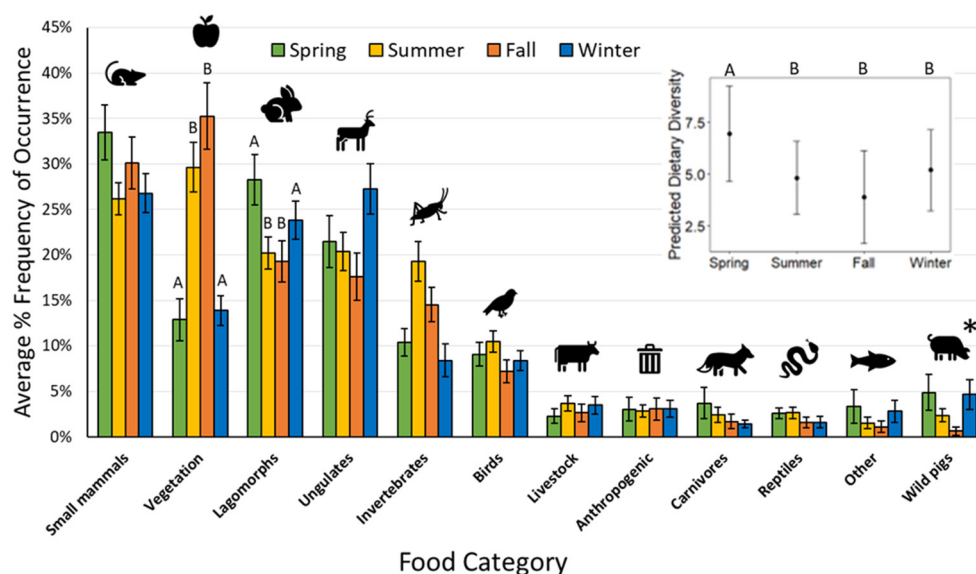


Fig. 1. Rangewide coyote *Canis latrans* diet. The main chart shows the mean percent frequency of occurrence (error bars represent standard error) for each of the 12 food categories in coyote diet in four seasons. Note that %FO can sum to >100% because each scat can contain more than one prey category. The letters above the vegetation and lagomorph bars indicate which seasons were significantly different from one another. Wild pigs *Sus scrofa* have an asterisk because their means were calculated only from studies which reported them, unlike the other food categories where 'zero' was entered if the category was not reported. The smaller chart shows model-predicted values of Levins' B from the dietary diversity analysis.

the centroid of each study site. We chose 50 km (7854 km² total area; Newsome et al. 2016) because it was a large enough buffer to encompass many coyote home ranges (mean home range: 18.7 km²; from Danner & Smith 1980, Kamler et al. 2006, Ward et al. 2018) and the entirety of the study area of nearly all studies, while not being so large as to include too much area outside of the zone where samples were collected. We used the Terra Snow Cover Daily Global 500 m data from the Earth Engine Data Catalogue (Hall et al. 2020) available from 2000 to present. We calculated the mean snow cover (based on the Normalised Difference Snow Index) within each 50 km radius buffer for each season from 2000 to 2015, then calculated the mean of those 16 values across years to obtain a single average snow cover value for each season. We estimated environmental productivity using the NOAA Climate Data Record of Normalised Difference Vegetation Index (NDVI) at a 0.05° resolution from the Earth Engine Data Catalogue (Vermote et al. 2020). We calculated the mean of NDVI values from 1981 to 2010 to estimate a single long-term value for each site (Doherty et al. 2018). We used long-term means for snow cover and NDVI because we wanted to include studies that occurred before these remotely sensed data were available. We calculated human footprint using the 1 km Global Human Modification dataset in the Earth Engine Data Catalogue (a cumulative measure of human modification that combines human settlement, agriculture, transportation,

mining, energy production and electrical infrastructure; Kennedy et al. 2019).

LARGE CARNIVORES

We used range maps of large carnivores (wolf, puma, jaguar *Panthera onca*, brown bear *Ursus arctos*, black bear *Ursus americanus*) from various sources to record whether each species was present on the landscape during each coyote diet study. We used Laliberte and Ripple (2004) for all large carnivores, which we supplemented with maps from Defenders of Wildlife for wolves (Defenders of Wildlife 2019) and Vaughan and Pelton (1995) for black bears. Wolves included red wolves *Canis rufus* and all North American subspecies of grey wolf, and we made sure to account for timing of reintroductions (National Park Service 2019). We used Panthera's range map for jaguars (Panthera 2016). We created three variables with these data: 1) wolf presence, 2) puma presence and 3) the number of large carnivores present (theoretical range: 0–5). We created a separate variable for wolves because of their propensity to interact with coyotes where they co-occur (both negatively, through killing coyotes, and positively, through provisioning carrion; Berger & Gese 2007, Sivy et al. 2017). We chose to separate pumas as well because they provide as much carrion to meso-carnivores as wolves (Prugh & Sivy 2020) and are sympatric with coyotes over ~50% of the coyote's current range.

ALTERNATIVE FOOD ITEMS

Like other carnivore diet meta-analyses (Lozano et al. 2006, Doherty et al. 2018), we were interested in how the consumption of core food items influenced dietary diversity and consumption of other core food items. For example, a negative relationship between a specific food item and dietary diversity would suggest that coyotes prioritise that food item. We used %FO of lagomorphs and %FO of small mammals because some researchers have suggested that coyotes exhibit selection for them (Bartel & Knowlton 2005, Prugh 2005), and %FO of ungulates because they are of general interest to wildlife managers.

Statistical analysis

We calculated dietary diversity for each dataset using Levins' measure of niche breadth (Levins' B ; Levins 1968), where Y is the total number of scat samples and N_j is the number of samples containing the j th food category of interest:

$$B = \frac{Y^2}{\sum N_j^2}.$$

In this context, Levins' B would be highest when %FO is equal across the six food categories and lowest when diet is composed of one food category. We log-transformed the Levins' B values and used the lme4 package (Bates et al. 2015) to test for multicollinearity among all of our predictor variables by measuring their variance inflation factor (VIF) using a global model with a negative binomial distribution and site as a random effect. We removed the 'number of large carnivores' variable so that all VIF values were <2.2 (Zuur et al. 2010). We then tested for pairwise correlations between the remaining continuous variables and found no Pearson's $r > |0.7|$. We centred and scaled continuous predictor variables (mass, snow cover, human footprint, productivity, small mammal %FO, lagomorph %FO and ungulate %FO), set 'autumn' as the reference category for season and set 'not present' as the reference category for wolves and pumas. We evaluated support for our various hypotheses (Table 1) by developing 18 a priori models (Appendix S6).

We used a similar statistical approach for our core food item analyses. We started with four global models, one for each food item, and tested for multicollinearity using the glmmTMB package (Brooks et al. 2017) with a negative binomial distribution and site as a random effect. We ultimately excluded the 'number of large carnivores' variable from all model sets, the season variable from the ungulate model set and the productivity

variable from the vegetation model set (Table 1) to ensure all variables had a VIF <2.2 . Depending on the dietary item, we developed 16 or 17 a priori models (Appendices S7–S10).

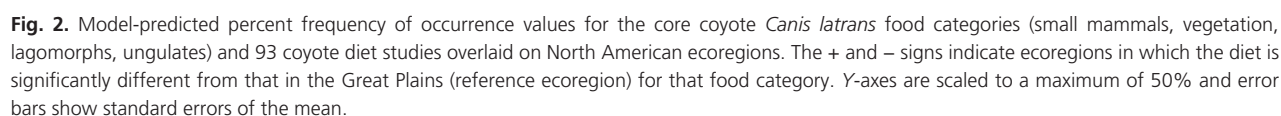
For each analysis, we checked model fit (dispersion parameter ~ 1) using the DHARMA package (Hartig 2020), and ranked models based on AICc weights using the MuMIn package (Barton 2009). We based inference on models with a delta AIC ≤ 2 (Burnham & Anderson 2002), and only reported effects from variables whose 95% confidence intervals did not overlap zero. We conducted all analyses in R version 4.0.2 (R Core Team 2020).

RESULTS

Ninety-three studies met all of our criteria for inclusion, which contained 294 seasonal records on which we based our analyses (Appendix S14). These studies represented 63341 coyote scats, with a mean sample size of 215 (standard error = 20). Most of the studies were from the USA ($n = 71$), followed by Canada ($n = 11$) and México ($n = 11$; Fig. 2). Seventy-eight studies reported data from multiple seasons; summer ($n = 95$) and winter ($n = 86$) were best represented, followed by spring ($n = 57$) and autumn ($n = 56$). For most of the studies ($n = 85$), the median year was after 1970. On average, small mammals occurred most frequently in the diets of coyotes (mean %FO $\pm$ standard error = $29\% \pm 1.2\%$), followed by vegetation ($23\% \pm 1.4\%$), lagomorphs ($23\% \pm 1.1\%$), ungulates ($22\% \pm 1.3\%$), invertebrates ($14\% \pm 1.0\%$), birds ($9\% \pm 0.6\%$), wild pigs ($3\% \pm 0.5\%$), livestock ($3\% \pm 0.5\%$), anthropogenic foods ($3\% \pm 0.5\%$), carnivores ($2\% \pm 0.5\%$), reptiles ($2\% \pm 0.5\%$) and other food items ($2\% \pm 0.5\%$; Fig. 1).

Ecoregional patterns

At least 80% of coyote scats in every ecoregion contained small mammals, vegetation, lagomorphs or ungulates, though there was variability among ecoregions in which supplementary foods made up the remainder of coyote diet (Appendix S4). Relative to the Great Plains, in northern forests, small mammal %FO was 16% greater, lagomorph %FO was 29% greater and ungulate %FO was 29% greater (Fig. 2, Appendix S11). In eastern temperate forests, vegetation %FO was 14% greater and ungulate %FO was 26% greater. In north-western forested mountains, ungulate %FO was 19% greater and lagomorph %FO was 12% less. In marine west coast forests, ungulate %FO was 18% greater. In North American deserts, lagomorph %FO was 15% greater and ungulate %FO was 7% less. In southern forests, lagomorph %FO was 12% less. We detected no ecoregional differences in invertebrate and bird %FO (95% confidence intervals overlapped zero; Appendix S11).



The top model for dietary diversity was a subglobal model (season + mass + human footprint + small mammal %FO + lagomorph %FO + ungulate %FO), which garnered 92% of model weight (Appendix S6). According to this model, coyote diet was 22% more diverse in spring than in autumn (Figs 1 and 3). Dietary diversity (Levins' B) increased by 0.9 for every 10% increase in human footprint, and decreased by 1.7, 1.4 and 1.1 for every 10% increase in small mammal, lagomorph and ungulate %FO respectively (Fig. 4).

The top predictive model for small mammals was a sub-global model (season + mass + human footprint + lagomorph %FO + ungulate %FO), which garnered 60% of the model weight and was ~3 times better supported than the next best model (Appendix S7). However, the only variable that did not overlap zero was ungulate %FO. Small mammal %FO decreased by 0.5% for every 10% increase in ungulate %FO, though the upper 95% confidence interval was zero (Fig. 5).

The top predictive model for lagomorphs was a subglobal model (season + mass + human footprint + small mammal

There were two top predictive models for the vegetation analysis: the global model (season + mass + productivity + snow cover + human footprint + wolf + puma + small mammal %FO + lagomorph %FO + ungulate %FO), which garnered 55% of the model weight, and a subglobal model (season + mass + human footprint + small mammal %FO + lagomorph %FO + ungulate %FO), which garnered 42% of model weight (Appendix S9). Season had the strongest effect in both models (Fig. 3), where vegetation %FO was 22% and 20–21% less in spring and winter, respectively, than in autumn (Fig. 1). The only other shared variable with 95% confidence intervals not overlapping zero was ungulate %FO – vegetation %FO decreased by 1.0–1.2% for every 10% increase in ungulate %FO (Fig. 5). The global model also predicted a 0.8% decrease in vegetation %FO for every 10% increase in lagomorph %FO, and a 5% decrease in vegetation %FO when sympatric with wolves (Fig. 5).

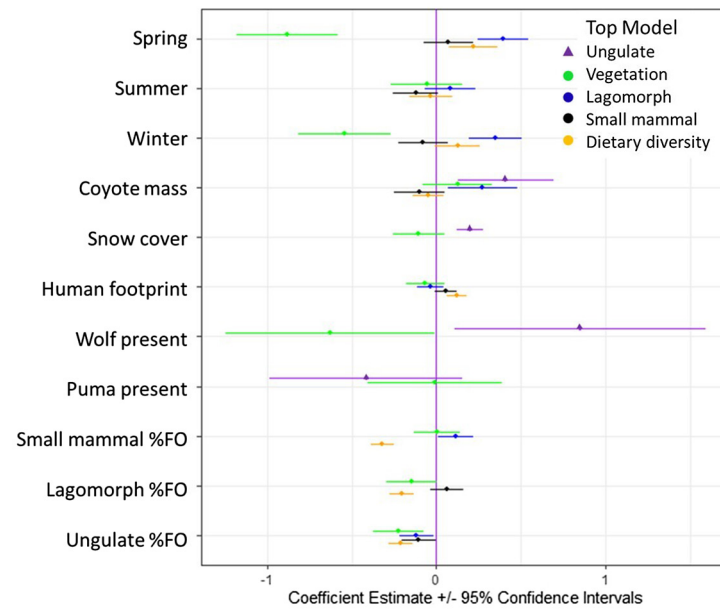


Fig. 3. A visual summary of the effects from variables in each of the top models from the coyote *Canis latrans* dietary diversity, small mammal, lagomorph, vegetation and ungulate analyses. The effects from season are relative to autumn, and the effects from wolf *Canis lupus* and puma *Puma concolor* are relative to those species not being present. There were two candidate models for the vegetation analysis and three for the ungulate analysis, yet we only show the model with the highest model weight for clarity (effects from other candidate models can be found in Appendices S9 and S10).

Ungulates

There were three top predictive models for the ungulate analysis: one of the subglobal models (mass+snow cover+wolf+puma) garnered 39% of model weight, a

more complex subglobal model (mass+productivity+snow cover+human footprint+wolf+puma) garnered 31% of model weight and the global model (mass+productivity+snow cover+human footprint+wolf+puma+lagomorph %FO+small mammal %FO) garnered 30% of model weight

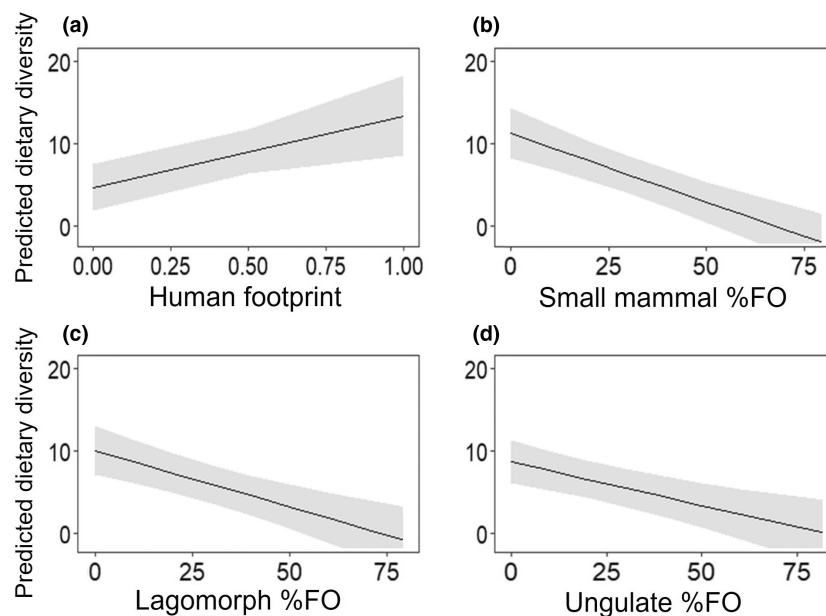


Fig. 4. Important non-categorical factors influencing coyote *Canis latrans* dietary diversity (Levins' B) from the top model: model-predicted values of dietary diversity against (a) human footprint, (b) small mammal % frequency of occurrence (FO), (c) lagomorph % FO and (d) ungulate % FO.

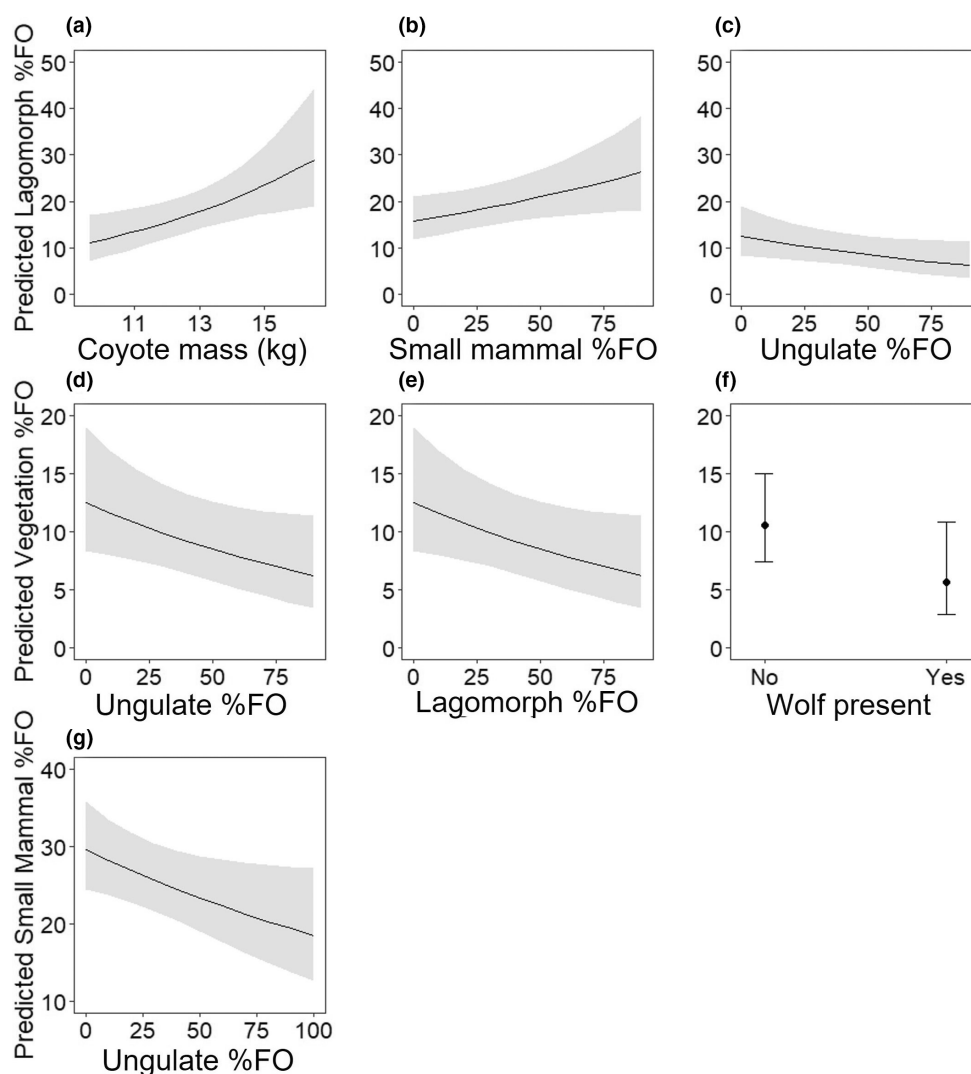


Fig. 5. Important non-season factors influencing coyote *Canis latrans* consumption of lagomorphs, vegetation and small mammals from the top models: model-predicted values of lagomorph % frequency of occurrence (FO) against (a) coyote mass (kg), (b) small mammal % FO (c) and ungulate % FO. We also show model predicted values of vegetation % FO against (d) ungulate % FO, (e) lagomorph % FO and (f) presence of wolves. Lastly, we show model predicted values of (g) small mammal % FO against ungulate % FO.

(Appendix S10). Despite this model selection uncertainty, the three variables with the strongest effects (mass, snow cover, and presence of wolves) were in all three models (Appendix S13). Ungulate %FO increased by 2.4–2.7% for every 1 kg increase in coyote body mass, increased by 1.4% for every 10% increase in snow cover and was 12% greater in areas coyotes were sympatric with wolves (Fig. 6). The more complex subglobal model predicted a 0.8% decrease in ungulate %FO for every 10% increase in human footprint (Fig. 6). The global model predicted a 0.1% decrease in ungulate %FO for every 10% increase in small mammal %FO (Fig. 6).

DISCUSSION

In this first range-wide meta-analysis of coyote diet, we found that coyotes had diverse diets dominated by small mammals, vegetation, lagomorphs and ungulates. Invertebrates and birds were consistent supplemental foods throughout the coyote's range, perhaps representing opportunistic consumption. Although the remaining food categories each only made up 2–5% of coyote diets on average, some of them highlight important ecological interactions. For example, while coyotes can be vexing sheep predators in some places (Mcinturff et al. 2021), our

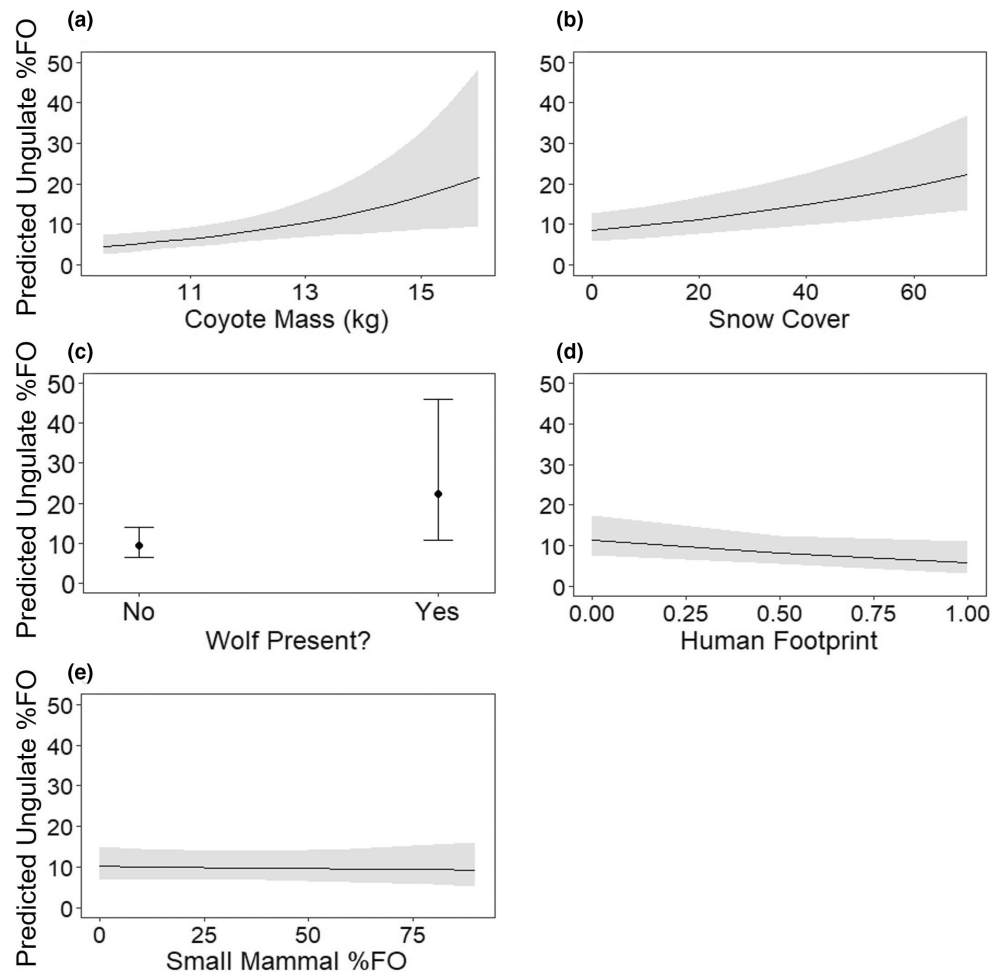


Fig. 6. Important factors influencing coyote *Canis latrans* consumption of ungulates from the top models: model-predicted values of ungulate % frequency of occurrence (FO) against (a) coyote mass (kg), (b) snow cover, (c) wolf presence, (d) human footprint and (e) small mammal % FO.

continental analysis showed that livestock were not an important part of coyote diets overall. By contrast, infrequent consumption of carnivores may not reflect the impact coyotes can have on smaller carnivore behaviour and abundance (Nelson et al. 2007). In the following sections, we discuss the factors that most influenced variation in dietary diversity and consumption of our core food categories.

Ecoregional patterns

Like the diet of other canids (Newsome et al. 2016, Doherty et al. 2018), coyote diet varied among ecological zones across their range. Coyotes were generally more carnivorous in temperate forests than in other ecoregions, which seems to be largely driven by greater ungulate consumption in temperate forests. Vegetation consumption being highest in eastern temperate forests likely reflects relatively high availability of wild fruits, as demonstrated by coyote diet studies from the

south-eastern USA (Schrecengost et al. 2008). Low lagomorph consumption in north-western forested mountains and southern forests could reflect less lagomorph availability; both ecoregions are primarily composed of mature forest or mountains, which do not provide an optimal combination of cover and forage for lagomorphs (Virgós et al. 2003).

Dietary diversity

Coyote dietary diversity was most related to mammal consumption, followed by season and human footprint. While small mammal, ungulate and lagomorph consumption each had a negative effect on dietary diversity, the effect of small mammals was 50% larger than that of lagomorphs and ungulates. This suggests that coyotes prioritise each of these mammals in certain contexts, and apparently do so with small mammals more often or more intensely than lagomorphs or ungulates. In Europe, wildcat *Felis silvestris* dietary diversity

is also negatively related to rodent consumption (Lozano et al. 2006), while Eurasian badger *Meles meles* dietary diversity is negatively related to rabbit *Oryctolagus cuniculus* consumption (Fedriani et al. 1998). However, badgers can specialise in other food sources like earthworms, insects or fruit, which suggests that they could be opportunistic to the point of local specialisation (Fedriani et al. 1998). It is possible that some coyote populations are also locally specialised – coyotes select for small mammals (Bartel & Knowlton 2005) or lagomorphs (Hernández et al. 2002) in some portions of their range. These more specialised coyote populations are likely to contribute less to community stability than generalist populations which more readily switch between food items (Murdoch 1969). However, we suspect that most coyotes' foraging strategies change throughout the year as relative abundances of foods change. For example, vegetation is most available in the summer and autumn, ungulate neonates are only available in the summer (and late spring in some regions) and ungulate carcasses are most available in the winter. The lower availability of these foods could explain why we found that dietary diversity was greatest in the spring. Indeed, although they were not included in our dietary diversity calculations, consumption of several less common food categories (carnivores, wild pigs and other foods) was also highest in the spring, providing further support that coyote foraging is most generalised in the spring.

Coyote diets were more diverse in areas with greater human development, which could be due to extrinsic and intrinsic factors. At large scales, human population density (a component of human footprint) has been demonstrated to be positively correlated with vertebrate diversity (Balmford et al. 2001, Chown et al. 2003), which could translate to higher predator dietary diversity. However, our raw data showed that dietary diversity was lowest at low levels of human footprint, highest at intermediate levels and moderate at high levels. This suggests that coyotes living in areas with relatively little human disturbance may be relatively specialised, while coyotes living in moderately disturbed areas are most generalised and have more diverse diets (Fedriani et al. 2001). Human footprint also had a moderate positive correlation with European red fox *Vulpes vulpes* dietary diversity, which the authors suggest could reflect increased habitat diversity resulting from fragmentation (Soe et al. 2017). By contrast, a global meta-analysis of grey wolf diet found no effect of human footprint (Newsome et al. 2016). It is possible that the dietary plasticity of red foxes and coyotes could in part explain their ability to tolerate, and even exploit, human development.

Lagomorphs and small mammals

Ungulate %FO had a weak negative effect on lagomorph and small mammal %FO, though maybe for different

reasons. For lagomorphs, the negative relationship with ungulates may primarily reflect ecoregional differences – lagomorph consumption was relatively high and ungulate consumption relatively low in North American deserts, and the opposite pattern was true in north-western forested mountains. These patterns could reflect differences in lagomorph and ungulate availability between these ecoregions. In contrast, small mammals were the most consistently eaten food items in all seasons and ecoregions, suggesting that large-scale differences do not explain the relationship with ungulate consumption. Our finding is potentially related to a combination of small mammal specialisation (see 'Dietary diversity' section), high ungulate consumption in some contexts (e.g. in snow-covered landscapes; see 'Ungulates' section) or bias in small mammal detection when ungulates are in scats (see 'Limitations' section).

Lagomorph consumption was also related to small mammal consumption, season and coyote mass. Our finding that lagomorph consumption and small mammal consumption were positively related was the only instance where the relationship between two food items was positive. Although the effect was weak, perhaps these two food items require similar foraging strategies, and therefore are somewhat coupled in coyote diets. Greater lagomorph consumption in the spring and winter may reflect reduced availability of other foods (Korslund & Steen 2006), increased availability of (inexperienced) juvenile lagomorphs born that year (in spring; Rogowitz 1992) or increased vulnerability in sparse understorey (in winter; Korslund & Steen 2006). We also found that larger coyotes ate more lagomorphs. This result makes intuitive sense from a metabolic perspective because larger coyotes cannot, on average, expend the same amount of energy pursuing small food items (i.e. small mammals, invertebrates) as smaller coyotes (Carbone et al. 1999).

Vegetation

Vegetation consumption was greater during the summer and autumn when many fruits are most available. This pattern is similar in other omnivorous canid species – reviews of Iberian red fox and golden jackal diets also found greater consumption of vegetation in the summer and autumn (Díaz-Ruiz et al. 2013, Lange et al. 2021). Indeed, the sharp increase in vegetation consumption during the summer and autumn we found could partially explain the negative relationship between it and both ungulate and lagomorph consumption. If this is true, increased vegetation consumption during these seasons appears to have no commensurate effect on small mammal consumption. Lastly, less vegetation consumption by coyotes that are sympatric with wolves may be a by-product of higher consumption of ungulates in areas of sympatry

(see ‘Ungulates’ section) or reflect lower availability of vegetation in those areas.

Ungulates

Coyotes ate more ungulates in areas of sympatry with wolves, which is likely to reflect coyotes scavenging wolf-provisioned carrion (Wilmers et al. 2003, Sivy et al. 2017). All 10 of the studies in our analysis where coyotes co-occurred with wolves were from western North America, where coyotes are rarely documented killing adult ungulates (except see e.g. Lingle & Pellis 2002). This suggests that, rather than niche partitioning taking place in areas of sympatry, coyote diets are more similar to wolf diets where they co-occur (Hinton et al. 2017). Wolves may not always augment coyote diet in this way, however; one study in Michigan, USA, found that coyotes ate less meat in areas where they were sympatric with wolves than where wolves were not present (Colborn et al. 2020). In contrast to wolves, pumas had no effect on coyote consumption of ungulates, even though they have been estimated to provision just as much carrion to mesocarnivores as wolves (Prugh & Sivy 2020). Perhaps, puma provisioning is more diluted given the much larger area in which they are sympatric with coyotes, or perhaps behavioural differences (i.e. caching or carrion defence) make puma kills more difficult for coyotes to exploit (Allen et al. 2015).

Snow cover is likely to facilitate consumption of ungulates by coyotes through several mechanisms. In northern latitudes and at high elevations, adult ungulate mortality is relatively high during the winter, when reduced forage availability can lead to starvation and increased vulnerability to predation (Coulson et al. 2001). This increases the availability of carcasses on the landscape, which also tends to last longer in the winter than in other seasons (Peers et al. 2020). Deep snow also hampers the ability of ungulates to escape from predators, including coyotes (Patterson & Messier 2003), and snow cover typically coincides with when other foods of coyotes are less available (Korslund & Steen 2006). While we were unable to determine the proportion of ungulates that were scavenged, the strength of the wolf and snow cover variables suggest that a substantial proportion of ungulate consumption by coyotes is likely to be scavenging (Prugh & Sivy 2020). Differentiating ungulate predation and scavenging in coyote diets is critical for contextualising their ecosystem function. Insight could be gained through differentiating between decomposed meat and fresh meat in coyote intestinal tracts (Best et al. 1981), observing coyote foraging behaviour (Lingle & Pellis 2002), ungulate cause-specific mortality studies (on both adults and neonates) and well-designed field experiments.

Our finding that larger coyotes ate more ungulates than smaller ones is likely to reflect a combination of increased predation and scavenging ability of larger coyotes. Previous research has shown that larger coyotes (in north-eastern North America) are capable predators of adult ungulates (Patterson & Messier 2003, Benson et al. 2017). While not as large as north-eastern coyotes, south-eastern coyotes are larger than western coyotes (Hinton et al. 2019), and have been documented killing adult white-tailed deer (Chitwood et al. 2014). One diet study in North Carolina, USA, showed that larger coyotes eat more ungulates than smaller ones, which the authors attribute to both predation and scavenging (Hinton et al. 2017). Moreover, south-eastern coyotes appear to be particularly adept at killing white-tailed deer fawns. On average, 44% of white-tailed deer fawn mortality in the southeast can be attributed to coyotes, compared to 16% in other regions of the eastern USA (Kilgo et al. 2019). Indeed, the mean ungulate %FO in the south-eastern states (Alabama, Florida, Georgia, Mississippi, North Carolina, South Carolina, Virginia, West Virginia) in our study was 42% – on a par with the northern forests ecoregion (where ungulate consumption was highest). Larger coyotes may also scavenge more, and be better able to defend carrion from other scavengers, than smaller coyotes (Macdonald & Sillero-Zubiri 2004). Regardless of how larger coyotes obtain ungulates, these results provide the first evidence that a carnivore’s mass influences diet throughout its range.

Limitations

Although we believe our findings represent an important step forward in coyote ecology, our methods and results have several limitations. First, %FO is not ideal for understanding diet from a metabolic perspective because it does not account for differences in energy content among different food items (Klare et al. 2011). A brown bear diet meta-analysis compared four methods of diet assessment and found that %FO under-represented vertebrate importance by three to four times, while over-representing vegetation importance by three to four times, relative to a method that used biomass estimates to account for the energy content of these food items (Bojarska & Selva 2012). Therefore, it is likely that vertebrates are more important and vegetation less important for coyote metabolism than we were able to show here.

Second, recent research has shown that relying on morphological or other cues to identify the depositor of scats in the field can lead to species misidentification, and genetic approaches should be used instead (Monterroso et al. 2019). While we do not believe misidentification was widespread enough to influence our findings based on 93 studies over a continental scale, we acknowledge that studies in our dataset may have included scats from other species (e.g.

bobcat *Lynx rufus*; Morin et al. 2016) and encourage the use of genetic approaches in future coyote diet studies where risk of misidentification in the field is high. Similarly, using genetics to identify the food items that were consumed (e.g. meta-barcoding) may reduce sources of bias in some cases. For example, Morin et al. (2019) found that detectability can vary among food items when using morphometrics, for example, deer hair can dominate a sample and obscure the presence of small mammal hair.

Third, considering the spatial and temporal extent of the studies we used in our analysis, we were limited by the availability of remotely sensed variables. For example, unlike snow cover and productivity (long-term averages), the human footprint data had a median date of 2016 (Kennedy et al. 2019), potentially not accurately representing human footprint from studies decades earlier. Likewise, a yearly measure of snow cover would have captured variation among years in a given study area, but snow cover data were only available beginning in 2000 (Hall et al. 2016), which would have limited the number of studies we could include.

Fourth, we were unable to test directly how our hypothesised factors influenced coyote diet. For example, it is possible that coyote diet also feeds back to influence coyote size (e.g. coyotes that eat more ungulates, grow bigger), in addition to the directionality that we suggest. We were also unable to quantify how the availability of food items influences diet. For example, it is possible that ungulate abundance is correlated with coyote mass, therefore also explaining the geographical patterns of ungulate consumption we found. Unfortunately, food availability data are not available at these large scales, supporting the need for continued localised studies of coyote foraging behaviour and dietary selection.

Looking ahead

Coyotes in North America have all but run out of land to colonise eastward (Hody & Kays 2018), but they are likely to continue to expand their range northward and southward. Warming temperatures at the northern edge of their range are likely to facilitate expansion farther north, while they also have been expanding closer to South America at the southern edge of their range (Méndez-Carvajal & Moreno 2014, Hody et al. 2019). Unfortunately, none of the studies that we included in our analyses was from Central America, and, despite searching in Spanish, we only found one study in our literature search from this region (El Salvador; Colacho Ponce 2009) which reported food categories too broadly for our use (e.g. 'mammals'). Nevertheless, coyote diet in the southern forests ecoregion is likely to be indicative of their diet farther south, and potentially of what they would be in South America as

well. We recommend that more coyote diet research be undertaken in Central America to increase our understanding of the potential impacts of coyotes in the Tropics.

CONCLUSIONS

Our results advance our understanding of coyote diet and broader ecology in several ways. First, while larger carnivore species are generally known to consume larger prey (Carbone et al. 1999), to our knowledge, this is the first time that variability in a species' mass has been correlated with differences in diet, where larger coyotes consumed more larger food items (ungulates and lagomorphs) than smaller coyotes. Second, we show that the presence of top predators (wolves and humans) is related to coyote diet, though in opposing ways. Coyotes consumed more ungulates and less vegetation where they were sympatric with wolves, and consumed less ungulates yet had more diverse diets in areas with greater human footprint. Third, although the diets of coyotes are flexible, they can be relatively specialised on (small) mammals in some circumstances – narrowing their dietary diversity. We also found that ungulate consumption was negatively related to consumption of all three other core food items, suggesting that coyotes prioritise ungulates in some contexts. Although we have long known that coyotes eat ungulates (Sperry 1933) and prey on adults in some circumstances, our results show that coyotes eat more ungulates in temperate forests, much of which they have colonised in the last 120 years. Scavenging appears to be an important foraging strategy for coyotes, though more work is needed to quantify where and when it occurs most.

Collectively, our findings emphasise the need for continued local or regional studies to understand the highly variable ecological effects of coyotes across their expanding range. The variable diets we observed, both seasonally and across their historical and newly expanded ranges, suggest that coyotes influence ecosystems at multiple trophic levels. Coyotes act as apex carnivores in large portions of their range (Gompper 2002), but understanding how coyotes influence ungulate populations (and act as analogues to wolves) will require continued investigations into their differential predation rates on ungulate life stages, and potential non-consumptive effects (Prugh et al. 2019). Coyotes also impact middle trophic levels (e.g. smaller carnivores, small mammalian herbivores and granivores) to varying extents throughout their range (Nelson et al. 2007), requiring investigations into their role as modulators of the abundance and behaviour of these important species. They also interact directly with the lowest trophic levels through vegetation consumption and seed dispersal (Roehm & Moran 2013). Indeed, these trophic interactions happen across a gradient of human

development, which will necessitate continued research at the interface of human–coyote conflict, ecology and evolution (Schell et al. 2018, Brooks et al. 2020).

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DATA AVAILABILITY STATEMENT

Data from our study are freely available online at Dryad: <https://doi.org/10.5061/dryad.866t1g1t0>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Flowchart illustrating the literature search process, criteria for inclusion, and the number of articles retained or excluded at each step.

Appendix S2. Search terms used to find coyote diet studies using Google Scholar, Web of Science, and ProQuest in English, Spanish, and French.

Appendix S3. Additional details about the eight criteria for inclusion we used to decide which publications to use in our analyses of coyote diet.

Appendix S4. Percent frequency of occurrence of all 12 food categories in coyote diet categorised by ecoregion.

Appendix S5. Locations of 65 datasets that weighed coyotes; compiled by Hinton et al. (2019).

Appendix S6. Model ranking results for the dietary diversity analysis.

Appendix S7. Model ranking results for the small mammal analysis.

Appendix S8. Model ranking results for the lagomorph analysis.

Appendix S9. Model ranking results for the vegetation analysis.

Appendix S10. Model ranking results for the ungulate analysis.

Appendix S11. Estimates and 95% confidence intervals from the ecoregion analysis on small mammals, lagomorph, vegetation, ungulates, invertebrates, and birds.

Appendix S12. Estimates and 95% confidence intervals for the top models ($\Delta AIC < 2$) from the dietary diversity, small mammal, lagomorph, and vegetation analyses.

Appendix S13. Estimates and 95% confidence intervals for the top models ($\Delta AIC < 2$) from the analysis investigating the consumption of ungulates.

Appendix S14. Metadata from the 93 studies we used in our coyote dietary meta-analysis.