OIKOS

Research article

Carnivore community reassembly provides a test of Eltonian niche conservatism

Mauriel Rodriguez Curras[1], **Philip J. Manlick**[2] **and Jonathan N. Pauli**[1]

[1]Department of Forest & Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA
[2]Pacific Northwest Research Station, USDA Forest Service, Juneau, AK, USA

Correspondence: Mauriel Rodriguez Curras (mauriel@berkeley.edu)

Oikos
2025: e10625
doi: 10.1111/oik.10625
Subject Editor: Sandra Hamel
Editor-in-Chief: Pedro Peres-Neto
Accepted 18 December 2024

The repatriation of species is common, especially in conservation efforts aimed at restoring trophic interactions. Whether the Eltonian niches of restored species are conserved in reassembled ecological communities is largely unknown. Within mammalian carnivores, we hypothesized that the Eltonian niches of sympatric competitors would be structured by trophic facilitation from subsidies provided by large carnivores (i.e. carrion) and humans (i.e. food subsidies). Using stable isotopes ($\delta^{13}C$, $\delta^{15}N$), we quantified the Eltonian niches of an apex predator, the grey wolf *Canis lupus* and two subordinate guild members, coyotes *Canis latrans* and red foxes *Vulpes vulpes*, from Michigan, USA across three periods that differed in community composition: a 'historical' carnivore community (1910–1930), a 'reduced' community which lacked wolves (1950–1970), and a 'reassembled' carnivore community featuring wolves as well as human food subsidies (2000–2020). In historical and reassembled communities, wolves constrained the niche space of coyotes via resource facilitation, regardless of human presence, such that the consumption of deer by coyotes increased by an average of 1.4–1.8-fold in the presence of wolves. Without wolves, coyotes exhibited an isotopic (dietary) niche breadth ~ 2–5× greater (3.33 ± 0.74‰^{2}) than in the historical (0.64 ± 0.11‰^{2}) and reassembled (1.66 ± 0.63‰^{2}) communities. Conversely, we found that the niche breadth of foxes was conserved across the historical (1.91 ± 0.41‰^{2}) and reduced (1.98 ± 0.75‰^{2}) communities but increased ~ 4-fold in the presence of human resource subsidies (7.52 ± 1.95‰^{2}). Notably, we found that trophic facilitation by wolves and resource subsidies from humans altered the foraging strategies of individuals, resulting in disparate foraging strategies for foxes in the reassembled community. Our results highlight that Eltonian niche conservatism in carnivore communities is driven by resource subsidies, both from the provisioning of carrion by large carnivores to meso-carnivores and from human foods subsidizing small carnivores. More broadly, our work suggests that large carnivore repatriation can restore some species interactions, while human resource subsidies can decouple others.

Keywords: Carnivore, Carnivora community, competition, niche conservatism, species interactions, suppression-facilitation

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

Niche theory provides a foundation for understanding competitive interactions (Grinnell 1917, Elton 1927, Hutchinson 1957). Competitors influence the critical components of a species niche (Case and Gilpin 1974), impacting resource utilization and trophic interactions (Macarthur and Levins 1967). Niche conservatism – the tendency of species to retain ecological characteristics across space and time – has emerged as a useful framework for ecologists to understand the roles of species within communities following the loss of community members (Peterson et al. 1999), the introduction of non-native invaders (Larson et al. 2010), and the putative replacement of species' ecological roles (Clark et al. 2021). Prior research has supported conservatism of phylogenetic (i.e. the tendency of related species to exhibit a similar niche space; (Losos 2008) and Grinellian (i.e. the retention of species–habitat associations through space and time; (Wiens and Graham 2005, Soberón 2007) niches. However, Eltonian niche conservatism has only recently been explored (Larson et al. 2010, Manlick et al. 2019, Medina and Almeida-Neto 2020). This comparatively limited advance could be due to the original nuanced definition of the Eltonian niche that emphasized the roles of species within the communities they lived in, namely their 'relations to food and enemies' and the comparison of a species niche to 'trades or professions or jobs in a human community' (Elton 1927, Dussault 2022). This focus on species interactions makes Eltonian niche conservatism inherently more difficult to examine, thereby complicating out ability to construct clear and testable hypotheses. Elton himself posited that the roles of species within their respective communities and ecosystems should be regarded as context-dependent characteristics rather than phylogenetic properties of organisms (Elton 1927). Thus, the functional role of a species (i.e. niche conservatism) is likely contingent upon the composition of the community and the ecosystem in which they occur (Dussault 2022). Eltonian niche conservatism, then, should be addressed in the context of community and trophic interactions between species – testing if species interactions, per se, are conserved as the environmental context changes.

The predictable characteristics of mammalian carnivore communities make them a useful model for understanding Eltonian niche conservatism. Large carnivores (Mammalia, Carnivora) shape ecological communities through both predation (Estes et al. 2011) and competitive interactions (Holt and Polis 1997). Carnivore communities are hierarchically structured by body size, whereby species that are between 2–5× larger than their competitors may physically harm or behaviorally displace subordinates (Palomares and Caro 1999, Donadio and Buskirk 2006). However, large carnivores may also provide meso- and small carnivores predictable and year-round scavenging opportunities through carrion (Wilmers et al. 2003, Roemer et al. 2009), especially during resource scarcity (Pereira et al. 2014). Not surprisingly, dietary overlap is a leading driver of interspecific competition and intraguild predation (Palomares and Caro 1999, Donadio and Buskirk 2006). Thus, resource provisioning by large carnivores draws subordinate carnivores into implicitly risky foraging locations – forcing decisions between food and safety. This hierarchical and nested structure of carnivore communities produces a dynamic interplay between suppression (e.g. interspecific killing) and facilitation (e.g. carrion subsidies (Prugh and Sivy 2020, Ruprecht et al. 2021); where competitive interactions are predicated by body size.

Resources provisioned by large carnivores, often in the form of ungulate carrion, are increasingly recognized as an important driver of community interactions (Wilson and Wolkovich 2011, Pereira et al. 2014, Perrig et al. 2023). These resources percolate through food webs (Selva and Fortuna 2007), supporting extensive networks of reticulate interactions, especially obligate and facultative scavenging (Wilson and Wolkovich 2011). Resource provisioning by large carnivores alters competition among subordinate species and, in some cases, offset the effect of suppression (Wilmers et al. 2003, Wilson and Wolkovich 2011). Indeed, carcasses provisioned by large carnivores can facilitate resource partitioning in carnivore communities by alleviating exploitative competition for small mammals (Sivy et al. 2018). Alternatively, human food subsidies in the form of agriculture, domestic livestock and human refuse can alter competition within carnivore communities (Newsome et al. 2015a, Manlick and Pauli 2020) and alter the co-existence dynamics between meso- and small carnivores (Murray et al. 2015, Pluemer et al. 2019). Determining how changes in large carnivore presence and increasing resource subsidies from humans influence dietary partitioning among carnivores is needed to better understand carnivore community dynamics, especially where carnivore abundance is expected to change as a result of anthropogenic activities (Chapron et al. 2014).

One of the most widely reestablished large carnivores, the wolf *Canis lupus*), is expected to have substantial top-down impacts on their primary prey and other carnivores at the community-level (Levi and Wilmers 2012, Ripple and Beschta 2012, Flagel et al. 2017). While previous research has focused on the top–down consequences of large carnivore extirpations and repatriations, less research has assessed how the functional return of large carnivores impacts the competitive interactions and niche characteristics of subordinate carnivores (Rodriguez Curras et al. 2024a). As large carnivores return to human landscapes (Chapron et al. 2014), it is critical to consider the impact of humans on the functional relationships that large carnivores could restore, and how they might deviate from our expectations. To our knowledge, however, no research has explicitly tested if the Eltonian niches of carnivores are conserved following the repatriation of a large carnivore to a landscape with increasing human use and anthropogenic resource subsidies.

To explore the consequences of large carnivore extirpation and subsequent recovery on Eltonian niche conservatism in subordinate carnivores, we quantified the resource use and trophic interactions between wolves, coyotes *Canis latrans*, and red foxes *Vulpes vulpes* across the Upper Peninsula (UP), Michigan, USA over 100 years of community change.

Notably, wolves were functionally extirpated from the UP by approximately 1950, before reestablishing populations in the early 1990s (Beyer et al. 2009, Hendrickson and Robinson 1975). In addition, the UP saw an exponential increase in tourism and housing density – though not necessarily a change in resident population size – over this period (Radeloff et al. 2005), likely altering the resource landscape via human food subsidies to wildlife (IPBES 2019, Manlick and Pauli 2020). Specifically, to understand how community reassembly and human disturbance interact to drive carnivore trophic relationships and Eltonian niches, we used bulk tissue stable isotope analysis of museum specimens and harvested carnivore tissues to quantify diets and niche overlap during three ecologically relevant time periods: 1) a historical carnivore community with wolves (1910–1930), 2) the community following the extirpation of wolves (which we refer to as 'reduced' throughout; 1950–1970), and 3) the reassembled carnivore community featuring wolves and high human subsidies (2000–2020). Within the context of Eltonian niche conservatism, we expect that the drivers of carnivore community interactions – specifically, suppression and facilitation – would be consistent through time. Accordingly, we hypothesized that the Eltonian niches of subordinate carnivores are structured by trophic facilitation, with different responses to resources provisioned by large carnivores and human food subsidies for meso- and small carnivores, respectively. Specifically, we predicted that the Eltonian niche of coyotes would be conserved in the presence of wolves due to facilitation – that is, coyote niche breadth would be narrower in the presence of wolves due to a higher proportion of deer carrion in their diet. Conversely, we did not expect carrion subsidies to support foxes given that dominant meso-carnivores like coyotes can monopolize this resource (Sivy et al. 2018). Specifically, we predicted that the Eltonian niche of foxes is more strongly mediated by non-wolf subsidies – that is, fox niche breadth would expand due to increased subsidies provided by humans. Accordingly, we expected dietary overlap between coyotes and foxes to be highest when wolves were absent due to a lack of carrion provisioning. The use of anthropogenic subsidies has been shown to increase dietary overlap between carnivores while simultaneously increasing co-occurrence due to exceedingly high convergence on human food subsidies (Manlick and Pauli 2020), so we expected the total community niche breadth to increase through time, which could lead to an increase in dietary overlap through time as human impacts increase. Finally, we predicted that dietary specialization would be highest for coyotes in the presence of large carnivores due to an increase in the consumption of deer, while human subsidies would drive higher diet variability.

Methods

Study area

The Upper Peninsula (UP) of Michigan, USA is characterized by boreal forest and mixed conifer and deciduous stands, with interspersed agricultural lands. The dominant vegetative community has been strongly influenced by human intervention during the last two centuries (Radeloff et al. 2005), with primary succession following industrial logging in the 19th century shifting landcover (Karamanski 1989). The region is highly seasonal, with mean temperatures ranging from −14°C in winter with up to 450 cm of snowfall and 25°C in summer with an average annual precipitation between 812–864 mm. The rate of land-use change over the past century has declined in the UP relative to the broader Great Lakes Region, while key prey like white-tail deer *Odocoileus virginianus* have increased in abundance (Supporting information). Following the crash in deer populations across North America, the UP was considered a white-tail deer refugia in the United States prior to modern management practices (Webb 2018). Although moose *Alces alces* – the only other substantial prey for wolves in the UP – occurred throughout the 20th century, their populations have been low (i.e. <200 individuals; (Beyer et al. 2011), and likely not significantly contributing to carnivore diets. The mammalian community has remained relatively stable, other than the extirpation of wolves in the middle of the century, and sympatric carnivores include black bears *Ursus americanus*, Canada lynx *Lynx canadensis*, bobcats *Lynx rufus*, American badgers *Taxidea taxus*, fishers *Pekania pennanti*, American marten *Martes americana*, least weasels *Mustela nivalis*, striped skunks *Mephitis mephitis*, racoons *Procyon lotor* and gray foxes *Urocyon cinereoargenteus*. Nevertheless, we were particularly interested in the canids within this community where we would expect the strongest competitive interactions due to their taxonomic relatedness, body size distributions, and diet, including evidence from both theoretical (Donadio and Buskirk 2006) and empirical (Levi and Wilmers 2012, Ripple et al. 2013, Newsome and Ripple 2014) studies. Generally, we were interested in testing the dynamics among the three most tightly coupled competing carnivores who serve as an ideal model for facilitation–suppression dynamics.

Design, data collection and preparation

We measured bulk tissue carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes from hair and bone collagen for 74 ($n_{Fox}=24$, $n_{Coyote}=35$, $n_{Wolf}=15$), 31 ($n_{Fox}=9$, $n_{Coyote}=22$), and 65 ($n_{Fox}=17$, $n_{Coyote}=17$, $n_{Wolf}=31$) individuals in the historic, reduced, and reassembled carnivore communities, respectively. Historical and reduced community samples were acquired from museum specimens while reassembled community samples were acquired from published data by Manlick and Pauli (Manlick and Pauli 2020) and include samples from fur auctions, museum collections, and collared animals. In addition, we sampled hair from the UP from the historical (*Myodes gapperi; n*=10, *Odocoileus virginianus; n*=8, and *Peromyscus* spp.; n=10) and reassembled (*Peromyscus* spp.; n=10) communities and compared these to contemporary (i.e. the reassembled community) samples from northern Wisconsin (n=70; (Carlson et al. 2014) to quantify isotopic variability in prey across time periods

(Supporting information); we included a total of 108 prey samples in our analysis (cf. Supporting information for all prey samples included in our analyses). We rinsed hair samples three-times with 2:1 chloroform methanol solution to remove surface oils, homogenized them with scissors, and dried samples for 72 h at 50°C (Pauli et al. 2009). Bone collagen samples were demineralized in 0.1N HCL, rinsed 5× with deionized water, and then lipid extracted in 2:1 chloroform methanol for three days and dried for ≥ 72 h at 50°C before homogenization in a mill mixer. Carbon and nitrogen isotope values were measured using an elemental analyzer coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer with internal reference materials calibrated against international reference standards (V-PDB for $\delta^{13}C$ and atmospheric N for $\delta^{15}N$). The within-run standard deviation for internal reference materials was < 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. All measurements were conducted at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM, USA). Prior to analyses and comparisons, we corrected all stable isotope samples for the Suess effect to pre-industrial values (ca 1750s) using data from Dombrosky (2020). Because the variability within time periods was equal to or less than the analytical precision of the mass spectrometer ($\delta^{13}C_{SD}$ < 0.2‰), we used an average value of the Suess-correction for all samples collected from the historical (1910–1930; −0.50‰), reduced (1950–1970; −0.80‰) and reassembled (2000–2020; −1.80‰) communities, respectively. All bone collagen samples exhibited high quality with C:N ratios within the acceptable range (C:N = 3.2 ± 0.3; (DeNiro 1985, Guiry and Szpak 2021).

Analyses

To test the mechanisms driving dietary variation across species and time periods, we used $\delta^{13}C$ and $\delta^{15}N$ values to estimate 1) isotopic niche breadth and pairwise isotopic niche overlap in 'δ-space' (Layman et al. 2007, Newsome et al. 2007, Jackson et al. 2011) and 2) the proportional assimilation of putative prey and dietary overlap based on stable isotope mixing models (Parnell et al. 2010). First, we quantified isotopic niche breadth and overlap – a proxy for dietary niche breadth and competition, respectively – as the 95% standard ellipses areas (B ‰^{2}) of each species (within time periods) and the overlap between species in each time period and across time periods for each species in the R package 'SIBER' ver. 2.1.6 (Parnell et al. 2010). We ran three chains of 300 000 iterations and removed the first 200 000 iterations as burn-in and then thinned posterior samples to every 10th sample. We calculated the total isotopic niche breadth (SEA_δ ‰^{2}) and the area of overlap between ellipses within each time-period. To quantify isotopic niche overlap, we used the single metric of niche overlap (O_δ) defined by the proportion of overlapping area of the two ellipse compared to the total area of the overlapping and non-overlapping areas, $O_\delta = O_{x-y}/((B_x + B_y) - O_{x-y})$, where O_{x-y} (= O_{y-x}) is the overlap between Species 1 and 2, B_x is the niche breadth of Species 1 and B_y is the isotopic niche breadth of Species 2; the resulting value ranges from 0 (no overlap) to 1.0 (complete overlap). Consistent niche breadth among meso- or small carnivores provided changes in the environmental context would support Eltonian niche conservatism.

To determine the proportional assimilation of dietary groups for each species across time periods we used a species and time period-specific suite of concentration dependent mixing models using the R package 'simmr' ver. 0.5.1.216 (Govan and Parnell 2019). We focused our efforts on mammalian diet items because they are generally available year-round and make up the predominant (> 75%) biomass consumed by canids in northern climates (Sivy et al. 2018, Fowler et al. 2021). Specifically, we excluded birds from our analysis as they are seasonally present and likely make up ~ 5–10% of the total diets of canids in this system (Petroelje et al. 2021). First, we tested differences between historical and contemporary samples of red-backed voles *Myodes gapperi*, white-tailed deer *Odocoileus virginianus*, and *Peromyscus* spp. collected across the UP and northern Wisconsin to test for baseline isotopic shifts through time. We used a PERMANOVA and a test of multivariate homogeneity in the R package 'vegan' ver. 2.6-2 (Oksanen et al. 2022) and found no evidence for isotopic differences in putative prey sources, so we combined historical and contemporary prey data for all downstream analyses (Supporting information). For all mammalian prey samples, we used biological considerations and results from a k-means clustering algorithm in the R package 'NbClust' ver. 3.0.1 (Charrad et al. 2014) to aggregate isotopically distinct prey items (Phillips et al. 2014). These considerations resulted in two isotopically distinct groups, 1) small prey (*Blarina brevicauda, Myodes gapperi, Peromyscus* spp., *Sorex cinereus* and *Tamiascirus hudsonicus*) and 2) white-tailed deer *Odocoileus virginianus* (Supporting information). To account for potential human resource subsidies in carnivore diets, we used the values inferred from human hair reported by Hülsemann et al. (2015) and Newsome et al. (2015b). Canids, especially in northern latitudes, grow their winter coat at the end of the summer when berries are available (Derbridge et al. 2012), therefore, we included berries in our analysis (Gable et al. 2018). This process resulted in four (4) isotopically distinct and biologically meaningful prey groups representative of the UP: 1) berries (*Rubus* spp. and *Fragaria* spp.; $\delta^{13}C = -28.5 \pm 1.4$ and $\delta^{15}N = -3.1 \pm 1.4$), 2) white-tail deer ($\delta^{13}C = -23.9 \pm 1.2$ and $\delta^{15}N = 2.8 \pm 1.2$), 3) small prey ($\delta^{13}C = -21.6 \pm 1.2$ and $\delta^{15}N = 3.5 \pm 1.2$), and 4) human foods ($\delta^{13}C = -20.3 \pm 1.3$ and $\delta^{15}N = 5.4 \pm 0.6$; see the Supporting information for further details).

We estimated proportional dietary inputs of species at the population- and individual-level by running three chains of 300 000 iterations and removed the first 200 000 iterations as burn-in and then thinned posterior samples to every 10th sample. We used uniform (i.e. even dietary proportions 1/N-sources = 0.25) priors throughout the modelling process (Parnell et al. 2010, Stock et al. 2018) with the exception of wolves. Because they are known to be large ungulate specialists in the region (Petroelje et al. 2019), we used loosely

informed priors for wolves based on past work in the Great Lakes region (Petroelje et al. 2019): human foods = 0.13 ± 0.06, deer = 0.67 ± 0.13, small prey = 0.13 ± 0.06, and berries = 0.08 ± 0.06. We used [C] and [N] data of berries ([C] = 0.48; [N] = 0.01), deer ([C] = 0.47; [N] = 0.14), and small prey ([C] = 0.47; [N] = 0.14) from (Carlson et al. 2014) and data from (Hopkins and Ferguson 2012) for the concentrations of anthropogenic-derived sources ([C] = 0.53; [N] = 0.07). For all carnivores, we used trophic discrimination factors of 2.6‰ (± 0.5) and 3.6‰ (± 0.5) for $\delta^{13}C$ and $\delta^{15}N$ for all hair and 3.8‰ (± 0.5) and 3.6‰ (± 0.5) for $\delta^{13}C$ and $\delta^{15}N$ for all bone collagen samples, respectively (Roth and Hobson 2000, Stephens et al. 2022). Because we sampled small prey and deer hair and not muscle, we adjusted our $\delta^{13}C$ discrimination factors by −1.0‰ for hair and bone collagen for those prey groups based on tissue specific discrimination factors (Roth and Hobson 2000, Newsome et al. 2015b). The samples of wolves in the reassembled community consisted of a mix of bone (n = 25) and hair (n = 6); thus, we ran two separate mixing models using the tissue-specific trophic discrimination factors (see the Supporting information for the community- and species-specific isoscapes used in our mixing models).

We first quantified prey use at the population level by grouping each canid species by time-period and estimated proportional use of the four potential prey sources (berries, deer, small mammals and human foods; Supporting information). At the population level, higher deer consumption for meso- or small carnivores in the presence of wolves would support our prediction of trophic facilitation by wolves. Furthermore, high deer consumption (i.e. carrion provisioning) in the face of altered human food subsidies would suggest that scavenging is a highly conserved trophic strategy. Then, we analyzed individuals separately to quantify consumption of each prey group and tested the impacts of community context on dietary variability, specialization and similarity, and the contribution of each diet item to dietary dissimilarity between individuals. For the population- and individual-level models, we identified model convergence using the Gelman–Rubin diagnostic value $\hat{R} < 1.01$ and the effective sample size of each estimate being > 10% of the thinned samples (i.e. 3000).

We estimated dietary niche breadth and overlap using our dietary proportion estimates of individuals across time periods. First, we performed a non-metric multi-dimensional scaling (NMDS) analysis on all median individual-level diet estimates across time periods in the R package 'vegan' using the Bray–Curtis dissimilarity distances. We included the median estimates of prey use for each individual carnivore across all time periods to be able to compare dietary overlap between species and across time. Using the two axis scores from our NMDS, we again used the R package 'SIBER' (www.r-project.org) to calculate the standard ellipse area in p-space (SEA_p unitless) and the total dietary niche overlap (O_p). We again report the proportion of overlapping area relative to the non-overlapping area of the two ellipses being compared relative to the non-overlapping area, ranging from 0 (no overlap) to 1.0 (complete overlap). To quantify the foraging strategies of individuals within each population in each time period, we used the individual proportional estimates of prey groups to quantify dietary specialization (Ɛ) and similarity (*s*) indices and visually inspected the density plots (Newsome et al. 2012). Here, Ɛ varies between 0 (an ultra-generalist) and 1 (an ultra-specialist) and *s* varies between 0 (exactly dissimilar from the population) and 1 (exactly similar to the population). Accordingly, the density plots can be subdivided into four quadrants: dietary specialists (Ɛ > 0.50) with diets dissimilar to the population (s < 0.50; dissimilar-specialists), dietary specialists with diets similar to the population (s > 0.50; similar-specialists), dietary generalists (Ɛ < 0.50) with diets dissimilar to the population (dissimilar-generalists), and dietary generalists with diets similar to the population (similar-generalists; Newsome et al. 2012). We classified dietary specialization and similarity from the posterior estimates of individual diets and generated density plots to classify the foraging strategies at the population level based on where the density distributions using a kernel function (Newsome et al. 2012) – foraging strategies are qualified as unique if there is little overlap between high density centers. Finally, we used a similarity percentage analysis in the R package 'vegan' to determine percent contribution of each prey group to the dissimilarity in diet composition between and among groups based on a Bray–Curtis dissimilarity matrix calculated from the estimates of each of prey group.

Results

Isotopic niche breadth and overlap

The isotopic niche breadth of wolves in the reassembled carnivore community was 2.5× greater than the historically observed value, increasing from (mean ± SD throughout) 1.12 ± 0.31‰^{2} to 2.95 ± 0.55‰^{2} (Fig. 1). Coyotes had a narrower niche breadth when wolves were present in the historical (0.64 ± 0.11‰^{2}) and reassembled (1.66 ± 0.43‰^{2}) communities, respectively, compared to the reduced community when wolves were absent (3.33 ± 0.75‰^{2}; Fig. 1). Alternatively, red foxes had a relatively narrow isotopic niche breadth within the historical (1.95 ± 0.42‰^{2}) and reduced (1.97 ± 0.74‰^{2}) communities, while isotopic niche breadth in the reassembled community was nearly 4× larger (7.54‰ ± 1.94‰^{2}). We found that the total breadth of the carnivore community increased through time in the UP (Historical = 1.24 ± 0.15‰^{2}, Reduced = 3.20 ± 0.60‰^{2}, and Reassembled = 4.49 ± 0.57‰^{2}).

The highest proportional isotopic overlap we observed between coyotes and foxes was in the absence of wolves ($O_{\delta\text{-Reduced}}$ = 0.40 ± 0.09) and it was lowest in the reassembled community ($O_{\delta\text{-Reassembled}}$ = 0.22 ± 0.06; Fig. 1). Isotopic niche overlap between wolves and coyotes decreased from the historical ($O_{\delta\text{-Historical}}$ = 0.43 ± 0.12) to reassembled ($O_{\delta\text{-Reassembled}}$ = 0.33 ± 0.08) communities, as did overlap between

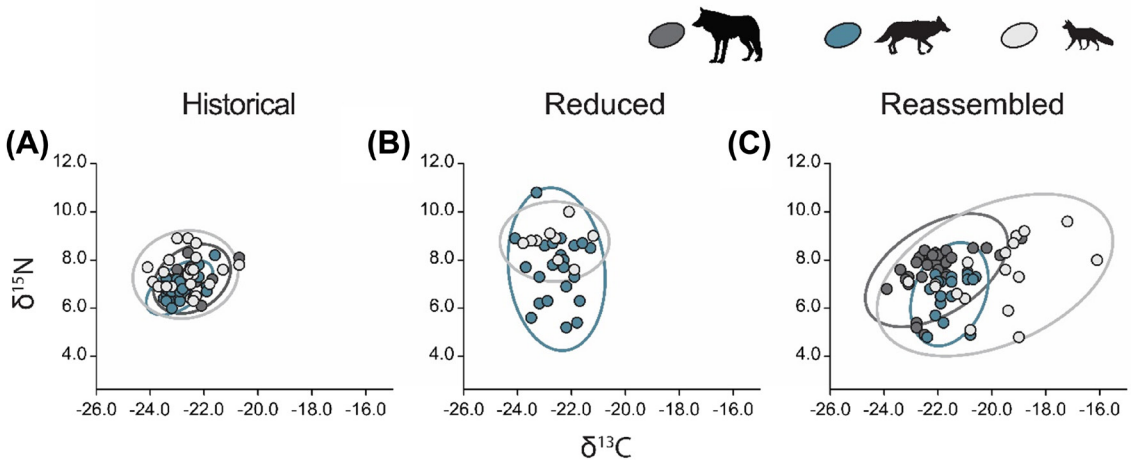

Figure 1. Standard ellipse area (SEAc; 95%) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values for wolves *Canis lupus* (gray), coyotes *Canis latrans* (blue), and red foxes *Vulpes vulpes* (brown) across the historical (1910–1930; A), reduced (1950–1970; B), and reassembled (2000–2020; C) carnivore community in the Upper Peninsula of Michigan.

wolves and foxes ($O_{\delta\text{-Historical}} = 0.50 \pm 0.11$; $O_{\delta\text{-Reassembled}}$ 0.30 ± 0.07; Supporting information).

Dietary contributions, dietary niche overlap and foraging strategies

Wolves consumed > 50% deer and their diets were relatively similar through time, though the mixing model estimates were strongly influenced by our priors (Fig. 2). On average, the consumption of deer by coyotes increased 1.4–1.8-fold when wolves were present on the landscape (Fig. 2) leading to a narrower dietary niche (Fig. 2). Specifically, deer consumption was greater in the historical (0.26 ± 0.07) and reassembled (0.35 ± 0.13) carnivore community than in the reduced community (0.19 ± 0.13, Fig. 2). Meanwhile, foxes consumed similar proportions of deer regardless of carnivore community context (0.15 ± 0.08, 0.23 ± 0.18 and 0.19 ± 0.11 in the historical, reduced and reassembled communities, respectively; Fig. 2).

Our NMDS diagnostics suggest good representation of the proportional data with low risk of drawing false inference (maximum residual error = 0.001; Stress = 0.041). Although the magnitude of isotopic and dietary niche breadth differed, the percent changes across time periods were similar (Supporting information). Using our informed estimates of wolf diets, our estimates of dietary overlap revealed limited wolf–coyote and wolf–fox overlap ($O_p < 0.01$). Like the observed isotopic niche overlap, the estimated dietary niche overlap between coyotes and foxes was highest in the absence of wolves, increasing ~ 1.3-fold when wolves became extirpated ($O_{p\text{-Historical}} = 0.34 \pm 0.13$, $O_{p\text{-Reduced}} = 0.44 \pm 0.13$) and then decreasing following community reassembly ($O_{p\text{-Reassembled}} = 0.14 \pm 0.05$). Generally, we observed a reciprocal pattern in the directional niche space overlap between species whereby the species with the largest dietary niche space greatly overlapped with the species of the narrower niche breadth (Supporting information).

Human foods were the leading cause of dietary dissimilarity among foxes at the individual-level in all communities, accounting for > 30% of the total dissimilarity among individuals (Supporting information). Coyote dissimilarity was driven by the consumption of human foods in the reassembled communities, while it was driven by berries in the historical and reduced community (Supporting information). Lastly, human food consumption drove variation in wolf diets in the historical and reassembled communities (Supporting information). Considering diets across communities, dietary dissimilarity was significantly high for foxes when comparing the historical and reduced diets to the reassembled carnivore community (Supporting information). Meanwhile, coyote diets were most dissimilar relative to the reduced community, but similar when wolves were present (Supporting information). Lastly, wolf diets were relatively similar during the historical and reassembled community, with the exception of differences in small mammal and deer consumption (Supporting information).

The trophic strategies of both wolves and foxes were largely synchronous in the historical and reassembled communities, becoming most variable in the presence of high anthropogenic resource subsidies (Fig. 3). Wolves were predominantly classified as highly similar ($s \geq 0.90$) and moderate generalists ($\varepsilon \approx 0.65$; Fig. 3). Alternatively, coyotes were classified as dietary generalists throughout (all $\varepsilon \leq 0.25$), though their trophic strategy was more variable, and they exhibited more dissimilar diets when wolves were absent ($s_{Reduced} = 0.77 \pm 0.14$) compared to the historical ($s_{Historical} = 0.86 \pm 0.09$) and reassembled ($s_{Reassembled} = 0.80 \pm 0.10$) communities (Fig. 3). Notably, although foxes were largely qualified as dietary generalists ($\varepsilon < 0.50$), two divergent foraging strategies emerged in the reassembled community whereby some individuals were quantified as highly generalists ($\varepsilon \approx 0.18$), while others were more specialized ($\varepsilon \approx 0.45$; Fig. 3).

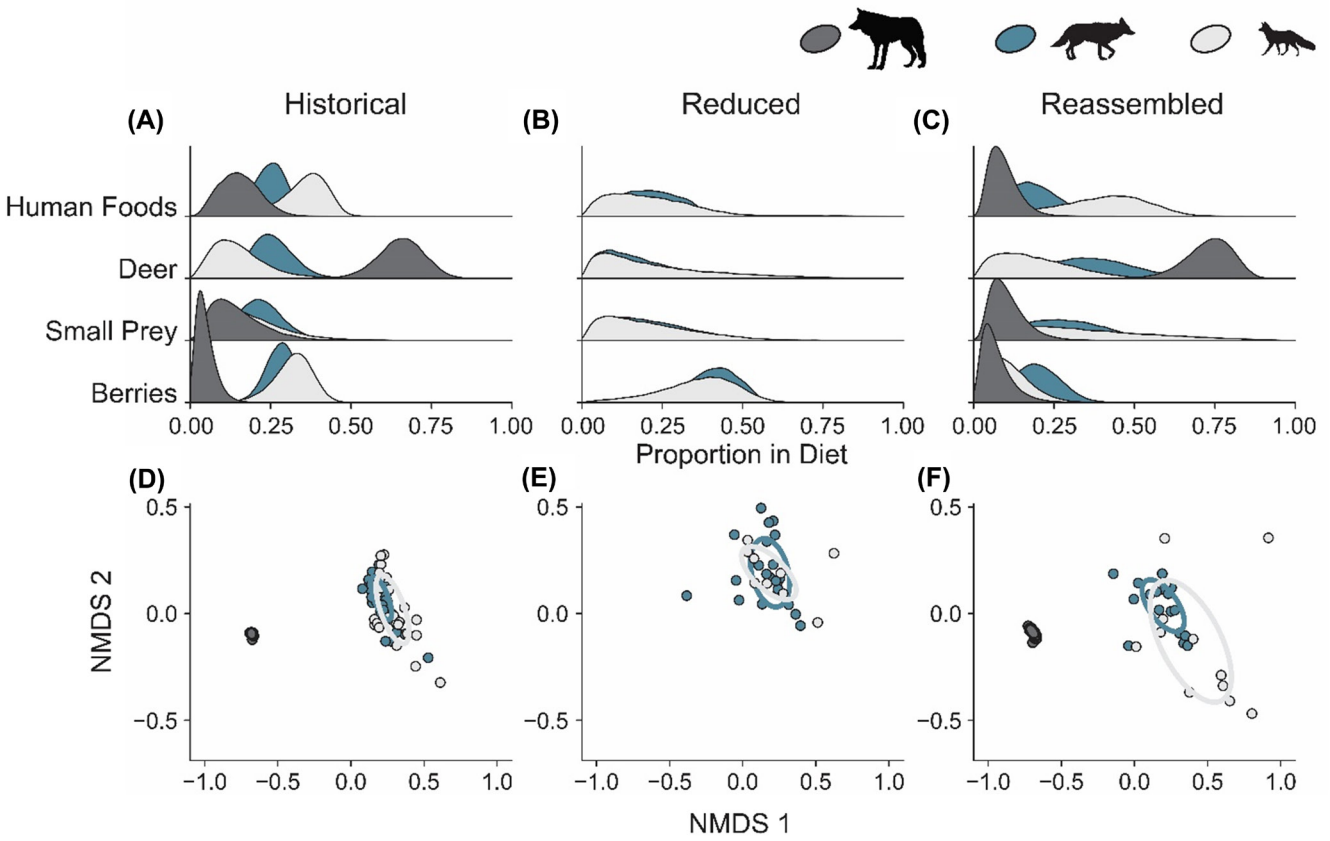

Figure 2. Posterior distribution of assimilated human foods, deer *Odocoileus virginianus*, small prey (e.g. Cricetids and Sciurids), and berries (*Rubus* spp. and *Ragaria* spp.) from wolf *Canis lupus* (dark grey), coyote *Canis latrans* (blue), and red fox *Vulpes vulpes* (light grey) tissues estimated via stable isotope mixing model (A–C). Note that we used uniform proportions (0.25) as priors for coyotes and foxes and informative priors for wolves based on a diet of ~ 70% deer. Population-level dietary overlap from the stable isotope mixing model results of individual (median) diet represented using non-metric multidimensional scaling (NMDS; D–F). Assimilated diet and dietary overlap are shown across the historical (1910–1930; A), reduced (1950–1970; B), and reassembled (2000–2020; C) carnivore community in the Upper Peninsula of Michigan.

Discussion

We quantified the diets of sympatric canids in the UP of Michigan over a century of ecological change to assess Eltonian niche conservatism and the consistency of trophic relationships through time. Historical and reassembled carnivore community interactions were markedly different than the reduced community and shaped by both large carnivore provisioning and human food subsidies. Indeed, we found that wolves structured the diets of meso-carnivores like coyotes, likely by facilitating access to deer carrion, resulting in the release of competition for smaller carnivores like red foxes. Furthermore, we show that humans can decouple competitive interactions within carnivore guilds by providing exceptionally high quantities of resource subsidies, especially to small carnivores. Notably, although our analysis lacked some secondary prey groups (e.g. passerines, grouse, etc.), our individual-level analysis of trophic strategies provided a means to make inference on the competitive pressure for individuals and human habituation exhibited by small carnivores, such as the red fox. Our results are consistent with recent studies illustrating the plasticity of mammalian carnivore diets (Sivy et al. 2018, Magioli et al. 2019, Manlick et al. 2019), and we highlight two contrasting mechanisms (i.e. the loss of large carnivores and the increase in anthropogenic resource subsidies) that can override Eltonian niche conservatism depending on body size.

Eltonian niche conservatism

Given Elton's (1927) emphasis on the functional role of a species within a community, Eltonian niche conservatism is contingent on the context of the community itself (Dussault 2022). Grinnellian niches have been hypothesized to be more labile than Eltonian niches (Larson et al. 2010), indicating that restored communities should maintain a similar structure to their historical counterparts. Accordingly, we hypothesized that large carnivores anchor the ecological interactions between meso- and small carnivores via resource facilitation; ultimately, these interactions cascade to shape the services that meso- and small carnivores provide to the broader community. Supporting our hypothesis, we found high levels of deer consumption by

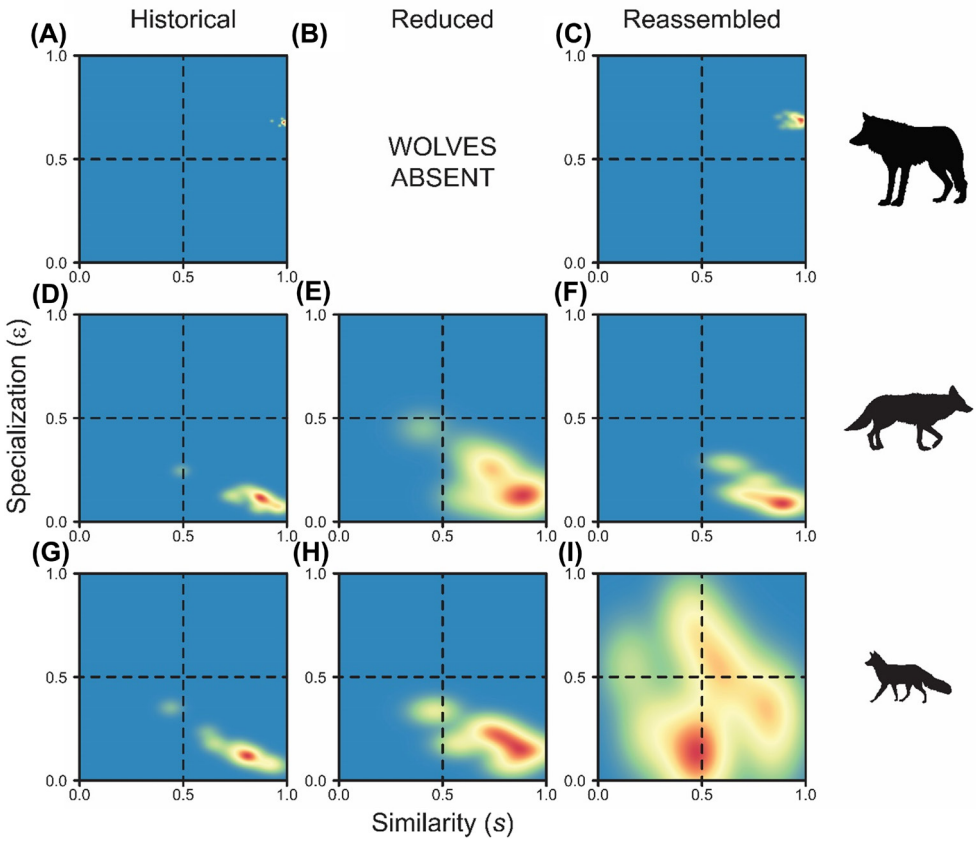

Figure 3. Foraging strategies represented as density plots of individual dietary similarity (x-axis) and specialization (y-axis) of wolves *Canis lupus* (A–C), coyotes *Canis latrans* (D–F), and red foxes *Vulpes vulpes* (G–I) in the respective historical (1910–1930; A, D, and G), reduced (1950–1970; E and H), and reassembled (2000–2020; C, F, and I) carnivore community in the Upper Peninsula of Michigan. Dashed lines represent the qualitative cutoffs identifying dissimilar individuals and generalists (Ɛ and $s < 0.50$) and similar individuals and specialists (Ɛ and $s > 0.50$).

coyotes when wolves were present in the historical and reassembled carnivore communities (Fig. 2), resulting in lower dietary overlap – and presumably competition – between coyotes and foxes (Supporting information). These results are supported by past empirical studies (Wilmers et al. 2003, Mark Elbroch and Wittmer 2012, Pereira et al. 2014), but further reinforce that scavenging resources facilitated by large carnivores is a highly viable strategy for meso-carnivores despite the potential interspecific conflict (Wilmers et al. 2003, Wilson and Wolkovich 2011, Ruprecht et al. 2021). This strategy appears conserved when large carnivores are present, regardless of environmental context or level of anthropogenic resource subsidies. Our framing differs from Eltonian niche conservatism as it has previously been tested, where conservatism is a lack of variation in the diet of a species across a geographical range (Manlick et al. 2019). Rather, we aimed to realign this modern concept with Elton's classical conceptualization of the species niche (Elton 1927, Dussault 2022). In our present framing of Eltonian niche conservatism, the provisioning of deer to coyotes when wolves are present was, indeed, conserved. Although the use of other prey groups slightly varied between historical and modern samples (Fig. 2), dietary overlap and the trophic strategies of coyotes were most similar in the presence of wolves (Fig. 2, 3), supporting Eltonian niche conservatism in the presence of wolves regardless of environmental context. We found similar support in the consumption of human food subsidies by foxes, though foxes became individually more varied in trophic strategy and diet in the reassembled carnivore community (Fig. 2, 3). The Eltonian niche of foxes, instead, was conserved in their consumption of human foods and berries. Notably, foxes exhibited an increasing disparity in foraging strategies through our study period, which coincided with increasing human food subsidies (Fig. 3). Globally, foxes are the most cosmopolitan carnivore and exhibit high variability in trophic strategies (Henry 1996), so it is not surprising that they have the behavioral and trophic flexibility necessary to expand their Eltonian niches when presented with novel opportunities such as human foods (Rodriguez Curras et al. 2024a).

Facilitation and competition

Globally, large carnivores provide > 1000 kg of carrion per individual per year to scavengers, with large allocations to meso-carnivores (Prugh and Sivy 2020). Although coyotes are effective predators of deer fawns, accounting for as much as 25% of fawn mortalities in the UP (Duquette et al. 2014), we

found that the proportion of deer in coyote diet increased by an average of 1.4–1.8-fold when wolves were present, thereby shaping the dietary niche of coyotes (Fig. 2). This was especially surprising in the context of the historical community (1900–1920), as deer and wolf abundances were lowest during this time period (Supporting information); although deer and wolf abundances were relatively lower in the historical community, we nevertheless detected high levels of trophic facilitation to coyotes in the form of deer carrion. Competitive interactions within carnivore communities are structured by body size differences between species (Donadio and Buskirk 2006) but agonistic interactions can be mitigated by minimizing overlap in resource use (Wilson and Wolkovich 2011, de Oliveira and Pereira 2014). Consequently, resource facilitation by large carnivores can lead to decreased competition between meso- and small carnivores via two mechanisms. First, provisioned carrion can decrease the impact of exploitative competition for a shared and limited resource base (Levi and Wilmers 2012, Allen et al. 2015). For example, resources provisioned by large carnivores are often high-quality, preferred, and monopolized by large-bodied meso-carnivores (Wilson and Wolkovich 2011, Prugh and Sivy 2020), while small-bodied carnivores scavenge depending on the relative availability of alternative resources (Pereira et al. 2014). Indeed, in the presence of wolves, we found evidence that coyotes consumed higher proportions of deer (Fig. 2). Further, small-bodied carnivores are often superior exploitative competitors (Polis et al. 1989, Holt and Polis 1997), thereby allowing them to avoid interference altogether by targeting lower quality (and hence low risk) resources (Robinson et al. 2014). Indeed, foxes exhibited the greatest isotopic and dietary niche breath in the historical and reassembled communities while their niches were relatively constrained in the reduced community and our analysis of directional dietary overlap suggested that foxes exploited the niche space of their larger, interspecific competitors (Supporting information). Our results suggest that although coyotes shifted their diets following the extirpation of wolves, the niche breadth of red foxes did not change (Fig. 1, 2). Second, facilitation by large carnivores can disproportionately impact large-bodied meso-carnivores via 'fatal attraction' to scavenging (Sivy et al. 2017). This higher reliance on provisioned resources by large-bodied meso-carnivores, like we found in coyotes, can enhance agonistic encounters with apex predators with population-level demographic consequences (Ruprecht et al. 2021), which has been observed in the UP (Fowler et al. 2021). These interactions, in turn, can release small-bodied meso-carnivores from competition with dominant meso-carnivores, and explain the indirect positive effects that large carnivores have on small carnivores (Rodriguez Curras et al. 2024a). While we did not test this hypothesis directly, wolves in our study area suppress coyote occupancy, with positive effects on fox occurrence (Flagel et al. 2017, Fowler et al. 2021). Our study suggests that provisioning by large carnivores facilitates dietary partitioning between sympatric meso- and small carnivores and may be the proximate mechanism that mediates the release of foxes from competition.

Although a low proportion of fox diet was comprised of deer, likely from scavenging, this may have placed them at an elevated risk of interference with both wolves and coyotes. Indeed, wolves and coyotes are known to displace foxes from their kills and carrion, respectively (Gese et al. 1996, Palomares and Caro 1999), suggesting that temporal partitioning might be important for deer consumption in red foxes – either avoiding the times that large and meso- carnivores are present or accessing carrion when the larger bodied species have given up (Fowler et al. 2021). Likewise, human resource subsidies can also release foxes from competition by providing a resource not tethered to immediate negative, competitive interactions (Pluemer et al. 2019). Indeed, foxes and coyotes have been found to co-occur at higher frequencies in the presence of humans – largely due to the consumption of human foods (Newsome et al. 2015a, Mueller et al. 2018). The divergent foraging strategies that red foxes developed following community reassembly (Fig. 3) shows the emergence of alternate strategies that competitors can utilize to co-occur with their larger competitors. Finally, the individual-level shift we observed in foxes towards anthropogenic resources can result in a reprieve of competitive pressure for some species, such as foxes, with consequences that can cascade through communities and food webs (Schell et al. 2021, Rodriguez Curras et al. 2022).

Human impacts to competitive interactions

Over the last century, the resident human population of the UP has remained relatively stable (~ 300 k), accompanied by a rural-to-urban migration, ≥ 50% decrease in agricultural lands (US Census Data), and a growing tourism industry (MEDC 2022). In the last 50 years, State and National Parks in the UP have reported park-visitor increases between 200–300% (NPS IRMA); today the UP receives > 6 million tourists a year (MEDC). Accompanying the change in industry, many of the UP forests have recovered from the excessive logging in the late-1800s and much of the UP has become designated as National or State Forest, designed for recreational tourism. The land-use changes in the UP over the past century have largely resulted in forest succession, with ecological processes resembling natural and undisturbed systems (Anderson et al. 2023). Nevertheless, we found that the isotopic niche breadth of the carnivore community increased through time (Fig. 1) and was accompanied by an increase in the consumption and specialization on human foods, especially at the individual-level by foxes (Fig. 2, 3). Although meso- and small carnivores exhibit much dietary plasticity across their ranges (Gittleman 1989) and can persist in contemporary human landscapes by consuming high levels of human foods (Newsome et al. 2015b, Manlick and Pauli 2020, Rodriguez Curras et al. 2024a), there is limited evidence that human food subsidies drive individual specialization (Manlick and Newsome 2021). Our work adds to the growing body of literature showing that human foods can increase individual specialization in carnivores – particularly small carnivores like foxes – with putative downstream consequences to the impacts of

suppression and facilitation. The human food system is particularly 'leaky', with an estimated one-quarter to one-third of food produced for human consumption lost or wasted each year (The World Bank 2014). Given the environmental context in the UP, we suspect the increasing dietary niche breadth and human food consumption has been due to an influx of human foods via refuse rather than agriculture (Manlick and Pauli 2020) or landscape homogenization. Our results, then, suggest that protecting and restoring community interactions cannot be accomplished by only protecting land from development and homogenization, and more emphasis should be placed on minimizing 'leakage' from human to natural food webs.

The niche expansion of the reassembled carnivore community was not reflected by coyotes, who possessed a narrower isotopic and dietary niche relative to the reduced community (Fig. 1, 2). Indeed, wolves appeared to constrain the dietary niche of coyotes via the facilitation of high-quality resources, as niche breadth was not impacted by human subsidies (Fig. 2). Canids are well equipped to exploit human landscapes because of their body size, dietary flexibility, and low risk they pose to humans (Kuijper et al. 2016), so it was surprising that coyotes did not more strongly track anthropogenic resources. At the highest human densities, consumption of human foods by contemporary coyotes has been found to be as high as 50% (Newsome et al. 2015b, Manlick and Pauli 2020), which is comparable to our estimates of the highest proportion of human foods in individual coyote diets (~40%). However, this value is lower than the overall consumption of human foods by foxes, where numerous individuals consumed > 60% human food subsidies. Alternatively, human food resources were the leading cause of dietary dissimilarity among coyotes and foxes (Supporting information), exemplifying the disproportionate importance of exploiting these resources. The use of human food subsidies by meso- and small carnivores can also result in behavioral changes with variable fitness consequences (Murray et al. 2015, Newsome et al. 2015a). On one hand, human food subsidies can actually increase co-occurrence among competing carnivores like coyotes and foxes (Mueller et al. 2018, Pluemer et al. 2019). On the other, human resource subsidies can also lead to the collapse of predator–prey (Rodewald et al. 2016, Parsons et al. 2022) and community interactions (Sapolsky and Share 2004, Manlick and Pauli 2020), as well as increased disease transmission (Murray et al. 2015) and ecological traps (Moss et al. 2016, Lamb et al. 2017). Given the current repatriation of large carnivores to human-dominated landscapes (Chapron et al. 2014), there is an urgent need to assess the degree to which human subsidies decouple interactions like facilitation and suppression that are predicted to be highly conserved.

Conclusion

Re-establishing trophic interactions has become a global ecological priority (Dobson et al. 2009, Estes et al. 2011), with anticipated benefits to biodiversity (Terborgh 2015) and ecosystem functionality (Ritchie et al. 2012). Carnivore restoration (particularly of large carnivores) has been promoted as an effective management tool to re-establish community interactions and lost functional roles (Pettorelli et al. 2019), particularly by mediating consumer–resource dynamics and top–down forcing (Ritchie et al. 2012, Ripple et al. 2014). However, ecologists still do not fully understand how the restoration of large carnivores will affect community-level processes and ecological functions (Ritchie et al. 2012, Pettorelli et al. 2019), particularly in the human-dominated landscapes of the Anthropocene (Chapron et al. 2014). Understanding and applying the concepts of Eltonian niche conservatism within the context of large carnivore repatriation is important because it can inform managers of the projected functional roles of reintroduced carnivores in novel ecosystems. Furthermore, applying this conceptualization to individuals within a broader population can refine the use of limited conservation resources to maximize impact and also provide a greater mechanistic understanding of ecological processes. In the context of Eltonian niche conservatism, we predict that horizontal interactions such as facilitation of carrion can be conserved among carnivores like wolves and coyotes, though these relationships could be decoupled by high resource subsidies from humans. Ultimately, as large carnivores repatriate their former ranges into cotemporary human-dominated landscapes we caution managers to expect variable outcomes, and our findings suggest that the realized functional roles of carnivores may be undermined by human food subsidies that permeate contemporary ecosystems.

Acknowledgements – We thank C. Thompson at the University of Michigan Museum of Zoology, L. Abraczinskas at the Michigan State University Museum, and K. Galbraith at the Northern Museum of Zoology for access and assistance with museum specimen sampling, D. Beyer at Michigan DNR for tissues from contemporary canids, and North American Fur Auctions for access to trapper harvested animals. We thank S. Peterson for laboratory preparation and analysis. We extend our sincere gratitude to Dr Dorothee Ehrich for her insightful and comprehensive review of our manuscript, who's thoughtful feedback greatly improved the quality of our work.

Funding – Support was provided by the Office of Naval Research (JNP: N00014-22-1-2625), the National Science Foundation (PJM: DGE-144752; JNP: DBI-1759849), and the American Society of Mammalogists (MRC).

Permits – All samples collected for this publication were sampled in accordance to the University of Wisconsin-Madison IACUC's committee (A006038-R01) and the appropriate museums from which the samples were collected (i.e. UMMZ, MSU and NMU).

Author contributions

Mauriel Rodriguez Curras: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Project administration (lead); Visualization (lead); Writing - original draft (lead); Writing - review and editing (lead). **Philip J. Manlick:**

Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (supporting); Resources (equal); Supervision (equal); Validation (equal); Writing - review and editing (supporting). **Jonathan N. Pauli:** Conceptualization (equal); Funding acquisition (equal); Investigation (supporting); Project administration (supporting); Resources (equal); Supervision (equal); Writing - original draft (supporting); Writing - review and editing (supporting).

Data availability statement

Data are available from the Figsharel Repository: https://doi.org/10.6084/m9.figshare.24886620.v2 (Rodriguez Curras et al. 2024b).

Supporting information

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

References

Allen, M. L., Elbroch, L. M., Wilmers, C. C. and Wittmer, H. U. 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. – Am. Nat. 185: 822–833.

Anderson, M. G., Clark, M., Olivero, A. P., Barnett, A. R., Hall, K. R., Cornett, M. W., Ahlering, M., Schindel, M., Unnasch, B., Schloss, C. and Cameron, D. R. 2023. A resilient and connected network of sites to sustain biodiversity under a changing climate. – Proc. Natl Acad. Sci. USA 120: e2204434119.

Beyer, D. E., Peterson, R. O., Vucetich, J. A. and Hammill, J. 2009. Wolf population changes in Michigan. – In: Wydeven, A. P., Van Deelen, T. R. and Heske, E. J. (eds), Recovery of grey wolves in the Great Lakes Region of the United States. Springer, https://doi.org/10.1007/978-0-387-85952-1_5

Beyer, D. E., Winterstein, S. R., Lederle, P. E. and Maskey, J. J. 2011. Moose in Michigan– : history, biology, and considerations for hunting. – Report to the Michigan department of natural resources and environment moose hunting advisory council. – https://www.michigan.gov/-/media/Project/Websites/dnr/Documents/WLD/Mgt/Moose_white_paper_28_Feb_2011_Final.pdf?rev=6f3dc747a2c843e2951bdc61ac588a17.

Carlson, J. E., Gilbert, J. H., Pokallus, J. W., Manlick, P. J., Moss, W. E. and Pauli, J. N. 2014. Potential role of prey in the recovery of American martens to Wisconsin. – J. Wildl. Manage. 78: 1499–1504.

Case, T. J. and Gilpin, M. E. 1974. Interference competition and niche theory. – Proc. Natl Acad. Sci. USA 71: 3073–3077.

Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes.pdf. – Science 346: 1517–1519.

Charrad, M., Ghazzali, N., Boiteau, V. and Niknafs, A. 2014. Nbclust: an R package for determining the relevant number of clusters in a data set. – J. Stat. Softw. 61: 1–36.

Clark, T. J., Vick, B., Newton, J., Marengo, I. and Wakefield, E. D. 2021. A wolf in fox's clothing? Using stable isotopes to quantify ecological replacement. – Conserv. Lett. 14: 1–8.

de Oliveira, T. G. and Pereira, J. A. 2014. Intraguild predation and interspecific killing as structuring forces of carnivoran communities in South America. – J. Mamm. Evol. 21: 427–436.

DeNiro, M. J. 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to paleodietary reconstruction. – Nature 317: 7–10.

Derbridge, J. J., Krausman, P. R. and Darimont, C. T. 2012. Using Bayesian stable isotope mixing models to estimate wolf diet in a multi-prey ecosystem. – J. Wildl. Manage. 76: 1277–1289.

Dobson, A., Allesina, S., Lafferty, K. and Pascual, M. 2009. The assembly, collapse and restoration of food webs. – Philos. Trans. R. Soc. B 364: 1803–1806.

Dombrosky, J. 2020. A ~1000-year 13C Suess correction model for the study of past ecosystems. – Holocene 30: 474–478.

Donadio, E. and Buskirk, S. W. 2006. Diet, morphology, and interspecific killing in carnivora. – Am. Nat. 167: 524–536.

Duquette, J. F., Belant, J. L., Svoboda, N. J., Beyer, D. E. and Lederle, P. E. 2014. Effects of maternal nutrition, resource use and multi-predator risk on neonatal white-tailed deer survival. – PLoS One 9: e100841.

Dussault, A. C. 2022. Functionalism without selectionism: Charles Elton's "functional" niche and the concept of ecological function. – Biol. Theor. 17: 52–67.

Elton, C. 1927, Animal ecology. – Macmillan Co.

Estes, J. A. et al. 2011. Trophic downgrading of planet Earth. – Sci. 333: 301–306.

Flagel, D. G., Belovsky, G. E., Cramer, M. J., Beyer, D. E. and Robertson, K. E. 2017. Fear and loathing in a Great Lakes forest: cascading effects of competition between wolves and coyotes. – J. Mammal. 98: 77–84.

Fowler, N. L., Kautz, T. M., Petroelje, T. R., Wilton, C. M., Kellner, K. F., O'Brien, D. J., Parsons, B., Beyer, D. E. and Belant, J. L. 2021. Marginal support for a trophic cascade among sympatric canids in peripheral wolf range. – Ecology 102: e03494.

Gable, T. D., Windels, S. K., Bruggink, J. G. and Barber-Meyer, S. M. 2018. Weekly summer diet of gray wolves (*Canis lupus*) in northeastern Minnesota. – Am. Midl. Nat. 179: 15–27.

Gese, E. M., Ruff, R. L. and Crabtree, R. L. 1996. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. – Can. J. Zool. 74: 784–797.

Gittleman, J. L. 1989. Carnivore behavior, ecology, and evolution (Gittleman, J. L., ed.). – Springer.

Govan, E. and Parnell, A. 2019. simmr: a stable isotope mixing model. – R package ver. 0.5.1.216, https://CRAN.R-project.org/package=simmr.

Grinnell, J. 1917. The niche relationships of the California thrasher. – Auk 34: 427–433.

Guiry, E. J. and Szpak, P. 2021. Improved quality control criteria for stable carbon and nitrogen isotope measurements of ancient bone collagen. – J. Archaeol. Sci. 132: 105416.

Hendrickson, J. and Robinson, W. L. 1975. Status of the wolf in Michigan, 1973. – Am. Midl. Nat. 94: 226–232. https://doi.org/10.2307/2424554

Henry, J. D. 1996. Red fox: the catlike canine. – Smithsonian Institution Press.

Holt, R. D. and Polis, G. A. 1997. A theoretical framework for intraguild predation. – Am. Nat. 149: 745–764.

Hopkins, J. B. and Ferguson, J. M. 2012. Estimating the diets of animals using stable isotopes and a comprehensive Bayesian mixing model. – PLoS One 7: e28478.

Hülsemann, F., Lehn, C., Schneider, S., Jackson, G., Hill, S., Rossmann, A., Scheid, N., Dunn, P. J. H., Flenker, U. and Schänzer, W. 2015. Global spatial distributions of nitrogen and carbon stable isotope ratios of modern human hair. – Rapid Commun. Mass Spectrom. 29: 2111–2121.
Hutchinson, G. E. 1957. Concluding remarks: the demographic symposium as a heterogeneous unstable population. – Found. Ecol. Class. Pap. Comment. 22: 415–427.
IPBES 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Brondizio, E. S., Settele, J., Díaz, S. and Ngo, H. T., eds). – IPBES secretariat, https://doi.org/10.5281/zenodo.3831673.
Jackson, A. L., Inger, R., Parnell, A. C. and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER – stable isotope Bayesian ellipses in R. – J. Anim. Ecol. 80: 595–602.
Karamanski, T. J. 1989. Deep Woods frontier: a history of logging in northern Michigan. – Wayne State Univ. Press.
Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K. and Cromsigt, J. P. G. M. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. – Proc. R. Soc. B 283: 20161625.
Lamb, C. T., Mowat, G., McLellan, B. N., Nielsen, S. E. and Boutin, S. 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. – J. Anim. Ecol. 86: 55–65.
Larson, E. R., Olden, J. D. and Usio, N. 2010. Decoupled conservatism of Grinnellian and Eltonian niches in an invasive arthropod. – Ecosphere 1: 1–13.
Layman, C. A., Arrington, D. A., Montaña, C. G. and Post, D. M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? – Ecology 88: 42–48.
Levi, T. and Wilmers, C. C. 2012. Wolves – coyotes – foxes : a cascade among carnivores. – Ecology 93: 921–929.
Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. – Ecol. Lett. 11: 995–1003.
Macarthur, R. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. – Am. Nat. 101: 377–385.
Magioli, M., Moreira, M. Z., Fonseca, R. C. B., Ribeiro, M. C., Rodrigues, M. G. and de Ferraz, K. M. P. M. 2019. Human-modified landscapes alter mammal resource and habitat use and trophic structure. – Proc. Natl Acad. Sci. USA 116: 18466–18472.
Manlick, P. J. and Pauli, J. N. 2020. Human disturbance increases trophic niche overlap in terrestrial carnivore communities. – Proc. Natl Acad. Sci. USA 117: 26842–26848.
Manlick, P. J. and Newsome, S. D. 2021. Adaptive foraging in the Anthropocene: can individual diet specialization compensate for biotic homogenization? – Front. Ecol. Environ. 19: 510–518.
Manlick, P. J., Petersen, S. M., Moriarty, K. M. and Pauli, J. N. 2019. Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations. – Funct. Ecol. 33: 335–345.
Mark Elbroch, L. and Wittmer, H. U. 2012. Table scraps: intertrophic food provisioning by pumas. – Biol. Lett. 8: 776–779.
MEDC 2022. Michigan Economic Development Corporation. – https://www.michiganbusiness.org/.
Medina, A. M. and Almeida-Neto, M. 2020. Grinnelian and Eltonian niche conservatism of the European honeybee (*Apis mellifera*) in its exotic distribution. – Sociobiology 67: 239–246.
Moss, W. E., Alldredge, M. W., Logan, K. A. and Pauli, J. N. 2016. Human expansion precipitates niche expansion for an opportunistic apex predator (*Puma concolor*). – Sci. Rep. 6: 39639.
Mueller, M. A., Drake, D. and Allen, M. L. 2018. Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. – PLoS One 13: e0190971.
Murray, M., Edwards, M. A., Abercrombie, B. and St Clair, C. C. 2015. Poor health is associated with use of anthropogenic resources in an urban carnivore. – Proc. R. Soc. B 282: 20150009.
Newsome, T. M. and Ripple, W. J. 2014. A continental scale trophic cascade from wolves through coyotes to foxes. – J. Anim. Ecol. 84: 49–59.
Newsome, S. D., Rio, C. M. del, Bearhop, S. and Phillips, D. L. 2007. A niche for isotopic ecology. – Front. Ecol. Environ. 5: 429–436.
Newsome, S. D., Yeakel, J. D., Wheatley, P. V. and Tinker, M. T. 2012. Tools for quantifying isotopic niche space and dietary variation at the individual and population level. – J. Mammal. 93: 329–341.
Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J. and Dickman, C. R. 2015a. The ecological effects of providing resource subsidies to predators. – Global Ecol. Biogeogr. 24: 1–11.
Newsome, S. D., Garbe, H. M., Wilson, E. C., Gehrt, S. D., Oecologia, S., Feature, S. and Niche, I. 2015b. Individual variation. in anthropogenic resource use in an urban carnivore. – Oecologia 178: 115–128.
Oksanen, J. et al. 2022 vegan: community ecology package. – R package ver. 2.6-2. https://github.com/vegandevs/vegan, https://vegandevs.github.io/vegan/.
Palomares, F. and Caro, T. M. 1999. Interspecific killing among mammalian carnivores. – Am. Nat. 153: 492–508.
Parnell, A. C., Inger, R., Bearhop, S. and Jackson, A. L. 2010. Source partitioning using stable isotopes: coping with too much variation. – PLoS One 5: e9672.
Parsons, M. A., Newsome, T. M. and Young, J. K. 2022. The consequences of predators without prey. – Front. Ecol. Environ. 20: 31–39.
Pauli, J. N., Ben-David, M., Buskirk, S. W., Depue, J. E. and Smith, W. P. 2009. An isotopic technique to mark mid-sized vertebrates non-invasively. – J. Zool. 278: 141–148.
Pereira, L. M., Owen-Smith, N. and Moleón, M. 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. – Mamm. Rev. 44: 44–55.
Perrig, P. L., Lambertucci, S. A., Donadio, E., Smith, J. A., Middleton, A. D. and Pauli, J. N. 2023. Risk effects cascade up to an obligate scavenger. – Ecology 104: e3871.
Peterson, A. T., Soberón, J. and Sánchez-Cordero, V. 1999. Conservatism of ecological niches in evolutionary time. – Science 285: 1265–1267.
Petroelje, T. R., Belant, J. L., Beyer, D. E. and Svoboda, N. J. 2019. Subsidies from anthropogenic resources alter diet, activity, and ranging behavior of an apex predator (*Canis lupus*). – Sci. Rep. 9: 13438.
Petroelje, T. R., Kautz, T. M., Beyer, D. E. and Belant, J. L. 2021. Interference competition between wolves and coyotes during variable prey abundance. – Ecol. Evol. 11: 1413–1431.
Pettorelli, N., Durant, S. M. and Du Toit, J. T. (eds) 2019. Rewilding (ecological reviews). – Cambridge Univ. Press.

Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., Semmens, B. X. and Ward, E. J. 2014. Best practices for use of stable isotope mixing models in food-web studies. – Can. J. Zool. 92: 823–835.

Pluemer, M., Dubay, S., Drake, D., Crimmins, S., Veverka, T., Hovanec, H., Torkelson, M. and Mueller, M. 2019. Red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*) in an urban landscape: prevalence and risk factors for disease. – J. Urban Ecol. 5: 1–9.

Polis, G. A., Myers, C. A. and Holt, R. D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. – Annu. Rev. Ecol. Syst. 20: 297–330.

Prugh, L. R. and Sivy, K. J. 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. – Ecol. Lett. 23: 902–918.

Radeloff, V. C., Hammer, R. B., Stewart, S. I., Fried, J. S., Holcomb, S. S. and McKeefry, J. F. 2005. The wildland–urban interface in the United States. – Ecol. Appl. 15: 799–805.

Ripple, W. J. and Beschta, R. L. 2012. Trophic cascades in Yellowstone: the first 15years after wolf reintroduction. – Biol. Conserv. 145: 205–213.

Ripple, W. J., Wirsing, A. J., Wilmers, C. C. and Letnic, M. 2013. Widespread mesopredator effects after wolf extirpation. – Biol. Conserv. 160: 70–79.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D. and Wirsing, A. J. 2014. Status and ecological effects of the world's largest carnivores. – Science 343: 1241484.

Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G. and McDonald, R. A. 2012. Ecosystem restoration with teeth: what role for predators? – Trends Ecol. Evol. 27: 265–271.

Robinson, Q. H., Bustos, D. and Roemer, G. W. 2014. The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. – Ecology 95: 3112–3123.

Rodewald, A. D., Shustack, D. P., Jones, T. M., Rodewald, A. D., Shustack, D. P. and Jones, T. M. 2016. Dynamic selective environments and evolutionary traps in human-dominated landscapes. – Ecology 92: 1781–1788.

Rodriguez Curras, M., Donadio, E., Middleton, A. D. and Pauli, J. N. 2022. Carnivore niche partitioning in a human landscape. – Am. Nat. 199: 496–509.

Rodriguez Curras, M., Romanski, M. C. and Pauli, J. N. 2024a. The pulsed effects of reintroducing wolves on the carnivore community of Isle Royale. – Front. Ecol. Environ. 22: e2750.

Rodriguez Curras, M., Manlick, P. J. and Pauli, J. N. 2024b. Data from: Carnivore community reassembly provides a test of Eltonian niche conservatism. – Figshare Repository, https://doi.org/10.6084/m9.figshare.24886620.v2

Roemer, G. W., Gompper, M. E. and Van Valkenburgh, B. 2009. The ecological role of the mammalian Mesocarnivore. – BioScience 59: 165–173.

Roth, J. D. and Hobson, K. A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. – Can. J. Zool. 78: 848–852.

Ruprecht, J., Eriksson, C. E., Forrester, T. D., Spitz, D. B., Clark, D. A., Wisdom, M. J., Bianco, M., Rowland, M. M., Smith, J. B., Johnson, B. K. and Levi, T. 2021. Variable strategies to solve risk-reward tradeoffs in carnivore communities. – Proc. Natl Acad. Sci. USA 118: e2101614118.

Sapolsky, R. M. and Share, L. J. 2004. A pacific culture among wild baboons: its emergence and transmission. – PLoS Biol 2: E106.

Schell, C. J., Stanton, L. A., Young, J. K., Angeloni, L. M., Lambert, J. E., Breck, S. W. and Murray, M. H. 2021. The evolutionary consequences of human–wildlife conflict in cities. – Evol. Appl. 14: 178–197.

Selva, N. and Fortuna, M. A. 2007. The nested structure of a scavenger community. – Proc. R. Soc. B 274: 1101–1108.

Sivy, K. J., Pozzanghera, C. B., Grace, J. B. and Prugh, L. R. 2017. Fatal attraction? Intraguild facilitation and suppression among predators. – Am. Nat. 190: 663–679.

Sivy, K. J., Pozzanghera, C. B., Colson, K. E., Mumma, M. A. and Prugh, L. R. 2018. Apex predators and the facilitation of resource partitioning among mesopredators. – Oikos 127: 607–621.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – Ecol. Lett. 10: 1115–1123.

Stephens, R. B., Ouimette, A. P., Hobbie, E. A. and Rowe, R. J. 2022. Reevaluating trophic discrimination factors ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) for diet reconstruction. – Ecol. Monogr. 92: 1–20.

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L. and Semmens, B. X. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. – PeerJ 2018: e5096.

Terborgh, J. W. 2015. Toward a trophic theory of species diversity. – Proc. Natl Acad. Sci. USA 112: 11415–11422.

Webb, G. K. 2018. Searching the Internet to estimate deer population trends in the U.S., California and Connecticut. – Issues Inf. Syst. 19: 163–173.

Wiens, J. J. and Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. – Annu. Rev. Ecol. Evol. Syst. 36: 519–539.

Wilmers, C. C., Stahler, D. R., Crabtree, R. L., Smith, D. W. and Getz, W. M. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. – Ecol. Lett. 6: 996–1003.

Wilson, E. E. and Wolkovich, E. M. 2011. Scavenging: how carnivores and carrion structure communities. – Trends Ecol. Evol. 26: 129–135.