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REVIEW AND SYNTHESES

Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores

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Abstract

Interactions among terrestrial carnivores involve a complex interplay of competition, predation and facilitation via carrion provisioning, and these negative and positive pathways may be closely linked. Here, we developed an integrative framework and synthesized data from 256 studies of intraguild predation, scavenging, kleptoparisitism and resource availability to examine global patterns of suppression and facilitation. Large carnivores were responsible for one third of mesocarnivore mortality (n = 1,581 individuals), and intraguild mortality rates were superadditive, increasing from 10.6% to 25.5% in systems with two vs. three large carnivores. Scavenged ungulates comprised 30% of mesocarnivore diets, with larger mesocarnivores relying most heavily on carrion. Large carnivores provided 1,351 kg of carrion per individual per year to scavengers, and this subsidy decreased at higher latitudes. However, reliance on carrion by mesocarnivores remained high, and abundance correlations among sympatric carnivores were more negative in these stressful, high-latitude systems. Carrion provisioning by large carnivores may therefore enhance suppression rather than benefiting mesocarnivores. These findings highlight the synergistic effects of scavenging and predation risk in structuring carnivore communities, suggesting that the ecosystem service of mesocarnivore suppression provided by large carnivores is strong and not easily replaced by humans.

Keywords

Carcass, carrion, cascade, fatal attraction, interspecific killing, intraguild predation, mesocarnivore, mesopredator, meta-analysis, scavenging.

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INTRODUCTION

The study of animal community ecology has been dominated by the paradigm that negative interactions such as competition and predation are the primary drivers of community structure (Elton 1927; Hutchinson 1957; Hairston *et al.* 1960; Paine 1966). Recently, ecologists have challenged this viewpoint and highlighted the importance of positive interactions and neutral processes in structuring communities (Hubbell 2001; Bruno *et al.* 2003; Jones *et al.* 2010; Augustine & Baker 2013; Barrio *et al.* 2013). Theoretical frameworks that integrate positive and negative interactions, such as successional theory and the stress gradient hypothesis, have greatly improved our understanding of plant community dynamics (Pickett *et al.* 1987; Bertness & Callaway 1994). Despite evidence that facilitation may be equally important in structuring animal communities (Stachowicz 2001; Bruno *et al.* 2003; Wilson & Wolkovich 2011), few studies have integrated positive and negative interactions in food web models (Thebault & Fontaine 2010; Fontaine *et al.* 2011; Pocock *et al.* 2012).

Terrestrial carnivore guilds present an ideal system for evaluating positive and negative pathways within animal interaction webs. Large carnivores can suppress populations of smaller carnivores (i.e., “mesocarnivores”) through direct killing, resource competition, or indirectly by inducing behavioural responses that slow population growth (Palomares & Caro 1999; Creel 2001; Berger & Gese 2007; Prugh *et al.* 2009; Ritchie & Johnson 2009; Ripple *et al.* 2013). Conversely, large carnivores can facilitate mesocarnivores by providing resource subsidies in the form of carrion (Moleón *et al.* 2014; Pereira *et al.* 2014). Recent syntheses concluded that scavenging is widespread and has major implications for food web structure, stability, population dynamics and nutrient cycling, but this unique interaction is often overlooked by ecologists (DeVault *et al.* 2003; Wilson & Wolkovich 2011; Moleón *et al.* 2014; Moleón & Sánchez-Zapata 2015; Barton *et al.* 2019). Opportunistic mesocarnivores commonly scavenge kills of larger carnivores, and this subsidy can be an important food source in areas where they coexist (Huegel & Rongstad 1985; Wilmers *et al.* 2003a; Prugh 2005; Atwood & Gese 2008; Dijk *et al.* 2008; Elbroch & Wittmer 2012; Schlacher *et al.* 2013; Sivy *et al.* 2018). The interaction between large carnivores and mesocarnivores may therefore range from facilitation to suppression, but a general conceptual framework to predict the strength and direction of these intraguild interactions has not been developed. As large carnivores recover in some regions and continue to decline in others (Chapron *et al.* 2014; Ripple *et al.* 2014), an improved understanding of positive and negative interactions among carnivores is needed for science-based conservation and management.

Carnivore ecology is often examined within the context of intraguild predation theory or the exploitation ecosystem hypothesis (e.g., Thompson & Gese 2007; Elmhagen *et al.*

2010; Letnic & Ripple 2017; Pasanen-Mortensen *et al.* 2017). Both theories predict that top carnivores should negatively affect mesocarnivores, with the strength and stability of interactions varying along productivity gradients (Oksanen *et al.* 1981; Holt & Polis 1997). The carnivore cascade hypothesis additionally predicts that top-down suppression of mesocarnivores by large carnivores should indirectly facilitate smaller carnivores (Levi & Wilmers 2012; Newsome & Ripple 2014), *sensu* "the enemy of my enemy is my friend." However, the carnivore cascade hypothesis has been demonstrated only among grey wolves (*Canis lupus*), coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in North America, and it is thus unclear how widespread these multilevel cascading effects may be. In addition, these top-down theories do not account for intraguild facilitation via carrion subsidies. Integration of top-down facilitation and suppression may help to explain why some carnivore communities do not appear to be structured by cascading top-down suppression (Schuette *et al.* 2013; Sivy *et al.* 2017).

The importance of carrion subsidies from large carnivores may increase when other resources are scarce, potentially outweighing negative effects of intraguild aggression (Selva & Fortuna 2007). The net effect of large carnivores on mesocarnivores may therefore switch from suppression to facilitation as systems become increasingly "stressful," which has been well-demonstrated to occur in plant communities (He *et al.* 2013). If facilitation dominates under conditions of high stress and suppression dominates under conditions of low stress, intraguild interactions may increase ecosystem stability by dampening spatiotemporal fluctuations in the abundance of mesocarnivores. Alternatively, carcasses may serve as foci of attraction for mesocarnivores, thereby increasing encounter rates with large carnivores and the likelihood of intraguild predation. This "fatal attraction" hypothesis thus proposes that carcass sites may amplify rather than ameliorate suppression (Sivy *et al.* 2017).

With the dawning of the "golden age" of scavenging research (Moleón & Sánchez-Zapata 2015), fundamental questions about facilitative and suppressive interactions among carnivores arise. Is the risk of intraguild predation linked to scavenging? What factors influence the strength of intraguild facilitation and suppression? Here, we address these questions by developing an integrated conceptual framework (Fig. 1) and conducting a global meta-analysis of studies that have quantified rates of intraguild mortality, scavenging, carrion provisioning and kleptoparasitism in terrestrial carnivore communities.

Previous reviews have found that intraguild predation within Carnivora is most common among pairs of species with intermediate body size ratios and less common among species pairs that are either very different or similar in size (Palomares & Caro 1999; Donadio & Buskirk 2006). Donadio & Buskirk (2006) also found that intraguild killing was more prevalent among species within the same family, potentially because these species have greater niche overlap than species in different families. We therefore predicted that mesocarnivore mortality rates caused by large carnivores would be greatest among species pairs with intermediate size ratios and among intrafamily pairs. If cascading effects of top-down suppression lead to positive indirect interactions among carnivores as predicted by the carnivore cascade hypothesis, we expected interactions among carnivores with one rank difference in the dominance hierarchy to be negative (e.g., wolves and coyotes), and interactions among species separated by two ranks to be positive (e.g., wolves and red foxes). We likewise expected that mesocarnivore body size would affect reliance on carrion and kleptoparasitism risk, with larger mesocarnivores better able to dominate abandoned large carnivore kills and defend their own kills from thieves.

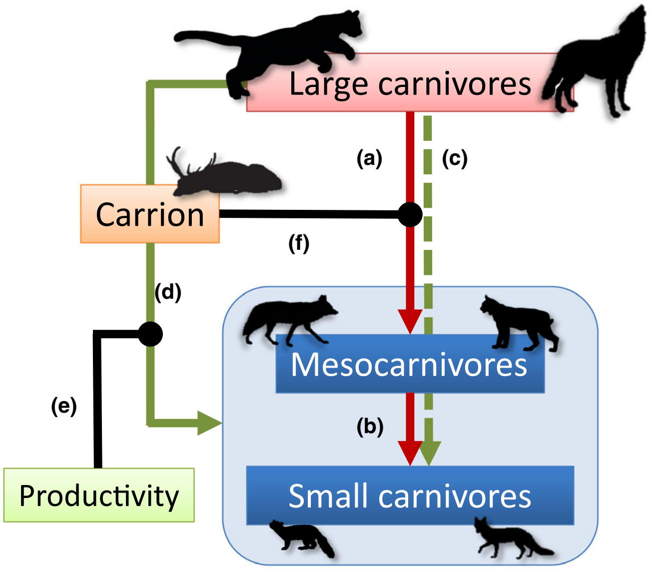

Figure 1 Conceptual framework integrating positive and negative interactions among carnivores. Positive effects are shown as green arrows, negative effects as red arrows, moderating effects are shown as black lines with circular ends, direct effects are solid and indirect effects are dashed. Large carnivores suppress mesocarnivores (path a) and mesocarnivores suppress smaller carnivores (path b) via direct killing and fear effects, which may lead to positive indirect effects of large carnivores on small carnivores (path c; carnivore cascade hypothesis). Large carnivores may simultaneously benefit smaller carnivores via carrion subsidies (path d), and the importance of these subsidies may increase as ecosystem productivity declines (path e; stress gradient hypothesis). However, carcass sites could increase the strength of suppression by large carnivores (path f) by functioning as hotspots of aggressive intraguild interactions (fatal attraction hypothesis).

We evaluated the stress gradient and fatal attraction hypotheses by examining latitudinal gradients in facilitation and suppression. If the stress gradient hypothesis applies to carnivore communities, we expected reliance on carrion to increase with distance from the equator due to the lower productivity and higher energetic demands of high-latitude systems. We also predicted that interactions among carnivores would be more positive in high-latitude systems due to a greater importance of carrion facilitation, and more negative at lower latitudes where competition and suppression should prevail. In contrast, the fatal attraction hypothesis predicts that a latitudinal increase in carrion reliance should strengthen negative interactions. An emergent effect of attraction leading to suppression should be scale-dependence, whereby local-scale associations among carnivores are positive (due to carcasses creating hotspots of carnivore activity) and landscape-scale associations are negative (due to intraguild killing; Sivy *et al.* 2017). We tested this scale-dependence by examining how study area size affected intraguild interactions. To provide context of how the biomass of carnivore-provided carrion compares to the biomass of small prey that are typically primary prey for mesocarnivores, we compiled data from studies reporting densities of small prey (lagomorphs and rodents) as well as studies reporting kill and consumption rates of ungulates by large carnivores to allow for a rough comparison. Together, these compiled datasets reveal new insights into the structure and functioning of carnivore communities.

METHODS

Data collection

We searched the Web of Science database for all relevant studies published to date in February 2018 (search terms specified below). We adopted a "snowball" approach, wherein we also reviewed relevant literature cited in studies located from Web of Science literature searches. After completing this process, we conducted a secondary search in Google Scholar and examined the first 200 papers (sorted by relevance) to determine whether additional papers with useable data were identified. This secondary search did not return additional useable papers. When publications reported findings from more than one study area or from distinct time periods with different carnivore communities, we recorded these as separate studies. Conversely, we pooled multiple publications into a single study in cases when findings from the same area and carnivore community were reported in more than one publication. For each study included in our database, we recorded the continent, latitude and longitude, study area size, season(s) of data collection, years and duration of study, dominant habitat type and vegetative cover class. Study area sizes reported by authors were recorded when possible. When size was not stated, we referred to study area maps, delineations of reserves or other boundaries referred to in the study to estimate the study area size. Dominant habitat was classified into one of 11 categories (see Table S1 in Supporting Information). Descriptions of the dominant vegetation were used to classify vegetation as open, closed or mixed, with "mixed" chosen when the proportion of open and closed habitats appeared to be roughly equal.

We conducted five separate literature searches to obtain data for different analyses:

Suppression

Studies reporting mortality and abundance relationships among smaller and larger carnivores were located using the terms "intraguild predation AND carnivor*", "mortality AND cause AND (telemetry OR collar) AND carnivor*," and "interspecific killing AND carnivor*." We restricted studies to regions with carrion-provisioning large carnivores, defined as large-bodied (>15 kg; Hunter 2011) non-ursid carnivores, as ursids (bears) tend to monopolize carcasses until thoroughly depleted (Allen *et al.* 2015). We restricted telemetry studies to those that collared subordinate carnivores (hereafter, "mesocarnivores"), defined as a carnivore that co-occurs with a larger, dominant carnivore. Each record consisted of a species pair for each study. We recorded the species names, total number of collared mesocarnivores (N_t), number of mortalities caused by each carnivore species (N_c), number of mortalities of unknown cause (N_u) and total number of mortalities (N_m). For each unique study-species pair combination, the proportion of known-caused mortality caused by the larger carnivore (*MortProp*) was calculated as:

$$MortProp = \frac{n_c}{n_m - n_u} \tag{1}$$

The proportion of individuals with known fate killed by the larger carnivore (mortality rate, *MortRate*) was calculated as:

$$MortRate = \frac{n_c}{n_t - n_u} \tag{2}$$

In cases when only data on mortalities was reported, *MortRate* could not be calculated. The numerators and denominators of each equation were used to construct binomial models of mortality risk (see *Statistical Analyses* below). Information on the gender and age class (adult, sub-adult or juvenile) of mesocarnivore was recorded when known. When mortality rates for juveniles were reported separately from adults, they were excluded, as most studies were of adults only. When studies allowed estimation of annual rates of cause-specific mortalities, these rates were also recorded.

We recorded correlations in abundance among species pairs (*AbundCor*) along with the sample size when available. We used only metrics that range from −1 to 1, which consisted of Pearson correlation coefficients, Spearman's rank correlation coefficients, species interaction factors (SIFs) and standardized path coefficients from structural equation models.

To test the carnivore cascade hypothesis, each species in the "suppression" data table was ranked according to its position in the dominance hierarchy of the carnivore guild in the study area. Top carnivores were ranked 1, which consisted of grey wolves, cougars (*Puma concolor*), Eurasian lynx (*Lynx lynx*), dingoes (*Canis dingo*), African lions (*Panthera leo*), tigers (*Panthera tigris*), spotted hyenas (*Crocuta crocuta*) and grizzly bears (*Ursus arctos*) in our dataset. Mid-size carnivores had a rank of 2 (e.g., coyotes, jackals [*Canis* spp.], bobcats [*Lynx rufus*], Canada lynx [*L. canadensis*]), smaller carnivores had a rank of 3 (e.g., foxes, small wild cats), and occasionally a small carnivore was assigned a rank of 4. For example, in Alaska wolves and grizzly bears = 1, wolverines (*Gulo gulo*), coyotes and Canada lynx = 2, red foxes = 3, and American marten (*Martes americana*) = 4. Aside from the top carnivores, the ranks of the other species could differ among systems. For example, American marten were ranked as 3 in a study in northeastern Oregon, where foxes and fishers (*Pekania pennanti*) were absent and the guild consisted of cougars (rank 1), coyotes and bobcats (rank 2), and marten (rank 3). For African large carnivores, lions and spotted hyenas were assigned a rank of 1, and leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) were assigned a rank of 2. Although leopards occasionally kill wild dogs and cheetahs, it was more appropriate to have all three species ranked directly below lions and hyenas for testing the carnivore cascade hypothesis, because wild dogs and cheetahs interact with lions and hyenas far more often than they interact with leopards (e.g., Mills & Gorman 1997; Gorman *et al.* 1998; Durant 2000a). We calculated the difference in ranks among pairs (*RankDiff*), and we classified pairs in one of three categories (*PairClass*): (1) large-meso (rank 1 vs. 2), (2) meso-small (rank 2 vs. 3), or (3) large-small (rank 1 vs. 3). Because of the small sample size of species ranked 4 ($n = 2$), these cases were excluded from analyses using *RankDiff* or *PairClass*.

Scavenging

Studies reporting the proportion of mesocarnivore diet comprised of carrion and visitation rates to carcasses were located using the search terms "carrion AND scaveng*," "mesopredator AND scaveng*," and "carnivor* AND scaveng*." As above, we excluded studies from areas that lacked carrion-provisioning large carnivores. We further restricted studies to those in which scavenging by mesocarnivores was confirmed by observation or in cases where the authors provided rationale for considering ungulate remains to be from scavenging rather than predation. For each study of scavenging, we recorded scavenger species, large carnivore(s) present, carrion source (when known), sample size and type, and carrion type. We recorded two metrics of carrion use depending on the study design: (1) *CarDiet*, the proportion of the diet comprised of carrion (from studies of scat or stomach contents), or (2) *CarVisit*, the proportion of carcasses visited (from observations at carcass sites).

Kleptoparasitism

Studies reporting data on kleptoparasitism among carnivores were located using the search terms "kleptoparasitism AND carnivor*." We recorded species names for each victim-thief pair, sample size (number of kills monitored), the number of kills stolen and densities of each species when reported. The proportion of kills kleptoparisitised was calculated as the number stolen divided by the number monitored (*KleptRate*).

Carrion provisioning

To estimate the amount of carrion provided to scavengers by large carnivores, we searched the literature for studies of kill rates. We first used the terms "carnivor* AND kill rate," and "carnivor* AND predation rate," but these searches yielded too few relevant results. We modified our search terms to specify the large carnivores present in each major ecosystem or continent (e.g., "wolf OR Canis lupus AND kill rate," "lion OR Panthera leo AND kill rate"). We recorded species-specific kill rates for each carnivore and prey species pair. The total biomass (kg) of carrion provided by an individual carnivore per year (*CarProv*) was calculated as:

$$CarProv = 365 * \sum (k_i * b_i) * r \tag{3}$$

where k_i is the number of individuals of ungulate prey species i killed per individual carnivore per day, b_i is the body mass of each ungulate species and r is the proportion of carrion biomass remaining after initial abandonment by the carnivore. The body mass of each prey species was obtained from each study based on the age and sex classes consumed, or from mean adult body masses in the PanTHERIA database if not reported (Jones *et al.* 2009). The proportion of carrion biomass remaining after abandonment was a constant (0.2788) calculated as the average across 26 studies reporting this metric based on visual observations (95% CI = 0.21–0.34).

To obtain a rough estimate of carrion provided by large carnivores per unit area for comparison to the biomass of live small prey for mesocarnivores (see below), we recorded all carnivore densities found in examined studies and supplemented with records from PanTHERIA ($n = 70$ estimates for 12 large carnivore species). We then multiplied *CarProv* by the average density for each carnivore species to obtain an estimate of carrion provided by each large carnivore species per km^2 over the course of a year.

Small prey biomass

When available, we recorded density (individuals/hectare) of rodents and lagomorphs reported in studies from the above literature searches, as these taxa are the primary year-round resources for most mesocarnivores (Macdonald & Nel 1986; Feldhamer *et al.* 2007). However, these data were often missing from carnivore studies. We therefore searched for studies of small prey density in regions where information was lacking using targeted searches for specific prey species or taxa based on knowledge of the primary prey bases in each ecosystem (e.g., hare OR Lepus AND abundance OR density). Thus, this search is not considered comprehensive but intended to provide a representation of small mammal biomass in areas throughout the world. We entered small mammal density data for each species (or, species combinations when reported together), season and year reported in the study. We then calculated average small prey density for each study, summing across species when densities of multiple small mammal species were estimated within a study. Small mammal density estimates were multiplied by the average adult body mass (obtained from the PanTHERIA database) to calculate biomass (kg per km^2).

Statistical analyses

We conducted meta-analyses to identify factors affecting rates of mortality, scavenging, kleptoparisitism and abundance correlations using the compiled datasets described above. For each model, Study ID was included as a random effect in a mixed effect general linear model. All variables used in models are described in Table 1.

Mortality, scavenging and kleptoparisitism models were run using the "glmer" function in R package *lme4* (Bates *et al.* 2015). We used the binomial family, with the response variable constructed as the number of "successes" and "failures." Because sample size information is inherently provided in these binomial response variables, weighting was not necessary. Qualitatively similar results were obtained using weighted mixed models with a Gaussian family and arcsine square-root transformed proportions, and back-transformed means and variances from these models were reported in tables and figures. We ran two mortality models, using

Table 1 Descriptions of all covariates and response variables, with the mean and range of values for continuous variables. Mean values here are unweighted and may differ from the means reported in results, which were weighted based on the sample size of each study. Mesocarnivore and large carnivore refer to the smaller and larger species, respectively, in a pair of interacting carnivores

	Description	Mean	Range
Covariates			
AbsLat	Absolute value of latitude for the study location	38.8	0.1–70
Area	Size of the study area (km^2)	78,591	0.7–1,700,000
Cover	Vegetative cover class (open, closed, or mixed)	--	--
Duration	Length of study (years)	6.1	1–80
MesoMass	Mesocarnivore body mass (kg)	18.74	0.87–110.5
LargeMass	Large carnivore body mass (kg)	65.7	4.8–196.3
MassRatio	Body mass ratio (ln*(LargeMass/ MesoMass))	1.38	−0.53 to 4.12
MesoFam	Taxonomic family of the mesocarnivore	--	--
LargeFam	Taxonomic family of the large carnivore	--	--
FamDiff	Are the large and mesocarnivores from the same or different families ("same" or "diff")?	--	--
RankDiff	Difference in dominance rank between the large and mesocarnivore	--	--
PairClass	Classification of the large-mesocarnivore dominance rankings (Rank 1vs2, 2vs3, 1vs3)	--	--
Response variables			
MortProp	Proportion of known-cause mortality caused by the large carnivore (see eqn 1)	0.26	0–1
MortRate	Proportion of radiocollared mesocarnivores killed by the large carnivore (see eqn 2)	0.11	0–0.54
AbundCor	Correlation among large and mesocarnivore abundances	−0.21	−0.92 to 0.81
CarDiet	Proportion of mesocarnivore diet comprised of carrion	0.26	0-0.93
CarVisit	Proportion of monitored carcasses visited by the mesocarnivore	0.31	0.02–1
KleptRate	Proportion of mesocarnivore kills stolen by large carnivores	0.24	0–1
CarProv	Total carrion biomass provided by an individual large carnivore (kg per year), see eqn 3	1597	314–5388

MortProp and *MortRate* to construct response variables (see eqns 1 and 2 above). In both models, “successes” were the numbers of individuals killed (n_c). “Failures” in the *MortProp* model were the numbers of known fate mortalities ($n_m - n_u$, see eqn 1), and “failures” in the *MortRate* model were the total numbers of individuals with known fate ($n_t - n_u$, see eqn 2). Mortality models included the following predictor variables: *Cover*, *FamDiff*, *RankDiff*, *MesoMass, LargeMass, MassRatio* and *MassRatio*^{2}. A polynomial fit was evaluated for *MassRatio* because prior syntheses found that intraguild predation risk was greatest at intermediate body size ratios among pairs of carnivores (Palomares & Caro 1999; Donadio & Buskirk 2006). To account for the effect that study duration could have on estimated mortality rates, we included *Duration* as a random effect in the *MortRate* model.

To examine how the diversity of carnivores in a system affects intraguild mortality rates, we summed mortalities caused by all larger carnivores for each mesocarnivore species within each study. We then conducted an ANOVA (weighted by sample size) using larger carnivore species richness as the predictor and the summed *MortRate* as the response variable. Carnivore richness was included as a categorical rather than numerical variable to facilitate comparison of mean mortality rates among systems with differing richness levels.

We ran two binomial scavenging models, one with the number of carcasses visited vs. not visited as the response variable (*CarVisit*), and one with the number of dietary items that were or were not carrion as the response variable (*CarDiet*). Scavenging models included the following predictors: *Cover*, *MesoMass* and *MesoFam*. Because the source of carrion was often unknown, information about provisioning large carnivores was not included in models. Kleptoparasitism models were constructed using the number of kills stolen vs. not stolen as the response variable (*KleptRate*), and *Cover*, *MassRatio*, *MassRatio*^{2}, *MesoMass, LargeMass, LargeFam* and *MesoFam* as predictors in single-factor models. Multiple factors could not be included in the same kleptoparasitism model due to low sample size. Type II Wald Chi-square tests were conducted to evaluate significance of the predictors using the R package *car* (Fox & Weisberg 2019).

Abundance correlation models were run using function “lme” of the *nlme* R package with a Gaussian family (Pinheiro et al. 2017). *Cover*, *FamDiff*, *RankDiff*, *MesoMass, LargeMass, MassRatio* and *MassRatio*^{2} were included as predictors. We used inverse variance weighting, which equals *n*-3 when the effect size is a correlation (Koricheva *et al.* 2013). Correlations were Fisher’s z-transformed prior to analysis, and back-transformed means and variances were reported. To test the carnivore cascade hypothesis, we used abundance correlations to construct a simple structural equation model that estimated direct and indirect effects of large carnivores on mesocarnivores and smaller carnivores. Abundance correlations among the three *PairClass* categories were used to calculate standardized path coefficients using variance partitioning equations in Grace (2006).

To test the stress gradient and fatal attraction hypotheses, we constructed general linear models examining latitudinal patterns of carrion provisioning, scavenging rates, mortality rates and abundance correlations. The absolute value of latitude (*AbsLat*) of each study location was the predictor variable, and *CarInd*, *CarDiet*, *CarVisit*, *PropMort*, *MortRate* and *AbundCor* were response variables in univariate models weighted by sample size. Scale dependence was tested using a weighted general linear model with log-transformed study area size (*Area*) as the predictor and *AbundCor* as the response variable. Study ID was not included as a random effect in these models, because latitude and study area size were key attributes of studies that likely explained random variation among studies. All statistical analyses were conducted in program R.

RESULTS

Summary of literature search results

We compiled data from 256 studies across all continents (except Antarctica), 67% of which were conducted in the northern hemisphere (Table S2, Appendix S1). Eighty six percent of studies took place in North America, Africa or Europe, while 14% of studies occurred in Asia, Australia or South America (Fig. 2). Mortality, scavenging and carrion provisioning data were obtained for 48 carnivore species in 9 families (Table S3).

Suppression

Our literature search yielded 58 estimates of intraguild mortality among 36 unique species pairs in 32 studies (Table S4). These records contained mortality data from 1,581 radio-collared individuals and 566 additional mortalities. The grand mean intraguild mortality rate (*MortRate*) was 4–7% for individual species pairs and 6–12% when summed across multiple agents of intraguild mortality for each mesocarnivore (Fig. 3a, Table 2). The mean proportion of mortality due to interspecific killing (*MortProp*) was 17% for species pairs and 27–32% when summed for each mesocarnivore (Table 2). Species richness of larger carnivores ranged from 1 to 3 among study systems. Increased richness caused additive or superadditive (i.e., more than additive) increases in intraguild mortality rates for mesocarnivores ($F_{2,28} = 9.31$, $P < 0.001$, $R^2 = 0.40$): mean mortality rates were 6.5% (95% CI = 1.5–11.4%), 10.6% (95% CI = 4.5–16.7%) and 25.5% (95% CI = 17.9–33.1%) for mesocarnivores in systems with 1, 2 or 3 larger carnivore species, respectively (Fig. 3b).

Intraguild mortality rates among species pairs were greatest when body mass ratios were intermediate, both species were in the same family, and in areas with closed vegetation cover (*MassRatio*^{2} $X_1^2 = 9.06$, $P = 0.01$; *FamDiff* $X_1^2 = 12.30$, $P = 0.002$; *Cover* $X_2^2 = 15.92$, $P < 0.001$). Risk of intraguild predation peaked when the larger carnivore was approximately four times larger than the mesocarnivore (Fig. 3c). Most large carnivores in the dataset were canids ($n = 17$) or felids ($n = 26$), so we tested for an interaction between *FamDiff* and *LargeFam* using this subset to determine whether the strength of intra- vs. interfamily aggression differed among families. Indeed, risk of mortality from large felids was identical for intra- and interfamily mesocarnivores (5.8%), whereas risk of mortality from large canids was more than five times higher for smaller canids (14.3%) than for mesocarnivores within other families (2.7%; Fig. 3d; *FamDiff* x *LargeFam* $X_1^2 = 8.73$, $P = 0.003$).

We obtained 45 records of abundance correlations among 21 carnivore species pairs in 22 studies (Table S5). The grand mean correlation between species pairs was −0.34 (95% CI = −0.26 to −0.41; Fig. 4). Correlations were more strongly negative in study areas with more open cover and among species pairs with one rank difference in dominance (*Cover* $F_{2,19} = 4.12$, $P = 0.03$; *RankDiff* $F_{1,18} = 18.9$, $P < 0.001$). Consistent with the carnivore cascade hypothesis, a simple structural equation model indicated that large carnivores directly suppressed mesocarnivores to a greater extent than they directly suppressed small carnivores (Fig. 5). The indirect positive effect of large carnivores on small carnivores due to suppression of mesocarnivores was 0.11, leading to a slightly positive net effect of 0.04 (Fig. 5).

Scavenging

We obtained 39 records of carrion occurrence in the diet of 18 carnivore species from 23 studies (Table S6), and 44 records of carcass visitation by 21 carnivore species in 19 studies (Table S7). The average proportion of carrion in the diet was

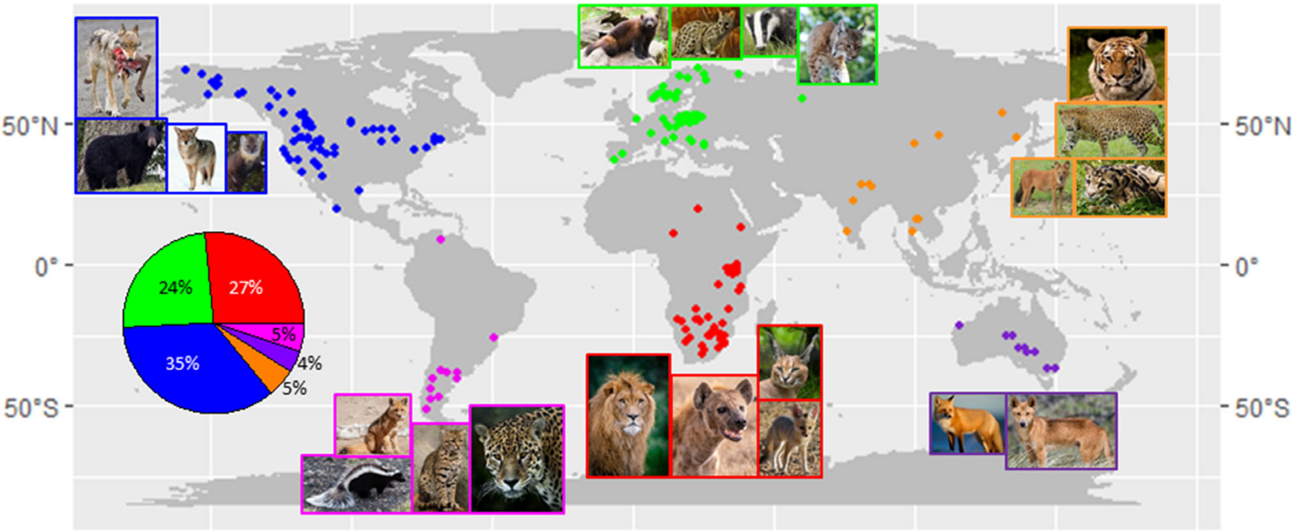

Figure 2 Locations of studies included in the meta-analyses ($n = 256$). Colours indicate continents (blue = North America, pink = South America, green = Europe, red = Africa, orange = Asia, purple = Australia). Pie chart indicates the percentage of studies from each continent. Photos show a subset of species studied in each continent. From top to bottom, left to right in each group: North America – Gray wolf, black bear, coyote, American marten; Europe – wolverine, common genet, European badger, Eurasian lynx; Asia – tiger, leopard, dhole, clouded leopard; Australia – red fox, dingo; Africa – African lion, spotted hyena, caracal, cape fox; South America – Culpeo fox, Humboldt's hog-nosed skunk, Geoffroy's cat, jaguar. See Table S3 for scientific names.

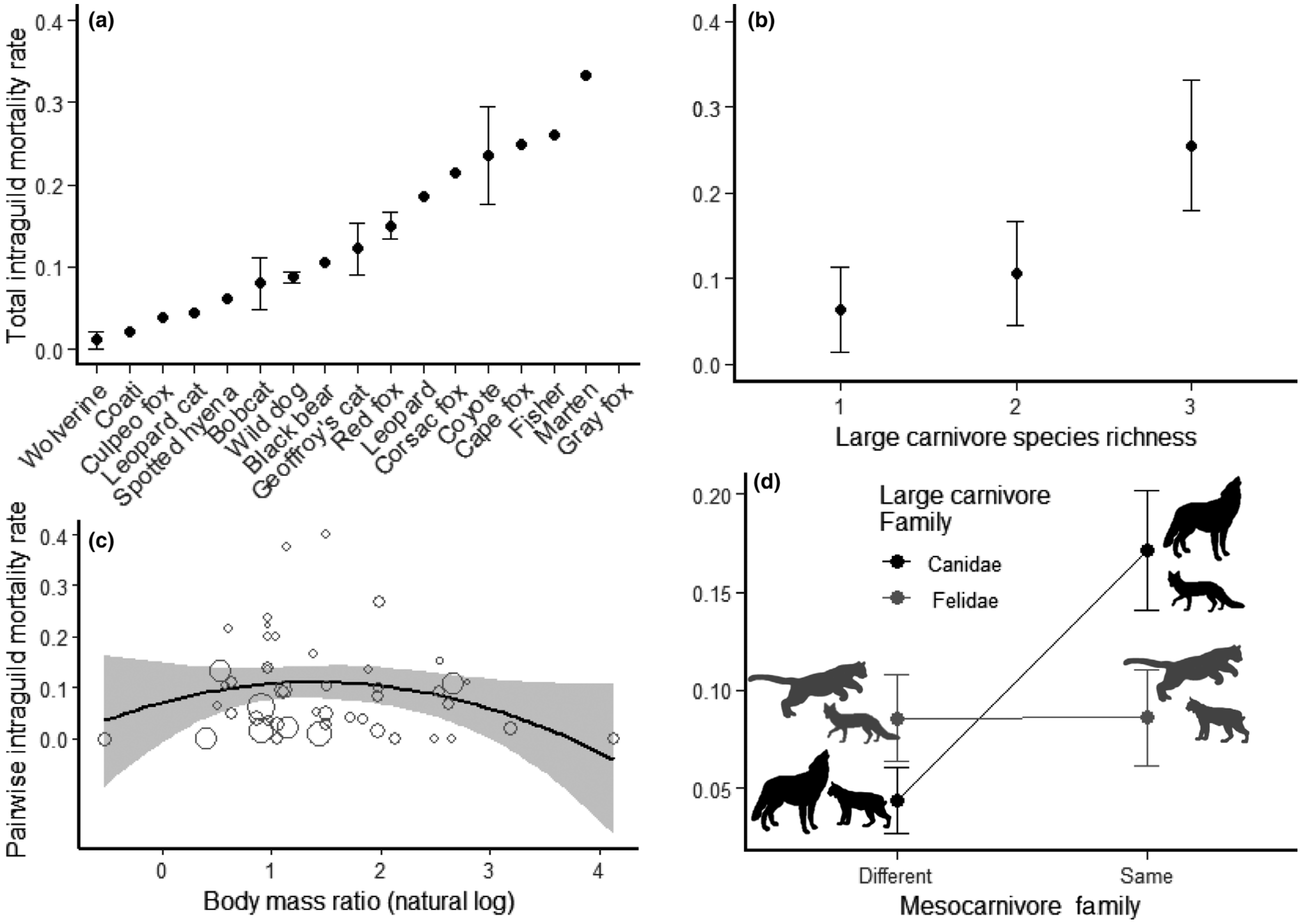

Figure 3 Patterns of intraguild mortality. Total intraguild mortality rates of (a) each mesocarnivore species, averaged across studies and ordered from lowest to highest average rate, and (b) mesocarnivore species in systems with either one, two, or three sympatric larger carnivore species. "Marten" = American marten, "wild dog" = African wild dog; see Table S2 for scientific species names. Weighted means and standard error bars are shown, with the sample size of collared animals in each study used as weights. Pairwise intraguild mortality rates were affected by (c) the body size ratio of the species pair, with the polynomial fit and 95% confidence interval showing highest mortality at intermediate size ratios (peak = 1.4). Body size ratios were natural log-transformed, so a ratio of 1.4 corresponds to a pair in which the larger species is approximately 4 times heavier than the smaller species. (d) Pairwise intraguild mortality rates caused by large canids were more than five times higher for canid mesocarnivores than for non-canid mesocarnivores, whereas mortality rates caused by large felids did not differ within and between families. Weighted means and 95% confidence intervals are shown.

0.30, and the average proportion of carcasses visited was 0.23 (Table 3). Visitation rates were similar to ungulate carcasses provided by large carnivores ($\bar{x} = 0.25$, $n = 20$), human hunters ($\bar{x} = 0.20$, $n = 8$) or a mix of hunters and carnivores ($\bar{x} = 0.22$, $n = 16$; $F_{1,41} = 0.05$, $P = 0.94$; Table S7). Carrion occurrence in the diet increased with mesocarnivore body size and was lower in study areas with open cover (Fig. 6, *MesoMass* $X_1^2 = 16.1$, $P < 0.001$; *Cover* $X_2^2 = 6.39$, $P = 0.04$). Carcass visitation rates increased with mesocarnivore body size, were highest in areas with mixed vegetation cover, and differed among families (Table 3, *MesoMass* $X_1^2 = 52.0$, $P < 0.001$; *Cover* $X_2^2 = 7.8$, $P = 0.02$; *MesoFam* $X_6^2 = 369.1$, $P < 0.001$). Canids were three times more likely to visit carcasses than felids or mustelids, although canids and mustelids had similar proportions of carrion in their diets (Table 3).

Kleptoparasitism

We identified 15 records of kleptoparasitism occurring between seven thief species and six victim species, documented by 12 studies (Table S8). Across all studies, thieves kleptoparasitized 8.4% (95% CI = 3.4–15.2%) of victims' kills. Risk of kleptoparisitism was primarily affected by the family of the thief (*LargeFam* $X_2^2 = 45.96$, $P < 0.001$). Ursids stole far more kills (40%, $n = 269$ monitored kills) than felids (4%, $n = 1,365$), canids (11%, $n = 54$) or hyaenids (11%, $n = 1,193$).

Carrion provisioning and small prey biomass

We compiled 64 records of kill rates by 10 carnivore species reported in 50 studies (Fig. 7, Table S9). Reported kill rates were overwhelmingly of ungulates, with the exception of caiman (*Caiman* spp), porcupines (*Erethizon dorsatum*) and red kangaroos (*Macropus rufus*). Large carnivores provided on average 1,351 kg (95% CI = 1,143–1,597) of carrion per individual per year. Carrion provisioning by cougars (1,350 kg, 95% CI = 1,069-1,707, $n = 19$ studies) was similar to that of grey wolves (1,239 kg, 95% CI = 863–1,779, $n = 13$ studies). The amount of carrion biomass provided by each large

Table 2 Intraguild mortality of radio-collared mesocarnivores. Weighted means, 95% confidence intervals and number of estimates (N) are shown for the intraguild mortality rate, which is the proportion of collared individuals with known fate that were killed by larger carnivores, and the proportion of known-caused mortality caused by larger carnivores. Mortality rates were weighted by the number of collared individuals, and proportion of mortality caused by larger carnivores was weighted by the number of mortalities to calculate weighted means. Rates were calculated for pairs of interacting carnivores ("species pairs"), and by summing across larger carnivores for each mesocarnivore within each study to estimate the total intraguild mortality rate ("summed mortality"). Rates were calculated using the total sample of collared individuals in each study, and annual rates were calculated when possible

	Mortality rate			Proportion of mortality		
Intraguild mortality	Mean	95% CI	*N*	Mean	95% CI	*N*
Species pairs, study total	0.07	0.05–0.09	51	0.17	0.13–0.22	58
Species pairs, annual	0.04	0.02–0.06	40	0.17	0.11–0.23	40
Summed mortality, study total	0.12	0.07–0.16	31	0.32	0.25–0.39	36
Summed mortality, annual	0.06	0.03–0.09	25	0.27	0.19–0.35	25

carnivore species per unit area was 42.2 kg per km^2 (95% CI = 30.2–58.7) per year, which was strikingly similar to the average standing crop of live small prey biomass (45 kg per km^2, 95% CI = 28.8–70.9, $n = 48$ studies, Table S10).

Stress gradient and fatal attraction hypotheses

As expected based on productivity gradients, the density of carnivore-provided carrion declined strongly with increasing latitude (Fig. 8a, $F_{1,48} = 39.1$, $P < 0.001$, $R^2 = 0.45$). Rates of carcass visitation and proportion of diet from scavenging did not vary strongly with latitude (Fig. 8b, *CarVisit* $F_{1,42} = 1.52$, $P = 0.22$; *CarDiet* = $F_{1,37} = 0.03$, $P = 0.87$). Correlations among larger and smaller carnivores became more negative with latitude (Fig. 8c, $F_{1,43} = 5.17$, $P = 0.03$, $R^2 = 0.11$), consistent with predictions of the fatal attraction hypothesis. Likewise, correlations became more negative as the size of study areas increased (Fig. 8d, F1,43 = 13.38, $P < 0.001$, $R^2 = 0.24$), supporting the scale dependence predicted by the fatal attraction hypothesis. Associations among carnivores were generally positive when study areas were less than 1,000 km^2 and negative when areas were larger (Fig. 8d).

DISCUSSION

Scavenging and intraguild killing are predominant interactions within carnivore communities, yet these contrasting phenomena are mostly studied separately, leading to two large and distinct bodies of literature. Our global synthesis of intraguild interactions among carnivores indicates that these positive and negative forces may be linked, with important consequences for carnivore community dynamics. Large carnivores accounted for one third of known-caused mortalities across mesocarnivore species, and ungulate carrion comprised approximately one third of the diet of mesocarnivores, highlighting the strength of both pathways. Scavenging and intraguild mortality were both mediated by body size, whereby larger mesocarnivores relied most heavily on carrion resources, and species pairs in which the larger carnivore was approximately four times heavier than the smaller carnivore had the highest rates of intraguild mortality. Large-scale abundance patterns supported the fatal attraction hypothesis rather than the stress gradient hypothesis, indicating that scavenging large carnivore kills may function more as an ecological trap than an easy meal for mesocarnivores. These findings highlight the potential riskiness of carrion as a food source, and call into question the common framing of carrion as a risk-free subsidy that benefits mammalian scavengers. Instead of facilitating mesocarnivore populations, carrion provided by large carnivores may facilitate suppression.

Global declines in large carnivore populations have coincided with marked increases in populations of mesopredators, an intraguild interaction known as mesopredator release (Soulé *et al.* 1988). The negative impacts of overabundant mesopredators are often used as arguments in favour of large carnivore restoration (Ritchie *et al.* 2012). We found superadditive effects of carnivore species richness on intraguild mortality rates, whereby subordinate carnivores in systems with three larger carnivore species had intraguild mortality rates that were more than twice as high as they were in systems with two larger carnivore species. Because our meta-analysis compared rates across systems rather than employing a stronger before-after-control-impact experimental design, it is possible these differences could reflect differential predation rates by carnivore guilds in different continents or cover types. However, studies were well-dispersed among ecosystems worldwide, and large carnivore richness did not differ among continents ($P = 0.45$) or cover classes ($P = 0.85$). In addition, our findings are unlikely to have resulted from omission of large carnivores that did not kill any collared mesocarnivores, because we added records with zero mortality in these cases ($n = 8$). Thus, these findings strongly suggest that emergent effects of multiple large carnivores may play a key role in suppressing mesocarnivore populations. While emergent effects have been shown to either reduce (e.g., via interference) or increase predation risk in other studies (Sih *et al.* 1998; Atwood *et al.* 2009), the vast majority of studies involving carnivores focus on single species (Moll *et al.* 2017; Montgomery *et al.* 2019). Our findings highlight the synergistic effects of carnivore diversity on the dynamics of lower trophic levels, indicating low redundancy.

In addition to the number of carnivore species in a community, our findings indicate that the composition of species within the carnivore guild may strongly affect dynamics. A prior synthesis reported higher frequency of intraguild killing within than between families (Donadio & Buskirk 2006), but our results indicate this pattern may not be consistent across taxa. We found large canids were far more likely to kill smaller canids than they were to kill smaller carnivores from other families. In contrast, large felids were equal opportunity killers. In regions where large canids such as wolves are the dominant large carnivore, suppressive effects on canid mesocarnivores are likely to be higher than for other species. This high level of canid-on-canid aggression is consistent with the fatal attraction hypothesis, because we also found that

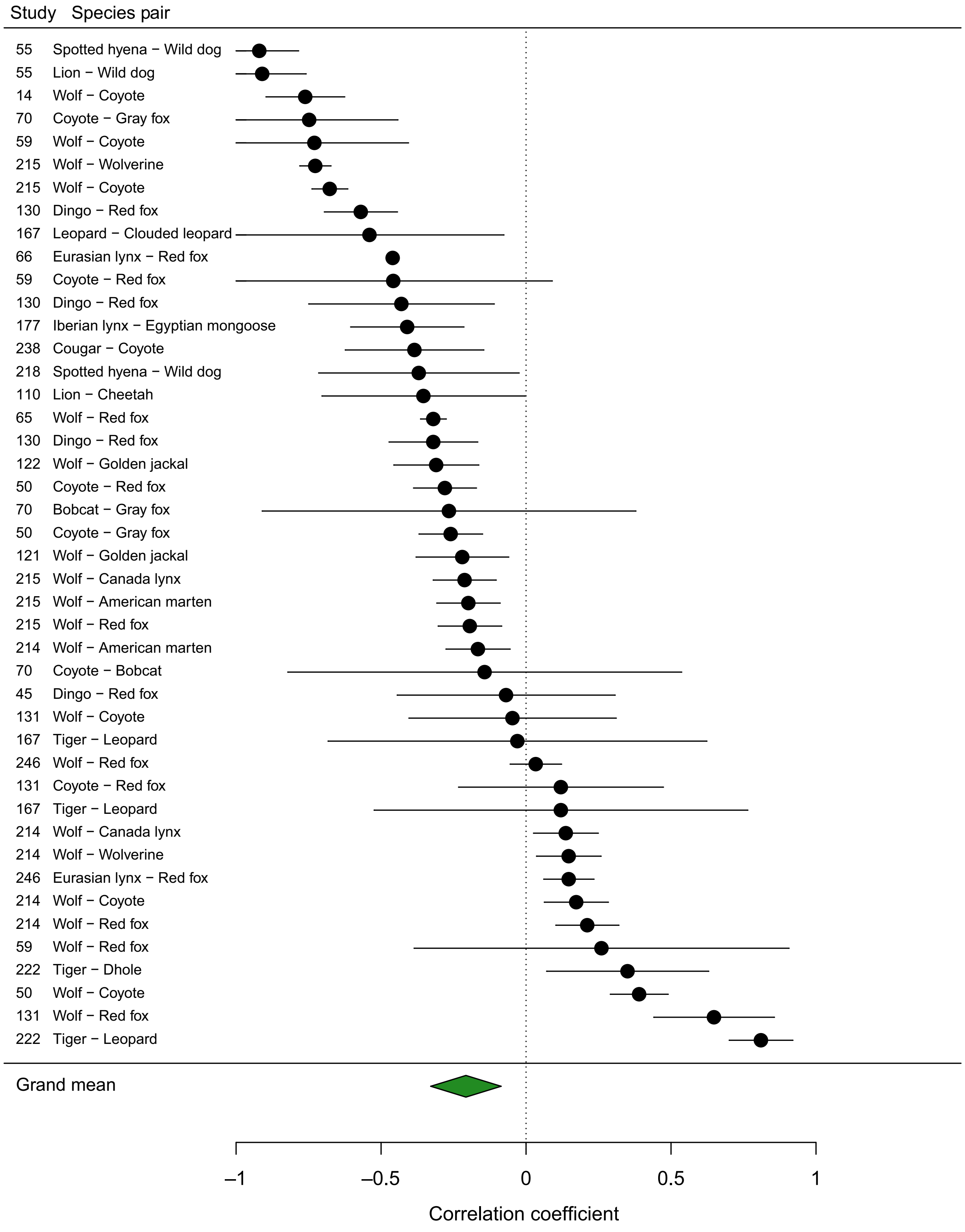

Figure 4 Forest plot of abundance correlations among pairs of sympatric carnivore species. The Study ID and common names of species in each pair are shown, with the larger species named first. Means and 95% confidence intervals are shown, with the variance of each study calculated based on the sample size used to estimate each correlation. The diamond indicates the grand mean and 95% confidence interval across all studies. Means were calculated using Fisher's z-transformed correlations (back-transformed values are shown), and inverse variance weighting was used to calculate the grand mean. Studies were ordered from most negative to most positive correlations.

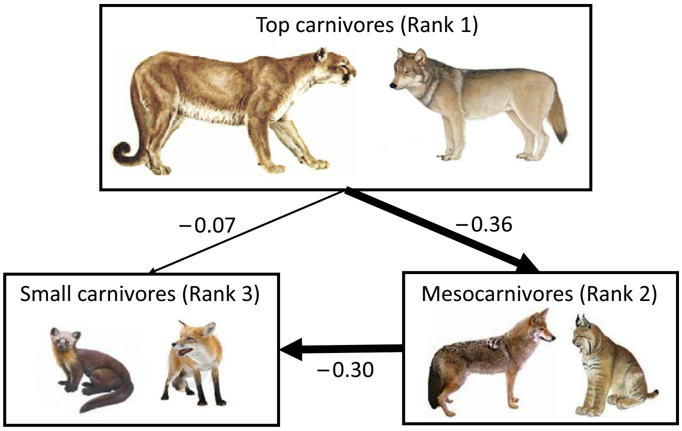

Figure 5 Path diagram of interactions among top carnivores, mesocarnivores, and small carnivores. Standardized path coefficients were calculated based on correlations among species pairs classified according to each species dominance ranking. The three classifications were large-meso (rank 1 vs. 2, $n = 29$ pairs), meso-small (rank 2 vs. 3, $n = 8$) and large-small (rank 1 vs. 3, $n = 5$).

canids were among the most avid scavengers. In contrast, large felids should suppress a wider array of mesocarnivore species, though less intensely. For example, recovery of Eurasian lynx may impact a wider array of mesocarnivore species than recovery of wolves in Europe, but wolves may have stronger suppressive effects on expanding golden jackal (*Canis aureus*) populations (Kusza *et al.* 2019).

While our synthesis indicates that a substantial proportion of mesocarnivore mortality is caused by large carnivores (*c.* 30%), annual rates of mortality were low enough (*c.* 6%) to have minimal impacts on population growth of mesocarnivores, which typically have high reproductive rates and can withstand considerable persecution (Conner & Morris 2015; Curveira-Santos *et al.* 2019). Despite these low intraguild mortality rates, abundance correlations among larger and smaller carnivores were typically negative, indicating net suppressive effects of large carnivores. Similarly, abundance and mortality datasets provided conflicting support for the carnivore cascade hypothesis. Patterns of abundance indicated that large carnivore suppression of mesocarnivores indirectly benefited small carnivores, but mortality rates were similar among species pairs with different dominance rankings. In fact, direct mortality rates from top-ranked carnivores were lower for mesocarnivores (rank 2, 5.2%) than for small carnivores (rank 3, 11.9%), although these differences were not significant. Caution should be used when interpreting these findings due to few records of interactions among apex and small carnivores ($n = 5$ abundance correlations and 6 mortality estimates). Nevertheless, these patterns indicate that factors other than direct killing may play an important role in mesocarnivore suppression. Mounting evidence suggests the fear of predation may limit population growth to an even greater extent than direct mortality (Preisser *et al.* 2005; Preisser & Orrock 2012; Clinchy *et al.* 2013; Suraci *et al.* 2016). We could not quantify fear effects of large carnivores on mesocarnivores, but these non-consumptive effects of predation are a plausible explanation for suppression despite low intraguild mortality rates. While a substantial body of literature has examined fear effects in carnivore-ungulate systems, far less is known about the relative importance of direct and indirect effects of large carnivores on mesocarnivores. Empirical studies specifically designed to quantify fear effects within carnivore communities are thus needed to fully understand the mechanisms of intraguild suppression (Prugh *et al.* 2019).

We hypothesized that the stress gradient hypothesis (SGH) could apply to carnivore communities, because the importance of carrion subsidies from large carnivores may increase when other resources are scarce (i.e., when stress is high), potentially outweighing negative effects of intraguild aggression (Bertness & Callaway 1994; Selva & Fortuna 2007). Because carcasses increase the likelihood of encountering an aggressor (Switalski 2003; Atwood & Gese 2008, 2010), mesocarnivores may avoid scavenging when other resources (e.g., small mammals) are abundant and increase use of carcasses when resources are scarce. For example, occurrence of ungulate carrion in the diet of coyotes increased by 67% when cyclic snowshoe hare (*Lepus americanus*) populations declined in Alaska (Prugh 2005). Although we found that ungulate carrion remained important despite its lower abundance in stressful environments (using absolute latitude as a proxy for stress), interactions among carnivores were increasingly negative rather than positive. Thus, intraguild suppression appears

Table 3 Rates of scavenging by carnivores. Weighted means, 95% confidence intervals, studies and total sample sizes are shown for proportions of carcasses visited and the proportion of diets comprised of carrion for carnivores within each family

	Carcass visitation rate				Proportion of diet			
Family	Mean	95% CI	*N* studies	*N* samples	Mean	95% CI	*N* studies	*N* samples
Canidae	0.33	0.21–0.46	22	3628	0.31	0.23–0.41	24	8479
Felidae	0.11	0.01–0.27	8	1259	0.02	0.41–0.67	2	125
Herpestidae	–	–	–	–	0.27	0.13–0.99	1	101
Hyaenidae	0.27	0.1–0.48	5	1193	0.35	0.16–0.56	4	1767
Mephitidae	0.1	0.01–0.47	1	316	0.12	0.01–0.54	3	382
Mustelidae	0.1	0–0.29	6	869	0.39	0.13–0.69	4	922
Procyonidae	0.07	0.02–0.41	1	316	–	–	–	–
Ursidae	0.67	0.07–0.99	1	116	–	–	–	–
Viverridae	–	–	–	–	0	0–0.42	1	170
Grand mean	0.23	0.17–0.31	44	7697	0.3	0.23–0.38	39	11946

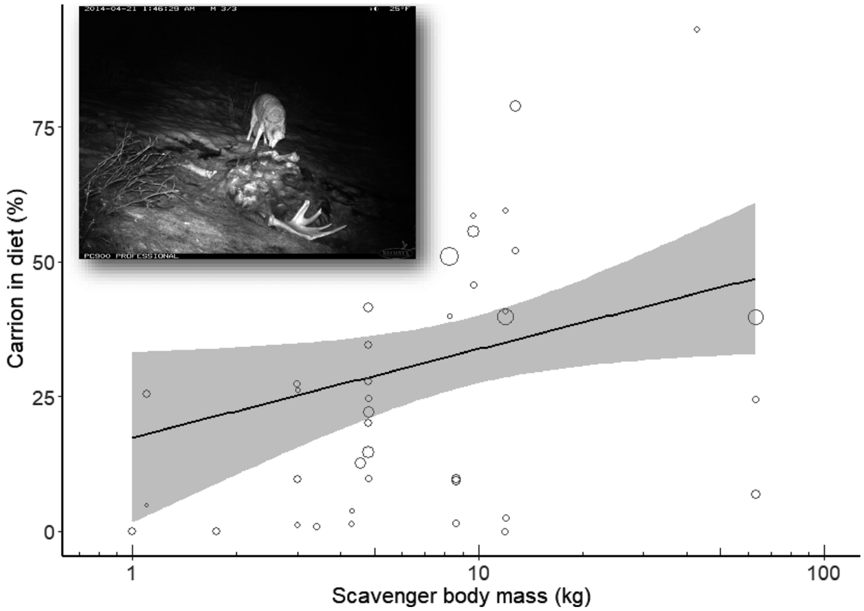

Figure 6 Reliance on scavenging increases with carnivore body size. Diets were estimated based on scat and stomach contents; proportion of diet comprised of ungulate carrion is shown. Each point represents an estimate from a study (*n* = 38), with point sizes scaled by sample size. The weighted regression line and 95% confidence interval are shown. Inset photo shows a coyote (average body mass = 12 kg) scavenging from a wolf-killed moose in Alaska (photo taken during Study 213, Sivy et al. 2017a).

to be enhanced in more stressful environments, contrary to SGH predictions.

Scavenging may be a risky strategy, but it is possible that avoidance of scavenging during lean times would lead to even higher mortality rates from starvation. If scavenging and intraguild mortality are linked, resource shortages may strengthen intraguild interactions due to increased risk-taking behavior, which may partially explain why large carnivores are more effective than humans at suppressing mesocarnivore populations, especially in less productive systems (Elmhagen & Rushton 2007; Prugh *et al.* 2009; Ritchie & Johnson 2009; Elmhagen *et al.* 2010). We expected rates of scavenging and intraguild mortality to covary, based on predictions from the fatal attraction hypothesis. The fatal attraction hypothesis proposes that scavenging should increase the risk of intraguild killing via two mechanisms: (1) increased resource competition, which provides the motivation for killing, and (2) increased encounter rates (Holling 1959), which provides the opportunity (Sivy *et al.* 2017). While several patterns we documented in this global-scale synthesis point toward a link between scavenging and intraguild suppression, we could not test this prediction directly because we found no studies that simultaneously quantified these factors. Likewise, the latitudinal patterns we documented suggest an important role of ecosystem productivity in mediating these interactions, which is supported by theory (Oksanen & Oksanen 2000; Elmhagen *et al.* 2010). However, many factors change with latitude. Empirical studies that examine (1) the fate of individuals in relation to scavenging behavior, (2) spatial associations between intraguild predation events and large carnivore kill sites, and (3) the influence of productivity metrics that are directly relevant to carnivores, such as live prey abundance, are needed to directly test the fatal attraction hypothesis and understand the mediating role of productivity. Specifically, studies where large carnivores and mesocarnivores are radio-collared in the same study area would allow investigation of mesocarnivore mortalities for potential intraguild killing and proximity to large carnivore kill sites, and stomach content analysis of killed mesocarnivores could indicate whether they had been scavenging. Clusters of locations made by collared large carnivores could help identify their kills, which could be monitored for scavenging activity using trail cameras and searches for signs of scavenger activity and mesocarnivore mortalities at or in proximity to kill sites.

Our findings highlight the importance of carrion as a food source for mesocarnivores and indicate that large carnivores provide carrion biomass during the course of a year that rivals the standing crop biomass of live rodents and lagomorphs. It is difficult to directly compare the profitability of these alternative resources, because estimates of carcass depletion rates were too scarce to calculate the standing crop density of carnivore-provided carrion, and live prey require energy spent hunting that carrion does not. Nevertheless, this rough comparison indicates that carnivore-provided carrion likely provides more than a trivial amount of resources to mammalian scavengers. These provisioning services may not be as substantial as they seem, however. All ungulates must die eventually, and removal of ungulate biomass by large carnivores may in fact reduce net carrion biomass rather than increase it. The effect of wolf recolonization on carrion supply was estimated in Yellowstone and Sweden, with conflicting results (Wilmers *et al.* 2003a; Wilmers *et al.* 2003b; Wikenros *et al.* 2013). Thus, net availability of ungulate carrion may be even greater in the absence of large carnivores, but substantial uncertainty remains.

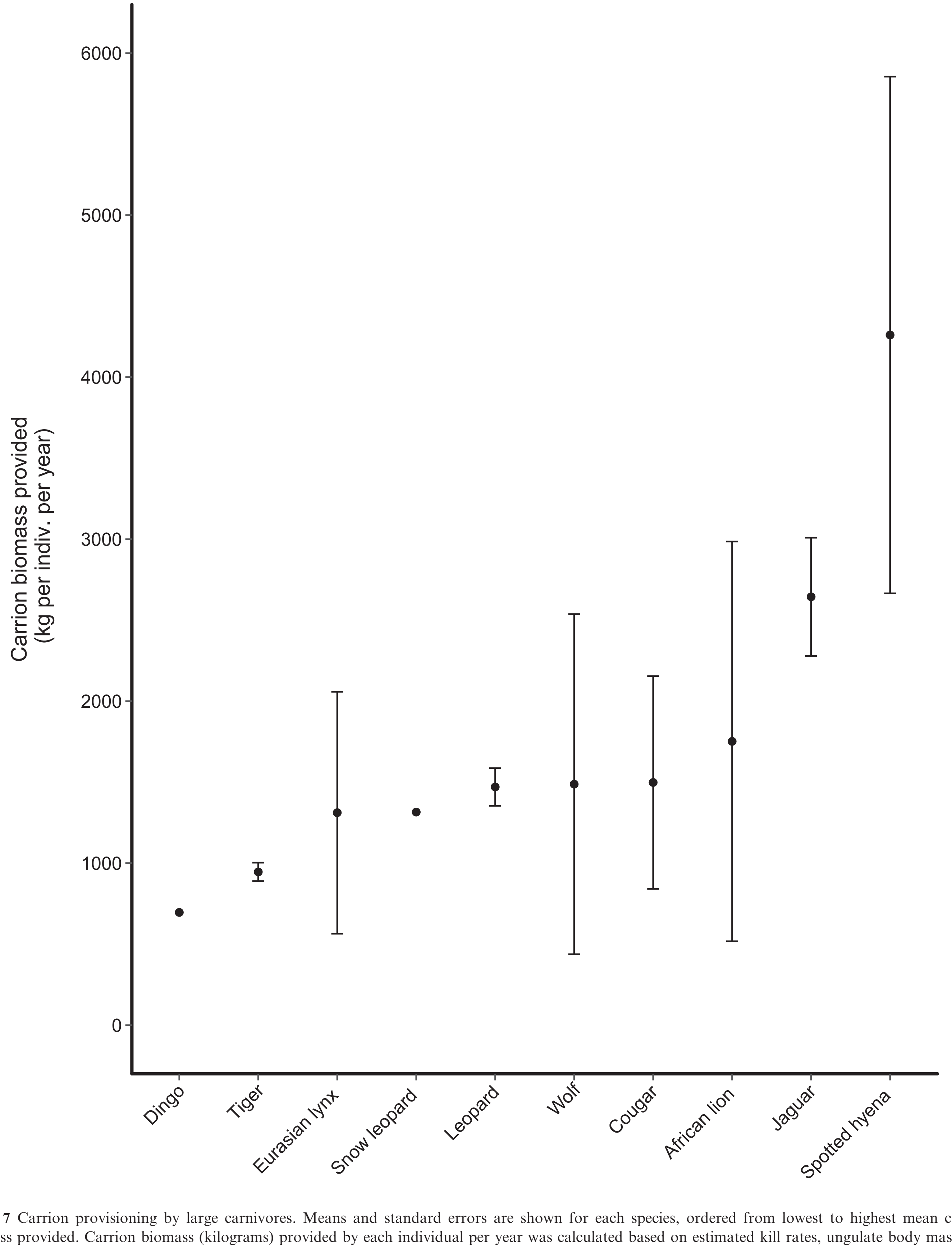

Figure 7 Carrion provisioning by large carnivores. Means and standard errors are shown for each species, ordered from lowest to highest mean carrion biomass provided. Carrion biomass (kilograms) provided by each individual per year was calculated based on estimated kill rates, ungulate body mass, and the proportion of the carcass typically consumed prior to initial abandonment. See Methods for details.

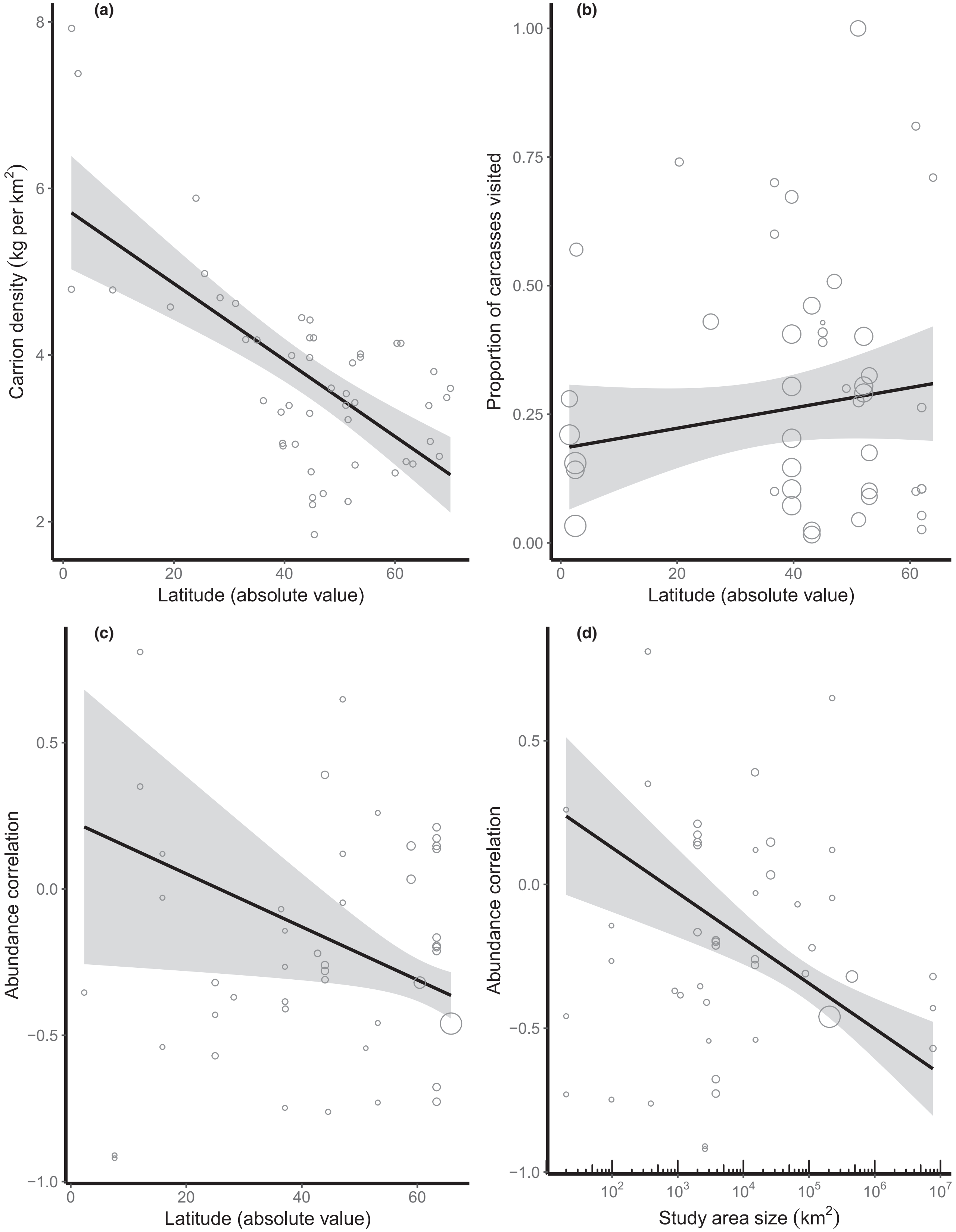

Figure 8 Latitudinal patterns of (a) the density of carrion provided by large carnivores (kg per km^2 per year), (b) visitation rates of scavengers to carcasses and (c) abundance correlations among sympatric pairs of larger and smaller carnivores. (d) Abundance correlations were more negative as the size of the study area increased, supporting the scale-dependence predicted by the fatal attraction hypothesis. Each point represents an estimate from a study, with point sizes scaled by sample size. Weighted regression lines and 95% confidence intervals are shown.

Although we restricted studies to regions with carrion-provisioning large carnivores, the source of carrion in the diet of mesocarnivores was often unknown in our dataset, and thus the contribution of carnivore-provided carrion relative to other sources is not known. Source of carrion was better known from studies that recorded visits to carcass sites, and mesocarnivores scavenged large carnivore kills at similar rates as hunter kills. We did not quantify carrion biomass produced by other agents of mortality, such as disease, starvation, human hunters, or vehicles. These sources may outweigh carnivore-supplied carrion in some systems, although the temporal availability of these carcasses may be more pulsed (e.g., hunter kills, overwinter starvation; Wilmers *et al.* 2003a; Wilmers *et al.* 2003b). In addition, avian scavengers can remove substantial amounts of carrion (especially vultures; Ogada *et al.* 2012; Morales-Reyes *et al.* 2017) and tend to dominate carcasses produced by vehicles and hunters (Wilmers *et al.* 2003b; Kaczensky *et al.* 2005; Selva *et al.* 2005). The effect of large carnivores on net carrion supply, and the relative importance of carrion provisioning by large carnivores compared to other sources, are key unknowns in understanding facilitation among carnivores.

While many large carnivores provide leftovers to scavengers, some large carnivores are more takers than givers, stealing kills from smaller carnivores rather than (or in addition to) providing them. For some mid-ranked carnivores such as cheetahs and leopards, avoidance of kleptoparisitism is a driving force in their ecology (Durant 2000b; Scantlebury *et al.* 2014; Balme *et al.* 2017; Hilborn *et al.* 2018). Kleptoparasitism has primarily been examined within east African carnivore communities; 7 of the 12 studies in our analysis occurred in Africa. Limited sample size precluded strong inferences regarding factors affecting kleptoparisitism rates, but strong taxonomic differences were apparent. Our analysis revealed that bears steal more kills than lions or hyenas, usurping 30–60% of kills from Eurasian lynx in Europe and cougars in North America (Table S8). Bears may thus strongly influence community dynamics by monopolizing carrion and increasing the rates by which felids must kill ungulates to pay this surprisingly high bear tax (Krofel *et al.* 2012; Elbroch *et al.* 2015). However, hibernation by bears provides a reprieve for other carnivores during part of the year. In contrast, kleptoparisitized carnivores in Africa must endure year-round thievery. Thus, systems with and without bears appear to differ substantially in the seasonal dynamics of resource provisioning and stealing among carnivores.

Carnivores are notoriously difficult to study, yet the complex interplay of competition, predation, and facilitation that occurs within terrestrial carnivore communities may be unique, and a better mechanistic understanding of these interactions is needed to accurately predict their system-wide effects (Mech 2012). Our synthesis indicates that scavenging is a critical yet overlooked factor that may determine both fear and the actual risk of mortality for mesocarnivores, creating hotspots of intraguild interactions across the landscape. The scale-dependence of these interactions has important implications for interpreting studies of intraguild interactions. Studies conducted at a local scale ($< 1,000$ km^2) that report positive associations among carnivores should not be interpreted as providing evidence that intraguild competition and predation can be ignored, because factors such as scavenging or coincidental habitat selection could lead to positive local-scale associations even if demographic effects of the intraguild interactions are negative. Our findings indicate that broader spatio-temporal scales need to be examined to accurately assess intraguild dynamics among carnivores, with strongest inference from studies that span multiple scales.

CONCLUSIONS

Populations of large carnivores have been eliminated or greatly reduced in many areas due to habitat loss and conflicts with humans, and the consequential weakening of top-down effects has triggered trophic cascades throughout the world (Estes *et al.* 2011; Ripple *et al.* 2014). As global change accelerates at a rapid pace, the need to better understand the role of large carnivores in ecosystems is urgent. Because mesocarnivores are centrally positioned in food webs and often have a generalist diet, their dynamics can have particularly strong effects on ecosystems and resources that people depend on (Myers *et al.* 2007; Roemer *et al.* 2009). Our synthesis indicates that carrion provisioning may enhance the strength of top-down suppression rather than opposing it, calling into question the assumption that carrion is a beneficial subsidy for mesocarnivores. A link between scavenging and mortality could partially explain the superadditive suppressive effects of large carnivores on mesocarnivores revealed by our synthesis. The suppression of mesocarnivore abundance despite low intraguild mortality rates suggests that large carnivores evoke fear effects, and mesocarnivore control may thus be an ecosystem service that large carnivores can provide most efficiently (Newsome *et al.* 2017). Our findings add to mounting evidence that large carnivores are integral to the functioning of ecosystems through a complex network of pathways (Estes *et al.* 2011; Ripple *et al.* 2014), thus highlighting the value of recovering their populations.

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AUTHORSHIP

LRP and KJS conceived of the study, collected the data and wrote the paper. LRP conducted the data analyses.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.n8pk0p2rv.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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