LETTER

Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide

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Abstract

The composition of local mammalian carnivore communities has far-reaching effects on terrestrial ecosystems worldwide. To better understand how carnivore communities are structured, we analysed camera trap data for 108 087 trap days across 12 countries spanning five continents. We estimate local probabilities of co-occurrence among 768 species pairs from the order Carnivora and evaluate how shared ecological traits correlate with probabilities of co-occurrence. Within individual study areas, species pairs co-occurred more frequently than expected at random. Co-occurrence probabilities were greatest for species pairs that shared ecological traits including similar body size, temporal activity pattern and diet. However, co-occurrence decreased as compared to other species pairs when the pair included a large-bodied carnivore. Our results suggest that a combination of shared traits and top-down regulation by large carnivores shape local carnivore communities globally.

Keywords

Camera trap, ecological traits, global assessment, interspecific interactions, local community structure, spatial co-occurrence.

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INTRODUCTION

The composition of ecological communities is shaped by interspecific interactions (Birch 1957; Hardin 1960; Rosenzweig 1966). Hutchinson's (1957) theory of a realised vs. fundamental niche was one of the first to evaluate species interactions and how they may cause an individual to occupy areas smaller than the area they would reside in the absence of competition and predation. Since then, area-specific assessments of species interactions have illuminated behavioural responses such as spatial partitioning between apex and mesocarnivores (Ritchie & Johnson 2009; Brook *et al.* 2012), temporal or spatial partitioning between predators and their prey (Miller *et al.* 2012; Davis *et al.* 2017) or between potentially competing carnivores (Di Bitetti *et al.* 2009, 2010) and local extinctions resulting from native species being

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outcompeted by exotics (Bailey *et al.* 2009; Farris *et al.* 2015a). As such, the concept of interspecific interactions has been, and is still, a central theme of ecological investigations (Wisz *et al.* 2013).

One of the primary ways in which interspecific interactions are evaluated is by assessing species' patterns of co-occurrence (i.e. species asymmetrical spatial distributions; Mackenzie *et al.* 2004; Richmond *et al.* 2010; Waddle *et al.* 2010). Co-occurring species often display niche segregation as it serves to reduce resource competition, promoting coexistence (Brown & Wilson 1956; Hutchinson 1959; Périquet *et al.* 2015). Niche segregation should occur when species directly compete for resources, and competition should be strongest in cases where species share similar life history traits (Brown & Wilson 1956). Alternatively, if competition and niche segregation are not the primary drivers of local species distributions, trait similarities should lead to greater co-occurrence because of shared environmental and resource affinities (i.e. habitat or environmental filtering; Van der Valk 1981; Keddy 1992; Weiher & Keddy 1999; Díaz *et al.* 1998; Weiher *et al.* 1998). Attempts to explain patterns of co-occurrence tend to focus on species' dietary and habitat preferences because the partitioning of resources can influence the degree to which competition occurs (Donadio & Buskirk 2006; Hayward & Kerley 2008; Yackulic *et al.* 2014).

Behaviour, morphology, and phylogenetic proximity also can play pivotal roles in influencing the strength and direction of interspecific interactions at local scales (Kronfeld-Schor & Dayan 2003; Donadio & Buskirk 2006; Davies *et al.* 2007; Yackulic *et al.* 2014). Species that exhibit different temporal activity patterns (e.g. diurnal vs. nocturnal) may be more likely to co-occur as they have a lower probability of direct competition compared to species which are active at similar times of the day (Kronfeld-Schor & Dayan 2003; Hayward & Slotow 2009; Bischof *et al.* 2014; Périquet *et al.* 2015). Alternatively, a species' overarching social structure (i.e. group, pair or solitary) can influence their resource requirements, detectability by other species and ability to outcompete interspecific competitors (Palomares & Caro 1999; de Oliveira & Pereira 2014). In turn, social structure could influence the likelihood that species co-occur. Body size may also influence co-occurrence via competition (e.g. Dayan *et al.* 1989, 1990; McDonald 2002) or direct aggression (e.g. Sidorovich *et al.* 1999) of similar-sized carnivores (Rosenzweig 1966), as well as top-down pressures of larger carnivores (Palomares & Caro 1999; Saether 1999; Terborgh *et al.* 1999; Elmhagen & Rushton 2007). Lastly, phylogenetic proximity may also shape patterns of co-occurrence because closely related species (e.g. within a family) are often similar in their resource requirements, thereby leading to greater competition among closely related taxa (e.g. within, rather than among, taxonomic groups; Gittleman 1985; Van Valkenburgh 1989; Donadio & Buskirk 2006).

The influence of interspecific interactions is particularly widespread within carnivore guilds (Rosenzweig 1966; Palomares & Caro 1999). Elucidating how carnivore interactions influence patterns of co-occurrence, and the ecological traits driving these interactions, is key to our understanding of niche dynamics, interspecies competition, mesopredator release (Dayan *et al.* 1989; Estes *et al.* 1998; Berger *et al.*

2001) and carnivore population dynamics (Robinson *et al.* 2014; Périquet *et al.* 2015). Interactions between carnivore species can also influence human perception and tolerance of carnivores, thereby affecting human-predator coexistence (e.g. Farhadinia *et al.* 2017). Despite the availability of detailed information on intraguild interactions at the site-specific levels, we have a poor understanding of global patterns in carnivore co-occurrence (Linnell & Strand 2000; Elmhagen & Rushton 2007; Périquet *et al.* 2015). Improving this understanding requires local occurrence data for carnivore communities across large spatial or temporal scales. Historically, resource constraints have limited our ability to collect such data sets for wide-ranging and often elusive species. In the last decade, however, the exponential increase in the use of camera trap surveys has opened the door to studying mammalian carnivore species in remote areas across the world (Rich *et al.* 2017; Steenweg *et al.* 2017). Collaborative research efforts and the aggregation of data collected across large spatial scales and international borders allow us to draw conclusions about patterns of spatial interactions across ecosystems rather than solely within a single study area, thus providing new and important insights into the underlying processes of community structure that are consistent across global scales (Steenweg *et al.* 2017).

Our goal was to investigate co-occurrence within the order Carnivora and determine which ecological traits influence the spatial distributions of sympatric species (i.e. the overlap or avoidance of two species in habitat use). To accomplish this goal, we used a pre-existing dataset (see Rich *et al.* 2017) consisting of remote camera trap data from surveys in 13 study areas in 12 countries, which included observations of 86 mammalian carnivore species in four of the five major biomes worldwide. We approached the analysis as a two-step process. First, we analysed these data using a pair-wise co-occurrence estimator to quantify relative co-occurrence of sympatric species while accounting for imperfect detection (Mackenzie *et al.* 2004; Richmond *et al.* 2010; Waddle *et al.* 2010). We then used estimates of co-occurrence (i.e. species interaction factor) to determine how shared ecological traits, including diet, body size, temporal activity patterns, social structure and phylogenetic proximity, correlated with co-occurrence probabilities. We predicted that species pairs with shared ecological traits (e.g. similar in body size or dietary preferences) would be more likely to compete for resources, and hence more likely to display spatial avoidance. Our analysis provides the first global assessment of carnivore spatial co-occurrence patterns, exemplifying a framework for other collaborative, global-scale studies on species interactions.

MATERIAL AND METHODS

Study areas

We used a pre-existing data set consisting of camera trap survey data (raw data previously published in Rich *et al.* 2017) from 13 study areas spanning 12 countries and 5 continents (Fig. 1). Study area size ranged from 42 to 18 714 km², and within each study area, between 22 and 319 ($\bar{x}$ = 143; SD = 85.5) camera stations (Table 1) were deployed. We only
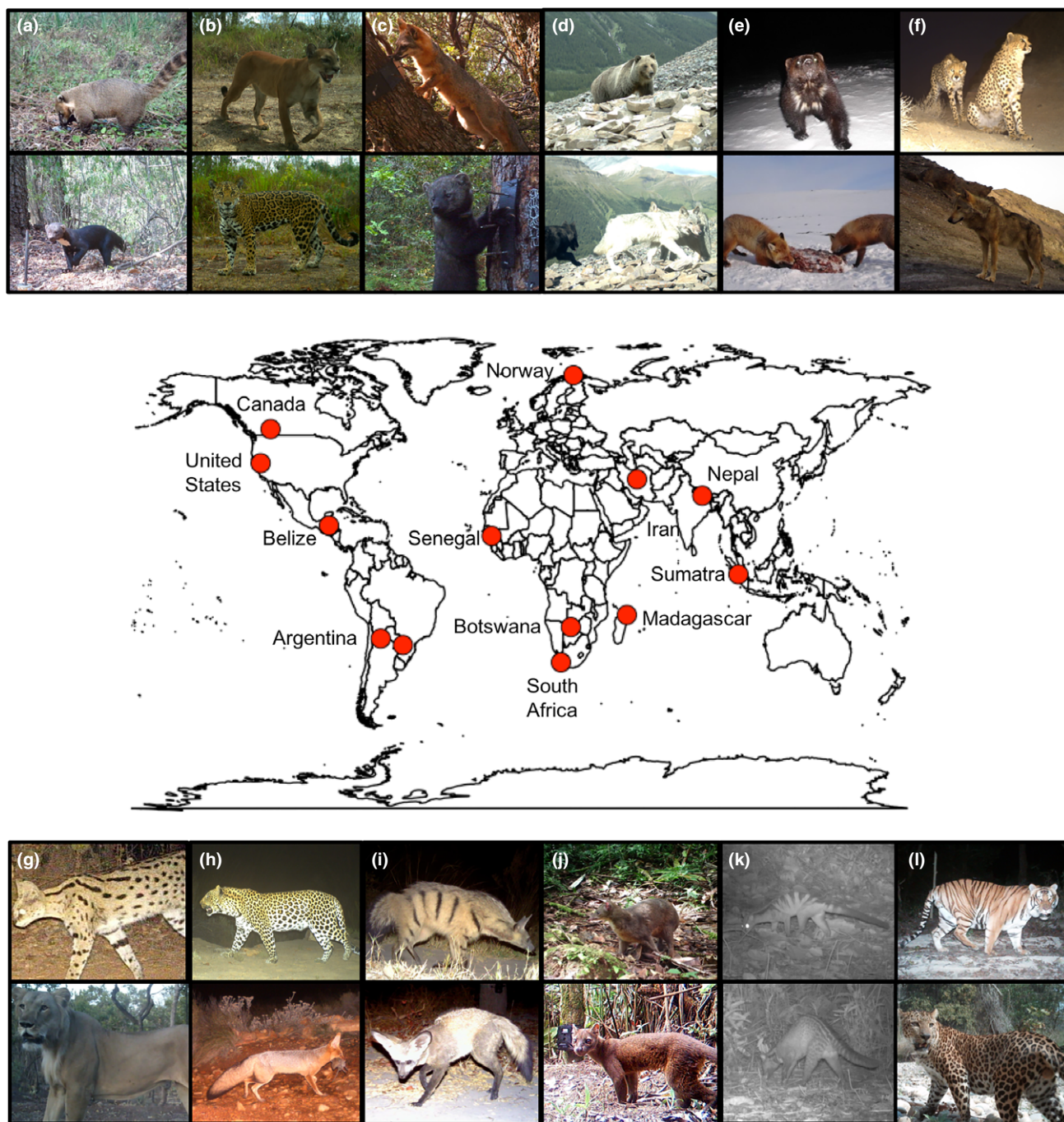
Figure 1 Locations of the 13 study areas, which include remote camera trap surveys conducted in 12 countries, spanning 5 continents and 4 of the 5 major biomes worldwide. Examples of co-occurring species pairs include: (a) *Nasua nasua* (South American coati) and *Eira barbara* (tayra) in Argentina, © M. Di Bitetti; (b) *Puma concolor* (puma) and *Panthera onca* (jaguar) in Belize, © Belize Jaguar Project/Virginia Tech; (c) *Urocyon cinereoargenteus* (grey fox) and *Martes pennanti* (fisher) in United States, © J. Tucker/US Forest Service; (d) *Ursus arctos* (grizzly bear) and *Canis lupus* (grey wolf) in Canada, © Park Canada; (e) *Gulo gulo* (wolverine) and *Vulpes vulpes* (red fox) in Norway, © S. Killengreen; (f) *Acinonyx jubatus venaticus* (Asiatic cheetah) and *Canis lupus* (grey wolf) in Iran, © Iranian Cheetah Society/CACP/DoE/Panthera; (g) *Leptailurus serval* (Serval) and *Panthera leo* (lion) in Senegal, © M. Kane; (h) *Panthera pardus* (leopard) and *Vulpes chama* (cape fox) in South Africa, © Q. Martins/Cape Leopard Trust; (i) *Proteles cristata* (aardwolf) and *Otocyon megalotis* (bat-eared fox) in Botswana, © L. Rich/Panthera; (j) *Eupleres goudotii* (falanouc) and *Cryptoprocta ferox* (fosa) in Madagascar, © Z. Farris; (k) *Hemigalus derbyanus* (banded palm civet) and *Paradoxurus hermaphroditus* (common palm civet) in Sumatra, © F. Widodo/WWF; (l) *Panthera tigris tigris* (Bengal tiger) and *Pantherus pardus fusca* (Indian leopard) in Nepal, © K. Thapa/WWF.

included study areas with > 1000 trap days, with realised effort ranging from 1170 to 35 441 ($\bar{x}$= 9007; SD = 8891) trap days (Table 1; Appendix S1).

North and Central American study areas included five national parks in western Canada (Steenweg *et al*. 2016), the Sierra Nevada Mountains of California, USA (Tucker *et al*.

Table 1 List of camera trap surveys included in our analysis and corresponding reference, detailing the number of camera stations, number of trap days, study area size, number of carnivore species detected and number of detected species pairs in each study area location

Study area	No. Camera stations	No. Trap days	Footprint (km^2)	No. Species detected[1]	No. Species pairs	References
Argentina						
Misiones	103	5104	1547	10	45	Di Bitetti *et al.* (2006)
Yungas	46	1258	376	8	28	Di Bitetti *et al.* (2011)
Belize	213	12 437	1030	11	55	Wultsch *et al.* (2016)
Botswana	179	5345	1154	21	210	Rich *et al.* (2016)
Canada	167	35 441	14 628	12	66	Steenweg *et al.* (2016)
Iran	220	12 768	4749	10	45	Farhadinia *et al.* (2014)
Madagascar	151	8795	42	6	15	Farris *et al.* (2015b)
Nepal	78	1170	509	7	21	Thapa & Kelly (2017)
Norway	66	1832	18 714	3	3	Hamel *et al.* (2013), Henden *et al.* (2014)
Senegal	58	3721	525	13	78	Kane *et al.* (2015)
South Africa	22	5077	2476	14	91	Martins (2010)
Sumatra	92	8009	524	12	66	Sunarto *et al.* (2015)
United States	319	7130	8453	10	45	Tucker *et al.* (2014)

[1]The number of species detected per study area that were included in our analysis, which does not include species with < 3 detections.

2014) and the Mayan Forest in Belize (Wultsch *et al.* 2016). We included two study areas in South America; the first from northeastern Argentina, in the Atlantic Forest of Misiones Province (Di Bitetti *et al.* 2006), and the second in the Yungas ecoregion in northwestern Argentina (Di Bitetti *et al.* 2011). In Africa, we included studies conducted in the Ngamiland District of northern Botswana (Rich *et al.* 2016), Niokolo Koba National Park in Senegal (Kane *et al.* 2015), Cederberg mountains of South Africa (Martins 2010) and Madagascar's Masoala-Makira protected area (Farris *et al.* 2015b). In Asia, we included the southern Riau landscape of central Sumatra in Indonesia (Sunarto *et al.* 2015), the Chitwan National Park in Nepal (Thapa & Kelly 2017) and several reserves across central Iran (Farhadinia *et al.* 2014). We also included a single European study area, located in northern Norway (Hamel *et al.* 2013; Henden *et al.* 2014).

Quantifying co-occurrence

We estimated co-occurrence probabilities for 768 species pairs. The number of species pairs ranged from 3 in Norway to 210 in Botswana (Table 1; see Appendix S2 for species list). In estimating patterns of co-occurrence, we were interested in determining whether species occurred at a site more or less often than expected under a hypothesis of independence (Mackenzie *et al.* 2004). Deviations from independence occur when distributions are non-random with respect to each other. To quantify these deviations, we used two-species occupancy models (Mackenzie *et al.* 2004; Richmond *et al.* 2010) to understand pair-wise carnivore co-occurrence patterns within each study area. This method allowed us to account for imperfect detection at a camera station (i.e. when a species is present but not photographed) by treating each trap day (i.e. 24-h. period) as a repeat survey (Dorazio & Royle 2005; Rich *et al.* 2016). These detection/non-detection data allowed us to estimate occupancy and detection probabilities for every combination of co-occurring species.

Species detected on < 3 occasions were not included in our analyses.

We fit models using a Bayesian formulation of the single-season two-species model parameterisation presented by Richmond *et al.* (2010). This parameterisation estimates conditional probabilities for both occupancy and detection (e.g. the probability species B is present given species A is present or absent and vice versa) and improves model convergence (Richmond *et al.* 2010). We were able to derive unconditional probabilities of species occupancy and detection from the conditional probabilities. We did not investigate covariate relationships on occupancy or detection, which allowed us to avoid classifying dominant/subordinate relationships between co-occurring species (Richmond *et al.* 2010).

We modelled latent occurrence of species A and B at camera station *j* as Bernoulli random variables,

$$z_{A,j} \sim \text{Bernoulli}(\Psi_A) \text{ and}$$
$$z_{B,j} \sim \text{Bernoulli}(\Psi_{Ba} \times (1 - \Psi_A) + \Psi_{BA} \times \Psi_A),$$

where ψ_A was the probability species A occurred in the study area, ψ_{BA} was the occupancy probability of species B given species A was present, and ψ_{Ba} was the occupancy probability of species B given species A was absent. ψ_B (occupancy of species B) was a derived quantity, given by $\psi_A \times \psi_{BA} + (1 - \psi_A) \times \psi_{Ba}$. We estimated the probability of observing species A and species B at camera station *j* as:

$$y_{A,j} \sim \text{Bernoulli}(z_{A,j} \times p_A) \text{ and}$$
$$y_{B,j} \sim \text{Bernoulli}(z_{B,j} \times p_B), \text{ respectively.}$$

The probability of detecting either species A or B at camera station *j* during a trapping session was a function of the probability of detecting the species (p_A and p_B) given it occurs at site *j* ($z_{A,j}$ and $z_{B,j}$). Our study focuses on the spatial rather than temporal co-occurrence between species pairs. In other words, $y_{A,j}$ and $y_{B,j}$ are the number of 24-h. time periods during which the respective species was photographed at site *j* and were modelled using a Binomial (rather than a Bernoulli)

distribution to speed up computation (Kéry 2010). This means we evaluated whether species occurred at the same site, but not necessarily at the same time. Co-occurrence here can be defined as overlap in the use of sites between species.

We then derived the species interaction factor (SIF; Richmond *et al.* 2010), or probability of co-occurrence, for each species pair as

$$SIF = \Psi_A \times \Psi_{BA}/(\Psi_A \times (\Psi_A \times \Psi_{BA} + (1 - \Psi_A) \times \Psi_{Ba}))$$

When the occurrence of one species is independent of the other, SIF = 1.0. When two species co-occur more frequently than would be expected under a hypothesis of independence, SIF and its credible interval will be > 1.0. When species occur less often than expected, SIF and its credible interval will be < 1.0. Note that SIF values < 1.0 indicate potential spatial avoidance, which may result from a habitat-mediated relationship or changes in the behaviour of one or both species. We were not able to disentangle these two mechanisms using our sampling framework. Instead, we use the term 'spatial avoidance' in situations where SIF and 95% credible intervals are < 1.0 to indicate that two species simply do not co-occur at the spatial scale we examine.

We estimated posterior distributions in R (R Core Development Team 2016) using the package R2Jags (Plummer 2011) to call JAGS (version 4.2.0). Estimates were generated from 3 chains of 50 000 iterations after a burn-in of 10 000 iterations. We drew uninformative priors from a uniform distribution of 0 to 1 for all parameters. We assumed model convergence when values of the Gelman-Rubin statistic were <1.1 (Gelman *et al.* 2004). R code is provided in Appendix S3.

Drivers of global co-occurrence

Using our pair-wise SIF estimates, we investigated global carnivore co-occurrence patterns to determine which ecological traits explain the spatial distributions of sympatric carnivores worldwide. We log-transformed mean SIF estimates for all species pairs. The log-transformed values provided a more symmetrical distribution and standardised deviations for cases where interactions were more and less likely (SIF is constrained between 0 and ∞, while ln[SIF] can range from –∞ to ∞). We then fit regression models to ln[SIF] that tested hypotheses about the drivers of mammalian carnivore co-occurrence.

Our primary prediction was that similarity of species pairs would affect the amount of spatial overlap. To assess similarity, we included information on species' temporal activity patterns, dietary habits, social structure, body size (both categorically and as a ratio), taxonomy at the family level (as a proxy for relatedness) and information on the study areas' species diversity and climate. Categorisation of species' temporal activity pattern, dietary habits, social structure and body size was based on a review of peer-reviewed literature, IUCN red-list species accounts (IUCN 2016, Appendix S2), and when necessary, expert knowledge of principal investigators from individual study areas. We assigned the temporal activity pattern for a species to be diurnal, nocturnal, crepuscular (i.e. active primarily at twilight) or cathemeral (i.e. irregularly active at any time of day or night). We designated the dietary habit for each species as strict carnivore, omnivore or insectivore. We used a species' tendency to exhibit grouping (i.e. > 2 individuals of the same species) vs. pairing and solitary behaviour to assign social structure. To account for body size, we characterised the mean weight ratio (heavier:lighter species) between two species, including it as a log-transformed continuous variable. We used the mean weight to accommodate for body size differences between sexes of the same species. We also assigned species to a body size group, with species categorised as small (< 2 kg), small–medium (2–5 kg), medium–large (5–15 kg) or large (>15 kg) body size. Our categorical and continuous variables characterising body size were never included in the same model. Finally, to account for relatedness, we categorised all Carnivora species included in this study based on their taxonomy at the family level. Our data included representative species of the families Canidae, Felidae, Herpestidae, Mustelidae, Procyonidae and Viverridae. Families represented by few species (Ursidae, Mephitidae, Eupleridae and Hyaenidae) were grouped together into a single category and classified as 'Other'.

We summarised the categorical variables of diet, temporal activity pattern, social structure, body size and taxonomic similarity in two ways. For the first coarse comparison method, we compared species with differing trait values (e.g. when species A | B are strict carnivore | omnivore) to those where pairs shared the trait value (e.g. strict carnivore | strict carnivore). In other words, species pairs were either labelled the 'same' or 'different' for all categorical variables of interest. For the fine-scale trait comparison, species pairs were categorically valued for all combinations of a trait (e.g. strict carnivore | strict carnivore = 1, strict carnivore | omnivore = 2, strict carnivore | insectivore = 3, etc.). By allowing for both types of comparisons, we were able to explore whether co-occurrence was driven primarily by coarse- (same vs. different) or fine-scale trait combinations. Lastly, to account for differences among study areas, we included covariates representing species diversity and climate. Specifically, we included fixed effects for the observed number of carnivore species in each study area and the study area's climate as determined by the Köppen-Geiger climate classification system (Kottek *et al.* 2006). Study areas were categorised into equatorial (n = 4), arid (n = 3), warm temperature (n = 4), snow (n = 1) or polar (n = 1) regions.

We had no *a priori* hypothesis on the combined influence of these variables, so we explored 864 model combinations. We estimated posterior distributions using R2Jags to call JAGS in R. Estimates were generated from 3 chains of 20 000 iterations after a burn-in of 5000 iterations (Appendix S3). We drew uninformative priors from a uniform distribution of 0 to 1 for all parameters. We used Deviance Information Criterion (DIC; Speigelhalter *et al.* 2002) to select among our competing models and present the subset of competitive models (i.e. ΔDIC <5) in Appendix S4. Models were considered equivalent with ΔDIC <2 and according to the parsimony principle, we chose the best model as the model with the lowest number of parameters (Burnham & Anderson 2002; Speigelhalter *et al.* 2002). We report coefficient estimates from this model in Appendix S5 and used these estimates to predict SIF ($\widehat{SIF}$) and 95% credible intervals (CI) for all species pairs.

We determined how sensitive our results were to changes in how the data were analysed and which data were included in our analysis. First, we compared our results to a Bayesian weighted regression approach to determine how parameter estimates for the three variables included in all competing models (i.e. body size, temporal activity pattern and diet category) were affected by the estimated uncertainty in mean SIF for each species pair. In addition, we assessed whether data-rich study areas, Botswana and South Africa, may have been driving the observed relationships for our global analysis. A full description of the methods for these sensitivity analyses can be found in Appendix S7.

RESULTS

Quantifying co-occurrence

The mean SIF value across all 768 species pairs was $\hat{x}$ [95% CI] = 1.24[1.19, 1.28], indicating that on average, species were more likely to co-occur than expected under a hypothesis of independence. Nonetheless, SIF variation was large within study areas, with some species pairs showing strong overlap in site use and others strong avoidance (Fig. 2). The largest SIF (4.84[2.25, 7.97]) was estimated for *Galerella sanguinea* Rüppell (slender mongoose) and *Cynictis penicillata* (G. [Baron] Cuvier) (yellow mongoose) in Botswana. Other species pairs exhibiting large spatial overlap included: *Vulpes ruepellii* Schinz (Rüppel's fox) and *Vulpes cana* Blanford (Blanford's fox) in Iran (4.25[2.22, 6.77]), and *Paradoxurus hermaphroditus* (Pallas) (common palm civet) and *Hemigalus derbyanus* (Gray) (banded civet) in Sumatra (3.60[1.53, 6.63]). Strong overlap in site use (mean SIF and 95% CI >1) was found for 91 species pairs (Fig. 2).

Spatial avoidance (mean SIF and 95% CI <1) was found for only 13 of our 768 species pairs (Fig. 2). Examples include: *Panthera pardus saxicolor* Pocock (Persian leopard) and *Hyaena hyaena* (L.) (striped hyena) in Iran (0.24[0.01; 0.83]), *Panthera leo* (L.) (lion) and *Ictonyx striatus* (Perry) (striped polecat) in Botswana (0.39[0.05, 0.94]) and *Urocyon cinereoargenteus* (Schreber) (grey fox) and *Conepatus semistriatus* (Boddaert) (striped hog-nosed skunk) in Belize (0.67 [0.39, 0.97]). The smallest SIF of 0.16[0.00, 0.53] was estimated for *Lycalopex gymnocercus* G. Fischer (pampas fox) and *Eira Barbara* (L.) (tayra) from the Yungas study area in Argentina. We provide species-specific estimates of mean occupancy and detection probabilities in Appendix S6.

Drivers of global co-occurrence

The predominant drivers of species' co-occurrence were body size, temporal activity pattern and diet category, being the three variables included in all competing models (Appendix S4). With the exception of large species, species pairs with similar body sizes occurred at the same sites more often than expected under independence (Fig. 3a). For species pairs categorised as different in size, small-sized species occurred more often than expected at the same sites as small-medium species (Fig. 3a). Species pairs that included a large-bodied carnivore exhibited depressed SIF values relative to all other pairs and to the global

mean, yet still indicated an overall independence (SIF = 1.0) in co-occurrence because credible intervals overlapped 1.0 (Fig. 3a). This pattern is particularly evident in large | large species pairs, where the mean predicted value was the only body size grouping with SIF <1.0, indicating that species of large body size tend to spatially avoid one another, though the 95% CI for this estimate slightly overlapped 1.0.

With respect to diet, same diet species pairs co-occurred at the same sites more frequently than expected for strict carnivores and particularly for insectivores, but not for omnivores (Fig. 3b). Species pairs with differing diets showed independent occurrence in general, with the exception of strict carnivore | omnivore species pairs that showed overlap in site use (Fig. 3b). Contrary to expectations, carnivores with similar temporal activity patterns co-occurred disproportionately more often than pairs that differed in temporal activity pattern (Fig. 3c). Within species pairs with similar temporal activity patterns, cathemeral, crepuscular and diurnal species showed the greatest overlap in site use. Species pairs with different temporal activity patterns showed an overall independence in spatial site occurrence (SIF = 1.0), with the exception of crepuscular | cathemeral species pairs showing a slight spatial overlap (Fig. 3c).

We found that parameter estimates were comparable (i.e. overlapping 95% CI) between the unweighted and weighted regression approaches, suggesting that our results were not sensitive to uncertainties in mean SIF (Appendix S7). Our results were also robust to whether data-rich study areas, Botswana and South Africa, were included in the analysis (Appendix S7).

DISCUSSION

The composition and structure of mammalian carnivore communities have far-reaching effects on the structure and function of terrestrial ecosystems (Roemer *et al.* 2009; Estes *et al.* 2011; Ripple *et al.* 2014). Local community structure depends on a combination of species-specific environmental affinities (i.e. habitat preferences or selection) and interactions among species (Leibold *et al.* 2004). Our study provides important insights into the role of each in shaping local carnivore communities across ecosystems. Overall, mammalian carnivores tended to overlap spatially, but there was wide heterogeneity across species pairs with some showing large spatial overlap and others showing large spatial avoidance. Specifically, we found that body size, temporal activity patterns and dietary habits were related to co-occurrence patterns, where species that shared similar ecological traits generally had greater overlap in site use. These results suggest that at the spatial scale of our study, shared ecological traits are not leading to competitive exclusion, but are rather causing species to select sites where resource availability is likely similar, and thus tend to co-occur. The overall trend of spatial overlap may be attributed to our coarse-scale analyses as we were unable to account for fine-scale differences in species' spatial and temporal activity patterns. Regardless, our study provides an important first step in understanding the drivers of carnivore co-occurrence at a global scale, and a foundation from which future studies interested in more fine-scale assessments of species-pair relationships can build.
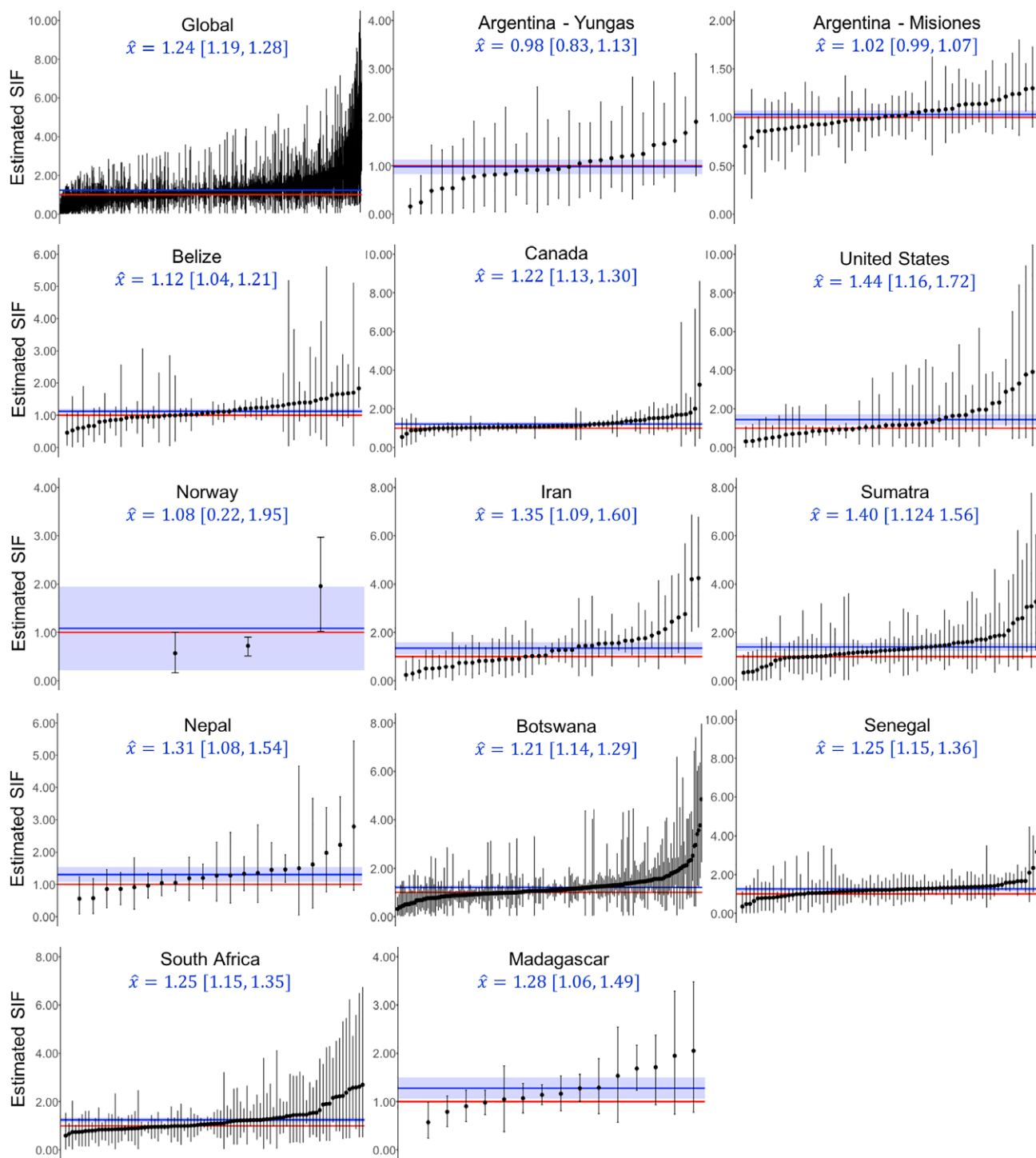
Figure 2 Estimated carnivore co-occurrence (SIF) for all 768 sympatric species pairs across our 13 study areas (and 95% CI). The red line indicates independently occurring species (SIF = 1) and the blue dotted line represents the estimated mean for each study area, with the light blue zone representing the 95% CI. SIF values > 1 indicate co-occurrence between two species, while SIF values < 1 indicate lack of co-occurrence.

Large carnivores reduce the abundance of co-occurring species through direct predation (Hakkarainen & Korpimaki 1996; Salo *et al.* 2008; Krauze-Gryz *et al.* 2012) and incite changes in behaviour (Creel *et al.* 2001; Ritchie & Johnson 2009) and resource use (Périquet *et al.* 2015), thus shifting the role that smaller carnivores play in ecological communities (Bischof *et al.* 2014; de Oliveira & Pereira 2014). Large

carnivores can also promote the abundance of small species by reducing the abundance of mesopredators (Estes *et al.* 1998; Ripple *et al.* 2014). The cascading effects of mesopredator release have been documented in a variety of systems and taxa worldwide (Terborgh *et al.* 1999, 2001; Brashares *et al.* 2010), often resulting in the widespread loss of biodiversity and ecosystem collapse (Estes *et al.* 1998; Berger *et al.* 2001;
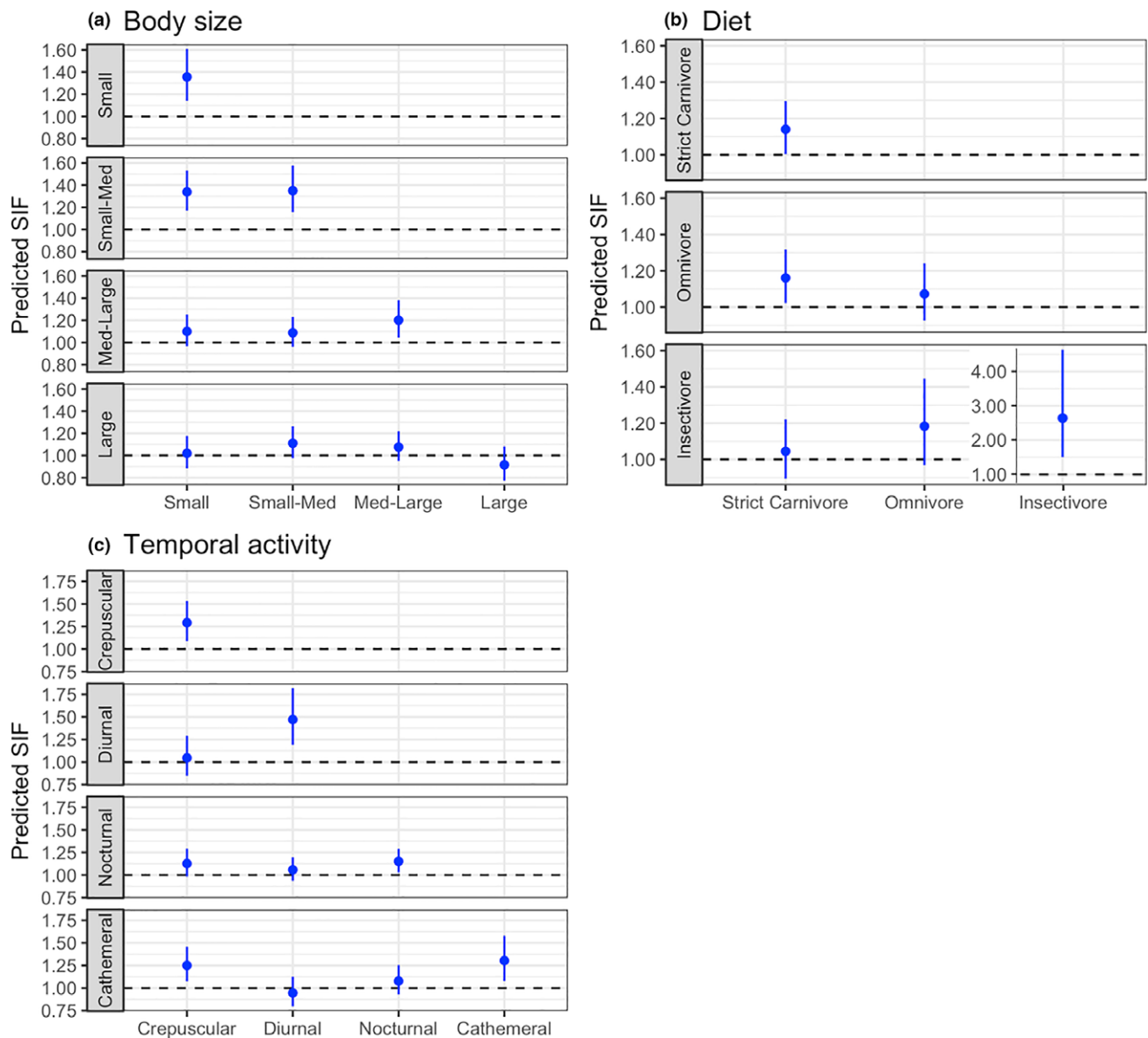
Figure 3 Predicted SIF and 95% CI) for each species trait combination of (a) body size, (b) diet, and (c) temporal activity pattern across the 13 study areas.

Ripple & Beschta 2006; Prugh *et al.* 2009). While our results do not suggest spatial avoidance among species of any body size, depressed SIF values in pairs that include a large or medium-large species supports the notion that large-bodied carnivores influence local community structure, particularly through the effects of large-bodied species on one another (Palomares & Caro 1999; Saether 1999; Terborgh *et al.* 1999, 2001; Elmhagen & Rushton 2007; Ripple *et al.* 2014; Swanson *et al.* 2016).

Species that overlap in space may reduce competition by exhibiting different activity patterns (e.g. diurnal vs. nocturnal; Kronfeld-Schor & Dayan 2003; Hayward & Slotow 2009; Di Bitetti *et al.* 2009, 2010; Bischof *et al.* 2014; Périquet *et al.* 2015). In our study, however, species sharing similar temporal activity patterns showed the strongest overlap in site use. For example, *Puma yagouaroundi* (É. Geoffroy Saint-Hilaire)

(jaguarundi) and *Nasua nasua* (L.) (South American coati) in Argentina are both medium-large, diurnal species that show strong co-occurrence but diverge in dietary habits (Appendix S2). Spatial coexistence also may be maintained through differentiation on another niche axis (e.g. vertical habitat partitioning, resource partitioning in prey size) or through fine-scale partitioning of temporal activity (i.e. differences in the time of peak activity; Farris *et al.* 2015c; Hayward & Slotow 2009; Sunarto *et al.* 2015). Again, there is wide heterogeneity in spatial overlap between species pairs within study areas, and similar species that show strong spatial overlap might also display temporal avoidance.

Differences in dietary niche breadths among species also influence the degree to which competition occurs (e.g. Hayward & Kerley 2008). We report high spatial overlap between species categorised as insectivores. In this case, heterogeneity in the

spatial and temporal availability of insect prey (e.g. termites) likely induces co-occurrence despite the strong overlap in dietary preferences (Pringle *et al*. 2010). In addition, species that both scavenge and actively hunt can exploit an ephemeral but consistent resource, thus reducing the reliance on a particular prey source during times of low prey abundance, unfavourable environmental conditions, or high competition (Devault *et al*. 2003; Selva & Fortuna 2007). Scavenging carnivores, such as *Crocuta crocuta* (Erxleben) (spotted hyena), *Panthera leo* (lion) and *Panthera pardus* (L.) (common leopard) in Botswana and Senegal occurred independently of one another, despite a high degree of overlap in dietary habit, temporal activity pattern and body size (Appendix S2). Previous studies have indicated that prey-switching (Höner *et al*. 2002) and changes in the scavenging behaviour (e.g. increased consumption of unfavourable elements, such as bones) of *C. crocuta* may alleviate strong competition with *P. leo* during times of low prey abundance (Kruuk 1972; Périquet *et al*. 2015). Coexistence can also be facilitated between species of similar dietary preferences through partitioned selection (e.g. by prey age or size) and use of food resources. For example, *Panthera onca* (L.) (jaguar) and *Puma concolor* (L.) (puma) in Belize partition their diet by preying on different species according to body plan. *Panthera onca*, as a stronger predator, prefers the slower but armoured *Dasypus novemcinctus* L. (nine banded armadillo), while the faster and more agile *P. concolor* preys on the more vulnerable but fast *Cuniculus paca* (L.) (paca; Foster *et al*. 2010).

Spatial avoidance can occur at various scales, but it can be challenging to differentiate microhabitat vs. macrohabitat resource partitioning (Bischof *et al*. 2014). When using data from remote camera trap surveys, assessments of co-occurrence patterns are often limited to the macrohabitat scale. Carnivore movements and responses to other carnivore species may occur at a finer spatio-temporal scale than we assessed in our analysis (Swanson *et al*. 2016; Dröge *et al*. 2017). Furthermore, factors such as ecosystem productivity, topographic features (e.g. mountains vs. open terrains), habitat patch size and quality (e.g. protected vs. degraded or fragmented), vegetation structure (e.g. grassland vs. rainforest), carnivore densities and resource availability (e.g. prey densities, water), or type of camera trap site (e.g. random vs. trails, baited vs. not baited), which we did not account for, also play an important role in determining carnivore co-occurrence at the landscape level (Elmhagen & Rushton 2007; Hoeinghaus *et al*. 2007; Bischof *et al*. 2014; Peoples & Frimpong 2015; Périquet *et al*. 2015; Hernandez-Santin *et al*. 2016).

Our analyses examined one key axis of co-occurrence, spatial overlap, but did not allow us to differentiate between a species' presence and the explicit use of resources. Additionally, while we assigned species according to their general temporal activity patterns, dietary habits and social structure, this categorisation may not adequately capture a species' behaviour at a particular study area or trap location. Temporal activity patterns, for example, are fluid and can be altered according to resource availability (Loveridge & Macdonald 2002; Hernandez-Santin *et al*. 2016), changes in the abundance or behaviour of co-occurring species (Creel *et al*. 2001; Ritchie & Johnson 2009) and human activity (e.g. McVittie 1979; Kitchen *et al*. 2000). Similarly, diet is closely tied to the availability of

resources at the local level (Höner *et al*. 2002; Ramesh *et al*. 2012). Co-occurrence at higher order interactions (i.e. among 3 + species) may also differ from the pair-wise interactions we examined, but computing SIF values based on multi-species occupancy modelling remains challenging. Nevertheless, our examination of pair-wise interactions allowed us to explicitly test, at the course spatial scale we examined, whether shared ecological traits affected co-occurrence by increasing competition due to niche overlap or by similar species sharing similar environmental and resource affinities.

Our study is the first global-scale assessment of species co-occurrence patterns and provides novel insights into the macro-ecological processes that influence the spatial distributions of sympatric mammalian carnivores worldwide. We demonstrated that species with similar ecological traits were often more likely to overlap spatially, suggesting that shared habitat affinities may influence occurrence patterns at coarse spatial scales. Therefore, competition and niche segregation were not the primary drivers of local species occurrence, though these patterns may change when considering the fine-scale differences in species' spatial and temporal activity patterns that we were unable to account for. We found a different pattern with respect to body size, with species tending to have a lower co-occurrence when paired with a larger carnivore. These results suggest that top-down processes may also be important in structuring carnivore communities. Moreover, the methods we employed highlight the utility of remote camera trap survey data to non-invasively study interactions among elusive species and offer a starting point for other collaborative, global-scale assessments (Butchart *et al*. 2010; Rich *et al*. 2017; Steenweg *et al*. 2017).

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad, https://doi.org/10.5061/dryad.7f9j57n

AUTHORSHIP

CLD and DAWM analysed the data and prepared the manuscript; LNR and ZJF initiated this global effort and coordinated the consolidation and management of data from all study areas; study design and data collection was performed by: MSD, YD and SA in Argentina; MJK, CW and BJH in Belize; JMT in United States; JW and RS in Canada; SH and NGY in Norway; MSF, NG and AT in Iran; KT and MJK in Nepal; SS, FAW and MJK in Sumatra; ZJF, AJM and MJK in Madagascar; QM in South Africa; LNR, DAWM and MJK in Botswana, and MDK and MJK in Senegal. All authors contributed input into the design and interpretation of the analysis and contributed to writing the final manuscript.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.7f9j57n

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SUPPORTING INFORMATION

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