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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space

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Abstract. Community ecology was traditionally an integrative science devoted to studying interactions between species and their abiotic environments in order to predict species' geographic distributions and abundances. Yet for philosophical and methodological reasons, it has become divided into two enterprises: one devoted to local experimentation on species interactions to predict community dynamics; the other devoted to statistical analyses of abiotic and biotic information to describe geographic distribution. Our goal here is to instigate thinking about ways to reconnect the two enterprises and thereby return to a tradition to do integrative science. We focus specifically on the community ecology of predators and prey, which is ripe for integration. This is because there is active, simultaneous interest in experimentally resolving the nature and strength of predator–prey interactions as well as explaining patterns across landscapes and seascapes. We begin by describing a conceptual theory rooted in classical analyses of non-spatial food web modules used to predict species interactions. We show how such modules can be extended to consideration of spatial context using the concept of habitat domain. Habitat domain describes the spatial extent of habitat space that predators and prey use while foraging, which differs from home range, the spatial extent used by an animal to meet all of its daily needs. This conceptual theory can be used to predict how different spatial relations of predators and prey could lead to different emergent multiple predator–prey interactions such as whether predator consumptive or non-consumptive effects should dominate, and whether intraguild predation, predator interference or predator complementarity are expected. We then review the literature on studies of large predator–prey interactions that make conclusions about the nature of multiple predator–prey interactions. This analysis reveals that while many studies provide sufficient information about predator or prey spatial locations, and thus meet necessary conditions of the habitat domain conceptual theory for drawing conclusions about the nature of the predator–prey interactions, several studies do not. We therefore elaborate how modern technology and statistical approaches for animal movement analysis could be used to test the conceptual theory, using experimental or quasi-experimental analyses at landscape scales.

Key words: food web modules; geospatial movement analysis; habitat domain; landscape of fear; multiple predator–prey interactions; predator consumptive effects; predator hunting mode; predator non-consumptive effects; spatial movement analysis; utilization distribution.

Introduction

Community ecology has traditionally been viewed as an integrative science. Its original goal was to blend the two enterprises of studying interactions between species and their abiotic environments with the study of species' geographic distributions and abundance in order to predict patterns of community structure and dynamics (MacArthur 1972). But the field has become increasingly subdivided with limited exchange between the two enterprises. There is now almost exclusive emphasis either on studying the nature and strength of biotic interactions within species assemblages (Loreau 2010, Paine 2010, Schmitz 2010, McCann 2011) or on analyses of pattern in species assemblage across geographic space (Franklin

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2010, Peterson et al. 2011). In the extreme, it has been argued that analyses of biotic interactions are altogether irrelevant to explaining geographic patterns (Pearson and Dawson 2003, Soberón and Nakamura 2009).

This divide has resulted in part because the two enterprises use altogether different methodologies and focus on different spatial scales. Studies of species interactions routinely involve manipulative experiments of small species ($\ll$1 kg) within small spatial locations (e.g., 0.5–2 m^2 experimental plots) to measure the nature and strength of interactions. By design, experimenting with small organisms at the small spatial extents of their natural habitats affords the ability to replicate treatments as well as control environmental variables, both of which are logistically challenging to do with large animals ($\gg$1 kg) that roam widely (e.g., many hectares to hundreds of square kilometers) across landscapes (Hairston 1990, Resetarits and Bernardo 1998, Schmitz 2004). Yet to remain relevant for community ecology at large, we must ask whether or not insights from small spatial extent manipulative experiments can be usefully scaled-up to explain patterns across broader landscapes and seascapes. Some ecologists have expressed doubt because the species used and the experimental conditions are idiosyncratic, making the scientific insights too contingent on the small, local conditions to make meaningful generalizations that apply to broader landscapes (Lawton 1999, Pearson and Dawson 2003, Ricklefs 2008, D'Amen et al. 2017).

The proposed alternative is to work at the large spatial extents of landscapes directly. Such approaches determine patterns of animal spatial occurrence using sophisticated statistical approaches that associate spatially explicit data on abiotic and biotic factors (e.g., climatic, topographic and land-use features, vegetation) to spatially explicit data on species occurrences across vast geographic space (Peterson et al. 2011, Dray et al. 2012, Gimenez et al. 2014, D'Amen et al. 2017). Yet such approaches often lack the nuanced natural history understanding or insights about species spatial interactions needed to *explain* and *predict* how and why species occur and interact the way they do across space (Paine 2010, Gimenez et al. 2014). Furthermore, the emphasis of statistical analysis of pattern has led to uneven emphasis on descriptive methodology at the expense of developing and testing conceptual theory (Scheiner 2013).

Our intention here is to help instigate a re-integration of the study of species interactions with the study of distribution and abundance. We focus on the community ecology of predators and prey as a starting point. This is because, as a field of inquiry, there is active, simultaneous interest in experimentally resolving the nature and strength of predator–prey interactions as well as explaining pattern and process across landscapes and seascapes (Schmitz 2005*b*, Fauchald 2009, Heithaus et al. 2009, Gorini et al. 2012, Sergio et al. 2014, Trainor and Schmitz 2014, Schmidt and Kuijper 2015). At its core, re-integrating the two enterprises requires answering a very fundamental question: How might we use insights from local experimental research to inform processes that occur across landscapes (Schmitz 2005*b*)? Our overarching answer is that, from a functional standpoint, most ecological systems can be viewed as systems of interacting carnivores, herbivores, and plants, regardless of whether or not the subjects of study are arthropods in very local, small meadows or large mammals moving broadly across vast landscapes. Thus, the exact spatial scale of each system is only *proximally* relevant. The ability to scale from one system to another, instead, rests on identifying fundamental principles that are evident among systems regardless of spatial scale (Petersen et al. 2003, Schmitz 2005*b*).

Here we convey a set of principles that are applicable regardless of species in question (which can have different spatial extents of movement, e.g., wolf spiders vs. gray wolves) and explain how to develop research and analyses that test them. We begin by describing a conceptual theory for spatial predator–prey interactions and distribution. We show how different spatial relations of predators and prey could lead to different emergent types of predator–prey interactions. We then review the literature on studies of large predator–prey interactions that describe movement and interactions at landscape scales. We evaluate how this theory fares in light of empirical insights. Finally, we elaborate how to use modern technology and statistical approaches for animal movement analysis to advance a priori quantitative tests of the conceptual theory, which in turn ultimately enhances predictive ability (Scheiner 2013). Advancing quantitative tests of the theory has practical implications for conservation, especially to increase understanding of how human transformation of landscapes, environmental change, or predator reintroductions to landscapes might reorganize community-level interactions between multiple species of predators and their prey.

Conceptual Theory of Multiple Predator–Prey Interactions

Background

A classic way to begin depicting interdependencies between predator and prey species is through the use of community modules (Holt 1997). Community modules can be used to characterize a range of species relationships, from simple single-predator–single-prey couplets to more complex configurations such as intraguild predation and interference competition. These depictions are, however, non-spatial representations of species interactions.

The interactions implied by the modules can be translated into spatial relations of predators and prey using the habitat domain-hunting mode concept originally derived from experimental research and synthesis of studies on arthropod and small vertebrate species (Schmitz et al. 2004, Schmitz 2005*a*, 2007, Northfield et al. 2012). An animal's habitat domain is the spatial extent

of area that an individual uses that is relevant to interspecific interactions (Schmitz et al. 2004, Preisser et al. 2007). Fundamentally, habitat domain describes the spatial extent of habitat over which individuals move in the course of their foraging. Habitat domain is to be distinguished from a home range, which is classically defined as the spatial extent of area routinely used by an animal to meet all of its daily needs (Burt 1943). Habitat domain of predator and prey populations can, in turn, be estimated by aggregating the habitat domain of each population member (Miller et al. 2014).

The population-level habitat domain offers a way to analyze and predict how predators and prey should interact as a consequence of contingencies in their spatial movement and overlap while foraging. The concept can be applied to widely different taxa because it is based on recognition of common, fundamental properties of organisms: their functional traits (like body size, hunting mode, and feeding mode Schmitz 2010, Gravel et al. 2016). Such a functional trait-based approach offers a common basis for principles that apply to a wide variety of species as well as spatial scales of analysis (e.g., wolf spiders and gray wolves can both be classified as "active" or "cursorial" hunters). These traits determine the spatial extent of movement of predators and prey and thereby can begin to explain emergent (sensu Sih 2005) patterns of predator and prey spatial occurrences and interactions.

The habitat domain concept also can explicitly consider the contingent ways in which predator and prey species interact spatially with each other due to factors like local variation in biophysical conditions of the landscape including (but not limited to) topography, thermal conditions, and vegetation or habitat. It offers a way to explain how and why species that co-occur in different locations may nonetheless differ in the nature of their interactions due to changing environmental contexts (e.g., Barton and Schmitz 2009, Schmitz and Barton 2014). As such, it helps make sense of context dependency that has been viewed as an important challenge to overcome in order to develop generalizations (Lawton 1999, Ricklefs 2008, Haswell et al. 2016). We do this by "turning context dependency on its head" and using it to deduce general conceptual principles about how spatial context leads to variation in the nature of species interactions (Schmitz 2010). Predicting context dependency in species interactions, essential to understanding geographic patterns in species distribution and abundance (MacArthur 1972), has not been accomplished well by conventional species distribution modelling (Trainor and Schmitz 2014).

Fundamentals: predator and prey functional traits and contingent habitat domains

The most basic community module is known as a predator–prey couplet (Fig. 1). This unit describes the trophic linkage between a predator species and prey species and thereby can become an essential building block to describe more complex modules involving multiple predator and prey species (Holt 1997). The couplet can also be used to develop mechanistic understanding of the contingent ways that a predator and prey species might interact. For example, predators may have both consumptive and non-consumptive (fear) effects on their prey (Abrams 2007). Indeed, the idea that predators cause prey to constantly live in a "landscape of fear" (Brown et al. 1999, Laundré et al. 2014), defined as living under conditions of chronic predation risk, has become a widely appealing and general notion. However, the habitat domain concept shows why this is not a general phenomenon. Empirical synthesis (Schmitz et al. 2004) suggests that whether or not consumptive or non-consumptive fear effects dominate in a system depends on predator and prey functional traits that determine their nature of movement and habitat domain sizes (Fig. 1).

Predator and prey body size is considered a key functional trait because it determines prey size selection and movement range (Lindstedt et al. 1986, Haskell et al. 2002, Sinclair et al. 2003, Jetz et al. 2004). But even within body size classes, predators and prey may exhibit different movement behaviors due to foraging mode and resource selection strategies (Haskell et al. 2002). For example, predators can adopt one of three general hunting modes (McLaughlin 1989): (1) sit-and-wait or ambush, when a predator remains primarily motionless and attacks a prey only when it moves within immediate catching distance; (2) sit-and-pursue, when a predator remains motionless until a prey moves within chasing distance; and (3) active or cursorial hunting, when a predator continuously moves through its environment to find, follow, and chase down prey. Across species within a given environmental context, habitat domain size appears to be consistent among predators with similar hunting modes (Miller et al. 2014). The trend is for actively roaming predators, at one extreme, to have large habitat domains and for sit-and-wait predators at the other extreme to have small habitat domains. However, predators may switch hunting modes (Helfman 1990, Olsson and Eklöv 2005, Donihue 2016), which could change space use and the nature of their interactions. Moreover, habitat domain size and spatial location in habitat space may change as the abiotic environmental context for predator and prey interactions changes (Barton and Schmitz 2009, Schmitz and Barton 2014, Trainor and Schmitz 2014). Smaller prey may forage locally, whereas larger prey may roam widely depending on their forage requirements in relation to the distribution of plant quality and productivity (Haskell et al. 2002). Moreover, prey could have different habitat domains in the absence vs. presence of predators (Korpimäki et al. 1996), as well as adjust their movement behaviors depending on the type of predator they face (Fischhoff et al. 2007, Merrill et al. 2010, Latombe et al. 2014, Miller et al. 2014).

Juxtaposing different predator and prey habitat domain sizes can then lead to four contingencies that

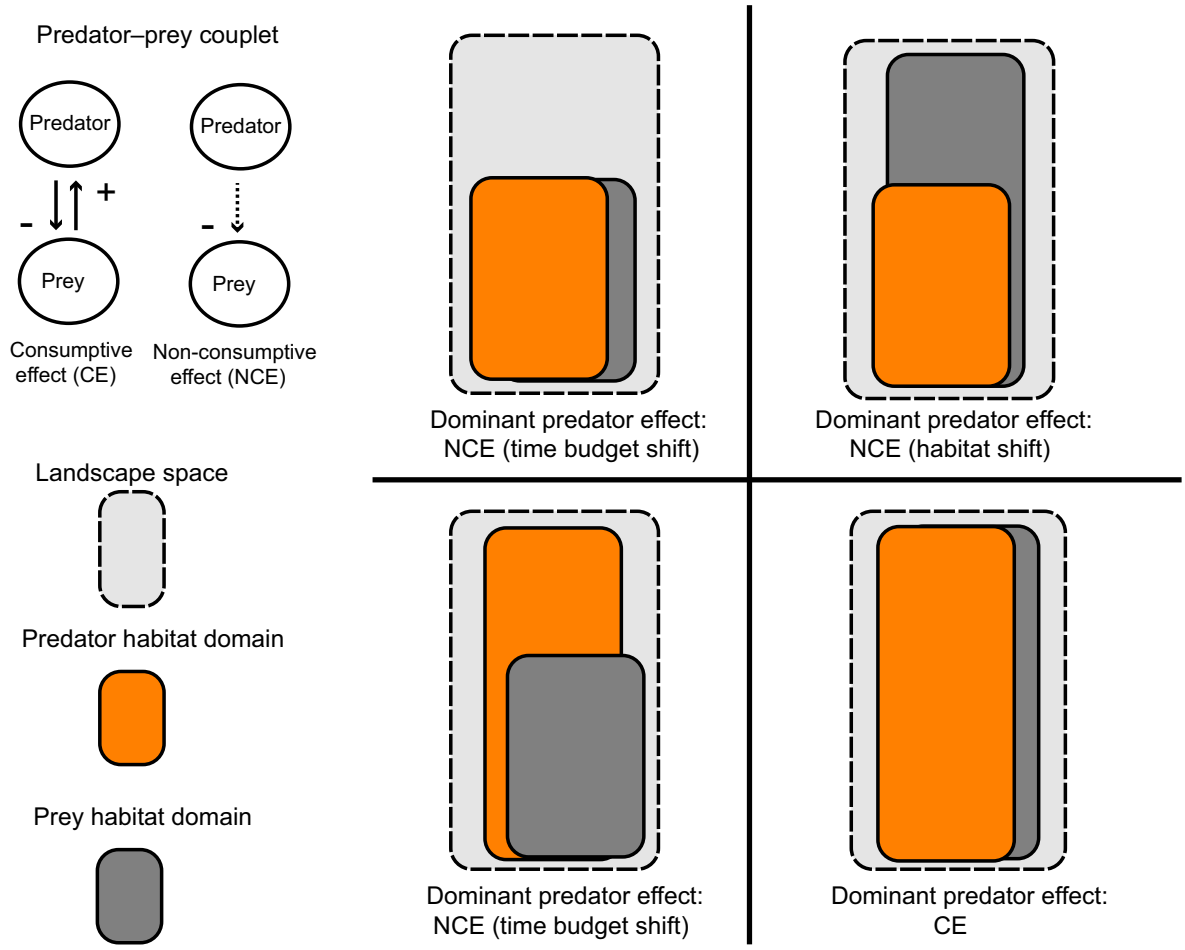

Fig. 1. Illustration of habitat domain (depicted as broad or narrow) and how it can lead to predictions about the nature of predator effects on prey. Habitat domain is the spatial extent in a designated landscape space (depicted by rectangle with dashed lines) that a predator or prey species uses in the course of foraging. Habitat domain can be broad (encompassing most of the landscape space) or narrow (encompassing a fraction of the landscape space). Predator effects on prey can be largely consumptive where they directly kill prey, or largely non-consumptive in which they induce anti-predator vigilance responses such as a reduction in feeding time or habitat shift to seek refuge. The spatial juxtaposition of the predator and prey habitat domains determines whether consumptive effects (CE) or non-consumptive effects (NCE) dominate.

explain when predator impacts on prey are predicted to arise largely from consumptive (direct mortality) or non-consumptive (chronic fear) effects (Fig. 1). The dominance of consumptive effects relative to non-consumptive effects will vary with the habitat domains of predators and prey (Fig. 1). Hence, prey species may not always live in a "landscape of fear." When non-consumptive effects do arise, they can come about via two mechanisms: (1) prey time budget shift due to increased vigilance or (2) prey habitat shift due to changes in space use. Empirical synthesis has shown that the relative habitat domain sizes of predators and prey determine which form of non-consumptive effect occurs (Schmitz 2005*a*).

Prey time budget shifts should be dominant responses when predators and prey completely overlap spatially within a small part of available landscape space (small habitat domains), or when prey are confined within a small space and predators have large habitat domains because they roam more widely (Fig. 1). Prey should merely change their time budgets in this case because they have no recourse to escape predators by seeking refuge habitats. Prey habitat shift should occur whenever predators are confined to a small part of landscape space and prey roam widely. In this case, prey have the opportunity to move into refuge habitat (Fig. 1). Finally, predator consumptive effects should dominate if both predators and prey have large habitat domains and roam widely over geographic space. In this case, predator and prey encounter each other infrequently, so it would be energetically inefficient for prey to engage in chronic risk avoidance behavior (Schmitz 2007). Instead, prey should respond only under imminent risk of attack (Schmitz 2007). These kinds of contingencies have been proposed to be plausible for large mammal predators and prey (Schmidt and Kuijper 2015) and now require empirical exploration.

Application to communities of multiple predators

The predator–prey couplet (Fig. 1) can be used to elaborate three slightly more complex, but commonly addressed, community modules comprised of two predators sharing a single prey (Fig. 2). The first module (Fig. 2a) is typically used to represent predator exploitative competition, where two consumers vie for a shared, limiting resource (Gotelli 2008). The second (Fig. 2b) represents interference competition, where predators preclude one another from spatial locations due to territoriality, etc. (Gotelli 2008). The third (Fig. 2c) represents intraguild predation, where exploitative competitors also prey on each other (Gotelli 2008). These community modules, as non-spatial representations of species interactions, are based on the assumption that predators and prey overlap completely, and therefore freely interact with each other everywhere. Yet placing the modules in a spatial context adds contingency because it changes the net effect of multiple predators on prey, even if the trophic linkages among the species remain unchanged (Fig. 2). This means that the type of predator–predator interaction implied by the classic non-spatial module may not always be upheld in a spatial context.

For example, in a non-spatial context, exploitative competition occurs whenever two predator species vie for a shared prey species. Classic models in ecology would predict that, in such conditions, the two predators should have additive (enhancing) effects on prey mortality (Gotelli 2008). In a spatial context, exploitative competition could arise in two ways: when prey have a large habitat domain and predators have small overlapping domains (Fig. 2a), or when predators have large overlapping domains that overlap prey with a small domain (Fig. 2a). In the first case, the prey species is assumed to shuttle between different spatial locations occupied by each predator. In the second case, the two predators are assumed to converge on the habitat occupied by the shared prey. The outcome of exploitative competition differs between these spatial scenarios. In the first case the predators have substitutive effects because, by being in separate locations, one predator compensates for the effects of the other predator (Schmitz 2007). Hence, multiple predator effects on prey mortality should be compensatory and thereby not enhance the net risk to prey. In the second case predators have complementary effects. Both predators should increase mortality risk to prey relative to their individual effects, leading to additive (or even multiplicative) mortality effects on the shared prey (Schmitz 2007).

Such spatial consideration reveals additionally a third spatial contingency (Fig. 2a) in which each predator could exploit a shared prey species but the common prey species occurs in spatially separated populations. The two predators thus technically would not compete, but rather operate as separate food chains involving their spatially corresponding prey population. This scenario also would enhance risk of mortality to the prey species across the landscape.

Predator interference (Fig. 2b) is predicted to occur when both predator species and prey overlap spatially. This may occur either when all predators and prey have large habitat domains, or when they all have small habitat domains. Examples in Appendix S1 show that whenever predators undergo interference competition they do so because one predator species preempts the other from gaining access to a spatial location occupied by the shared prey. In such cases, predator species reduce their net effects on the prey by engaging in interference interactions, including one predator species killing (but not

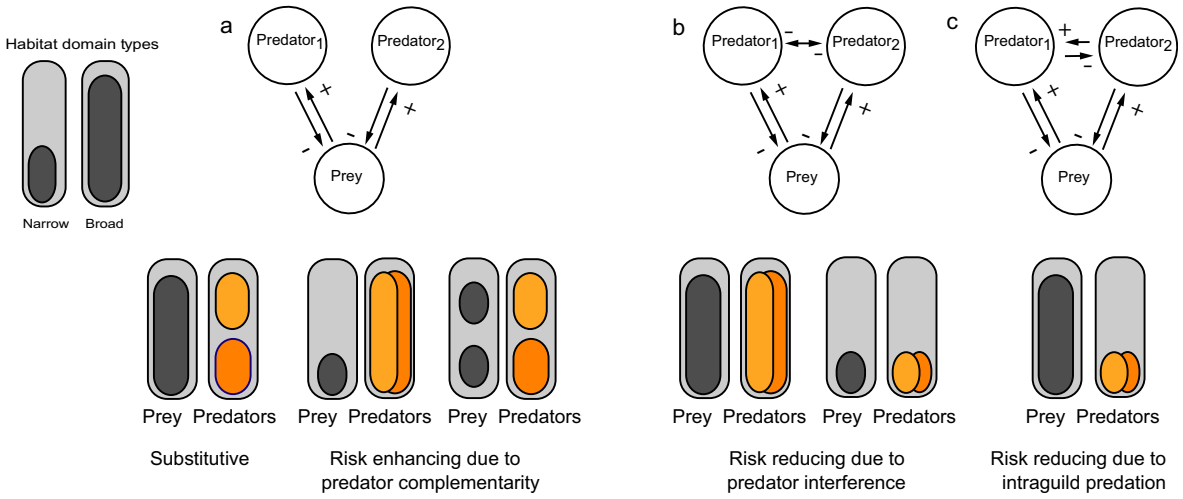

FIG. 2. Translating classic non-spatial food web modules describing (a) exploitative competition, (b) interference competition, and (c) intraguild predation into a spatial context using the habitat domain concept. The figure predicts a priori conditions needed for different natures of multiple predator–prey interactions to emerge. It also illustrates that spatially there may be more than one type of emergent effect for a particular food web module.

necessarily eating) another predator species. Hence predation risk to the prey becomes reduced by interspecific interactions between predators (Schmitz 2007).

Intraguild predation is predicted to arise when predator species have small, overlapping domains and prey have large habitat domains. In this case, prey can spatially evade both predators. Without recourse to capture other prey, one predator species attacks and consumes the other. Hence, risk of predation to prey is again reduced, but this time because prey can evade spatial locations where the predators exist (Schmitz 2007).

Depicting interactions in the context of habitat domain underscores an important point that merely studying the movement ecology of predators without studying movement of their prey can lead to equivocal conclusions about the nature of predator effects on prey (i.e., consumptive vs. non-consumptive effects; Fig. 1) and the nature of predator-predator interactions (Fig. 2). For example, predator species should occupy small, overlapping habitat domains in different types of multiple predator–prey interactions (cf. Fig. 2b, c). Thus, it is the habitat domain of their shared prey that determines whether the predators engage in intraguild predation or interference competition. Similar considerations arise in the case of substitutive vs. complementarity multiple predator effects on prey (Fig. 2a).

Empirical Insights from Large Vertebrate Predator–Prey Studies

The habitat domain conceptual framework (Fig. 2) has explained multiple predator–prey interactions in a wide range of arthropod systems (Schmitz 2005*a,b*, Miller et al. 2014). It has also been explicitly used to explain interactions in large vertebrate predator–prey systems (e.g., Thaker et al. 2011, Gervasi et al. 2013, Vanak et al. 2013). There are numerous other analyses of large vertebrate multiple predator–prey communities that infer interactions (e.g., interference, intraguild interactions), and these studies offer the means to begin evaluating whether conclusions about the interactions align with theoretical expectations (Fig. 2).

We identified these studies by searching the literature using Web of Science and Google Scholar (*available online*).[7],[8] We used the search keywords: ("spatial" OR "habitat domain" OR "home range" OR "utilization distribution") AND ("attack" OR "encounter" OR "hunting mode" OR "predator strategy" OR "predation risk") AND ("carnivore" OR "predator") AND ("intraguild" OR "predator–prey interaction" OR "prey") NOT ("invertebrate" OR "insect"). Articles were included in our evaluation if they involved interactions between two or more non-human carnivorous vertebrate predators. Studies could be both experimental and observational (manipulative experiments with vertebrate carnivores, especially large carnivores, are rare, but carnivore species reintroductions offer treatments analogous to experiments); reviews and meta-analyses were omitted. The studies had to involve interactions between live predators and shared live prey (e.g., studies reporting on effects of predator cues such as urine, feces or sounds were not be used, nor were studies inferring predator–prey interactions based on predator diets). Theoretical discussions and simulation models of predator–prey interactions without mention of specific species were excluded because the context of hunting mode and/or habitat domain could not be determined. We compiled studies and recorded the predator and prey species, the type of interaction between predators (if any), the evidence used in the study to make these conclusions and any missing evidence that would prevent a definitive evaluation of the conceptual framework.

Our search as of May 2015 identified 19 studies that met our search criteria completely (Appendix S1: Table S1). Another 30 studies were missing some pieces of evidence necessary to evaluate our framework. Out of all 49 articles, 46 studies (94%) involved mammal (canid, felid, ursid, hyenid, or mustelid) predators, seven (14%) involved avian (eagles, cormorants) predators, and one (2%) involved fish (shark) predators (percentages exceed 100% because some studies involved more than one taxonomic family). Terrestrial prey species included mammals (rodents, rabbits, ungulates, and primates) and birds (geese) and marine prey species were fish. No studies of reptile predators or prey were found.

The number of articles published on large vertebrate multiple predator spatial interactions gradually increased from an average of one per year between 1994 and 2002 to an average of three per year between 2003 and 2015 (Fig. 3). Most studies concluded that predators engaged in interference competition (23 papers or 47%), followed by risk enhancement (14 papers or 29%) and substitutive effects (12 papers or 24%), and only four studies (8%) involved intraguild predation (note that some studies involved more than one type of competitive interaction and the interaction type was not identifiable in four papers). Of the 30 studies that were missing information, 24 (80%) did not contain information on prey spatial movement and/or distribution. The majority of these studies likewise did not report on predator spatial movement and/or distribution, which, according to the conceptual framework (Fig. 2), creates uncertainty about the conclusions. Hence, the results support the need to propose steps for explicitly and quantitatively evaluating the habitat domain conceptual framework.

Moving Forward: Developing Quantitative Assessment of Large Vertebrate Predator–Prey Habitat Domains

The predator and prey habitat domains, as depicted in Figs. 1, 2, and 4, effectively represent the spatial extent of hunting and foraging behavior in terms of animal

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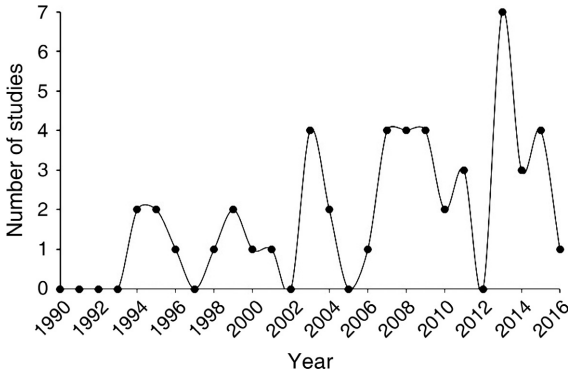

FIG. 3. The number of peer-reviewed studies on interactions between large vertebrate multiple predator–prey communities published each year. Note that, since the literature search was conducted in May 2015, 2015–2016 do not reflect the total number of studies published in these years.

spatial utilization distributions (sensu Van Winkle 1975, Millspaugh et al. 2006, Barraquand and Murrell 2013). The outer bound of a utilization distribution circumscribes the extent of foraging movements by an individual predator or prey within their home range. Thus, habitat domain size is controlled by the variance of an individual predator or prey's movement distribution across space. For example, in arthropod systems, individual sit-and-wait predators have narrow habitat domains and individual actively roaming hunting predators have either narrow or broad habitat domains (Miller et al. 2014). The relationship between predator hunting mode and habitat domain size requires further testing in large mammal communities to explore its consistency across different organismal scales. Here we propose how habitat domains and their degree of overlap may be quantitatively assessed in four steps (Fig. 4).

First, sequential movement data by an individual predator or prey across a landscape must be attained through telemetry or other means of tracking, and foraging locations identified (Fig. 4a). An individual's utilization distribution should then be generated by plotting two-dimensional probabilities of spatial locations associated with foraging behavior across a landscape (Fig. 4b; a three-dimensional utilization distribution could be estimated if vertical movements are tracked, e.g., movement in forest canopies [McLean et al. 2016]). The habitat domain is represented by the probability isopleth that circumscribes the data within the behavior-specific utilization distribution according to a set probability threshold, e.g., 95% or 99% probability (Fig. 4c). Finally, the degree of overlap between predator and prey habitat domains should be calculated to inform predictions on how predators and prey should interact spatially (Fig. 4d). We next elaborate on these steps.

Movement by predator and prey individuals can come about for many reasons (Hebblewhite et al. 2005, Merrill et al. 2010, Courbin et al. 2013). The trick in deriving a habitat domain is to decompose the hierarchy of movement analysis into components related to predator hunting and prey availability (Hebblewhite et al. 2005, Merrill et al. 2010, Courbin et al. 2013). While we recognize that a predator can exert risk effects on prey independent of its behavioral state, our focus is on identifying locations when the predator is actively engaged in hunting behavior (Fig. 4a). A variety of analytical techniques exist to infer behavioral states from relocation data, including metric-based approaches such as first-passage time analysis (Fauchald and Tveraa 2003), time-series approaches like behavioral change point analysis (Gurarie et al. 2009), and mechanistic modeling approaches such as multistate random walk models (Morales et al. 2004). Trade-offs associated with these methods are compared and discussed in two recent reviews (Gurarie et al. 2015, Edelhoff et al. 2016). Alternatively, the application of ancillary devices such as collar-mounted accelerometers or internal temperature sensors afford direct identification of hunting behavior that may be paired with GPS or telemetry relocations, and are becoming increasingly common as technologies advance (Brown et al. 2013, Wilson et al. 2013, Whitlock et al. 2015, Abrahms et al. 2016). For prey animals, with species-specific exceptions, we consider that they are always available to be preyed upon throughout their home range, regardless of behavioral state; we therefore operationally define the habitat domain of prey as synoptic with their home range. Finally, we note that the extent of an animal's space use can be sensitive to the time period of inquiry (Fieberg and Börger 2012); therefore it is important to assess a habitat domain over a biologically relevant time period (for example, a season).

Once the locations suitable for assessing habitat domain have been attained (i.e., active hunting locations for predators, all locations for prey), it is then a matter of estimating utilization distributions from these points (Fig. 4b). One estimating approach, the kernel density estimator (KDE), maps the probability density of animal space use over a landscape (Worton 1989). It is methodologically straightforward and remains one of the most popular methods for utilization distributions estimation (Fieberg and Börger 2012). However, several recent alternative approaches, including Brownian Bridge Movement Modeling (Byrne et al. 2014), Autocorrelated KDE (Fleming et al. 2015) and Time Local Convex Hulls (Lyons et al. 2013), aim to overcome the assumption of data independence required by KDEs. While these methods are computationally intensive, they may be more appropriate if the spatiotemporal resolution of the data violates the assumption of independence between relocations.

The spatial extent of the habitat domain is determined by the bounds of a probability isopleth estimated from the utilization distribution (Fig. 4c). For instance, the 99% isopleth of a utilization distribution circumscribes the area in which there is a 99% probability of a relocation observation (Worton 1989). In animal movement analysis, the 95% probability isopleth is most commonly

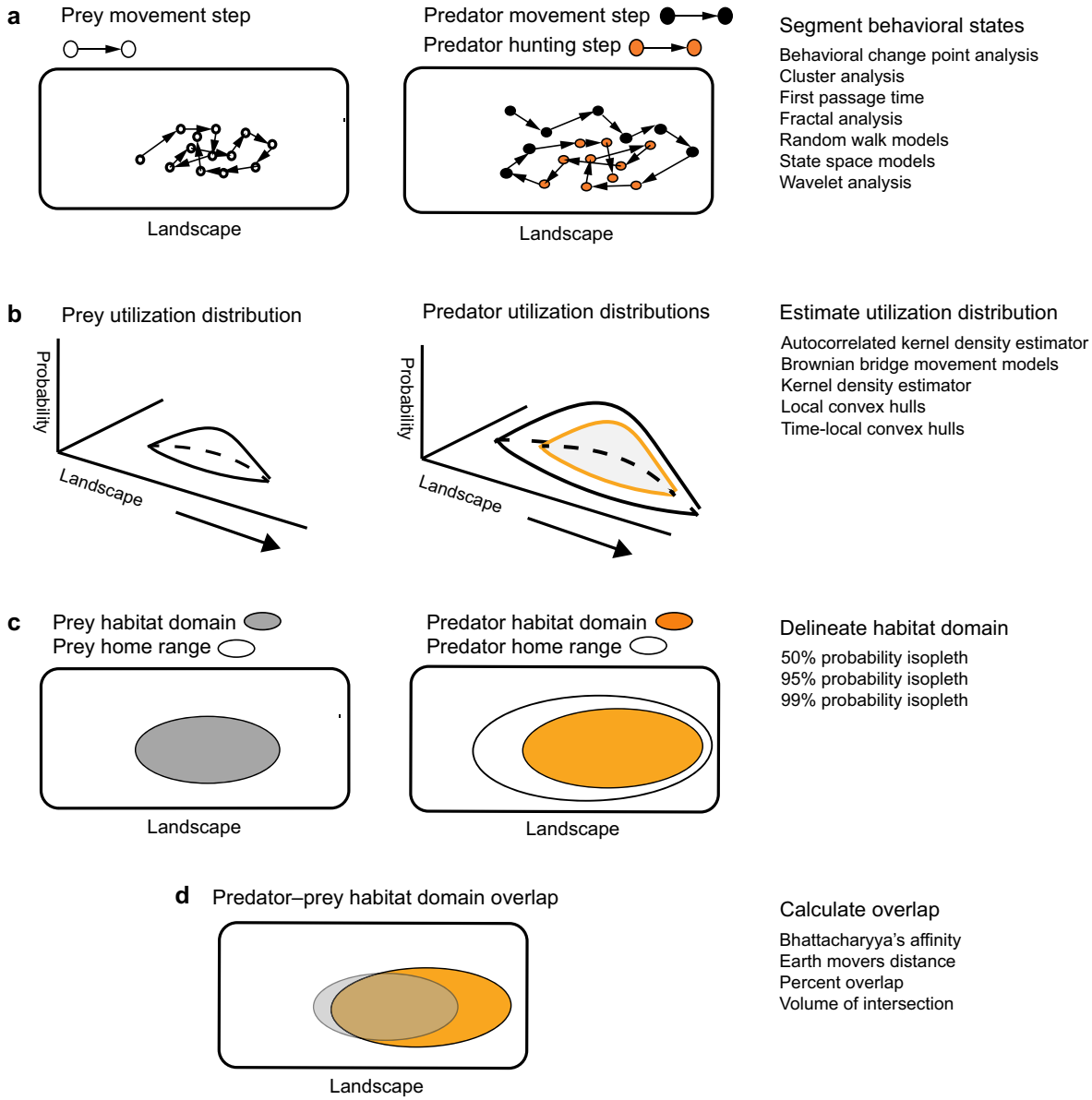

FIG. 4. Steps for quantifying habitat domains of prey (left) and predators (center), and associated methods (right): (a) first, relocations for prey and hunting-specific relocations for predators are collected; (b) second, utilization distributions are constructed for each set of relocations; (c) third, habitat domain extents are delineated as a percent probability isopleth of each utilization distribution. For prey this is synoptic with home range; for predators this represents the spatial extent of their space use for hunting activities; and (d) overlap between predator and prey habitat domains is calculated to inform predictions.

used for estimating home range extent, while the area circumscribed by the 50% isopleth is considered an animal's "core area" (White and Garrott 1990). Because the choice of isopleth threshold depends on the inquirer, the habitat domain size could become arbitrary if due consideration of the ecology of the species in question is not made.

The analysis described here considers habitat domains of individual population members. Deriving a population-level habitat domain is merely a matter of aggregating the behavior-specific utilization distribution of each population member (Miller et al. 2014).

The conceptual theory presented thus far provides a basic scaffolding for considering different predator–prey interactions in the context of species spatial movements. One can infuse into it richer within- and between-species behavioral ecological detail embodied in many of the studies listed in Appendix S1, to increase realism. For example, food or habitat availability can determine the nature of animal movement, which in

turn influences the intensity of use of a particular habitat area (Van Moorter et al. 2016). Habitat structure within landscape space can cause the same species to exhibit different habitat utilizations in response to predation risk (Schmitz 2005*a,b*). Prey species may also associate into social groups to decrease predation risk (Brown 2016, Laursen et al. 2016), or associate closely with certain predators to gain protection from other predators (Jones et al. 2013, Greeney et al. 2015). The many density-dependent territorial interactions listed in Appendix S1 could determine how population members become assorted across space. These kinds of behavioral detail could act to modulate population habitat domain size and should be important considerations in future research.

Finally, to inform predictions on predator–prey interactions and distribution, the spatial overlap between predator and prey habitat domains must be quantified (Fig. 4d). Several metrics exist to calculate an overlap index. Simple metrics, such as percent overlap, calculate the overlap in total extent of the domains while ignoring relative probability of use (Fieberg and Kochanny 2005). Alternatively, metrics such as volume of intersection (Kernohan et al. 2001) or Bhattacharyya's affinity (Bhattacharyya 1943) incorporate utilization distribution probabilities to account for differential intensities of space use within the domains. We refer readers to Fieberg and Kochanny (2005) for a helpful review and comparison of overlap metrics. A more recently developed method, earth mover's distance, builds on previous methods to consider the spatial proximity of utilization distributions, rather than the amount of overlap exclusively (Kranstauber et al. 2016).

Once overlap values are calculated, they can be used to deduce the nature of the multiple-predator–prey interaction and this deduction can then be compared with empirical observations of predator–prey interactions across landscapes. According to norms of multiple-predator–prey analyses in community ecology (Sih et al. 1998, Schmitz 2007), such observations should be made at least using quasi-experimental (if not experimental) approaches that compare predator–prey interactions in locations where each predator exists alone with a prey (single predator treatment) as well as where multiple predators overlap (multiple predator treatment). Both should be compared to locations where prey occur alone (predation control). This then ultimately overcomes the experimental-statistical methodology divide by bringing back an experimental tradition to analyses of species interaction and distribution across broad landscapes. We appreciate that such experimentation can be challenging, given that logistical constraints can limit the possibility for the needed systematic comparisons. But wildlife management using predator control or predator reintroductions across large landscapes could provide opportunities for such experimentation and evaluation of community ecological processes at the landscape scale (Trainor and Schmitz 2014).

Conclusions

Modern concerns about human alteration of landscapes have instigated a herculean effort to examine how species move and assort themselves in geographic space. The research has produced considerable descriptive insight about species distribution and redistribution. This is especially true for arising research on large carnivores that are being reintroduced to their former ranges or expanding their distributions beyond existing ranges, at the same time that humans are encroaching on or altering their habitats. Such a descriptive approach, however, does not offer the insight needed to predict how landscape changes will reconfigure ecological communities of predators and prey. Here we have offered a way to begin making such analyses more predictive by introducing a conceptual framework, rooted in traditional community ecology, to predict how the spatial juxtaposition and movement of predator and prey species determines the nature of their interactions. We elaborate on how this framework can be tested with modern geospatial movement analyses. We therefore show how to advance mechanistic research on species interactions at landscapes scales in order to re-instigate the consideration of community ecology as the integrative study of species interactions and distribution and abundance.

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Supporting Information

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Appendix S1

Table S1. Peer-reviewed studies examining interactions between large vertebrate multiple predator-prey communities, with information on the study predator and prey species, conclusion, main evidence used to make those conclusions and missing evidence that would prevent an evaluation of the habitat domain conceptual framework for predicting predator-prey interactions.

Missing evidence	Study	Predator species	Prey species	Study conclusion	Evidence
No evidence missing (sufficient test of interactions)	Atwood et al. 2009	Cougar (*Puma concolor*), gray wolf (*Canis lupus*)	Mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*)	Risk enhancement: habitat separation in predation by predators	Predator habitat selection during encounters with prey and kills
No evidence missing (sufficient test of interactions)	Berger et al. 2008	Coyote (*Canis latrans*), gray wolf (*Canis lupus*)	Pronghorn antelope (*Antilocapra americana*)	Interference: wolves displaced coyotes spatially	Fawn survival rates with and without wolves
No evidence missing (sufficient test of interactions)	Bischof et al. 2014	Altai mountain weasel (*Mustela altaica*), stone marten (*Martes foina*), red fox (*Vulpes vulpes*)	Large-eared pika (*Ochotona macrotis*), Royle's pika (*O. roylei*)	Risk enhancement: Weasel temporally avoids marten and fox and likely pursues prey in unique habitats	Temporal activity patterns

No evidence missing (sufficient test of interactions)	Carter et al. 2015	Leopard (*Panthera pardus*), tiger (*P. tigris*)	Wild pig (*Sus scrofa*), spotted deer (*Axis axis*), muntjac (*Muntiacus muntjak*), hog deer (*Hyelaphus porcinus*), gaur (*Bos gaurus*), sambar (*Rusa unicolor*)	Interference interaction: Leopards spatially but not temporally avoid tigers	Leopard, tiger and prey occurrence and temporal activity
No evidence missing (sufficient test of interactions)	Durant 2013	Cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), lion (*Panthera leo*)	Thomson's gazelle (*Eudorcas thomsonii*), hares (*Lepus* spp.), wildebeest (*Connochuetes tatirim*), Grant's gazelle (*Gazella granti*)	Interference: Cheetah avoids dominant predators by shifting space use to lower-density prey areas	Predator and prey densities and spatial distribution
No evidence missing (sufficient test of interactions)	Fedriani et al. 1999	Red fox (*Vulpes vulpes*), Iberian lynx (*Lynx pardinus*), Eurasian badger (*Meles meles*)	European rabbit (*Oryctolagus cuniculus*)	Substitutive: foxes avoid lynx habitat but badgers do not compete directly for prey	Predator diet, activity patterns and habitat use
No evidence missing (sufficient test of interactions)	Husseman et al. 2003	Wolf (*Canis lupus*), cougar (*Puma concolor*)	Elk (*Cervus elephus*), mule deer (*Odocoileus hemionus*)	Risk enhancement: Differential prey selection due to hunting behavior; stalking cougars select hunting sites at finer spatial scales than courser wolves	Prey age and characteristics at kill sites

No evidence missing (sufficient test of interactions)	Karanth and Sunquist 2000	Tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpinus*)	Chital (*Axis axis*), sambar (*Cervu sunicolor*), muntjac (*Muntiacus muntjac*), gaur (*Bos gaurus*), wild pig (*Sus scrofa*), Hanuman langur (*Presbytis entellus*)	Risk enhancement: Predators coexist largely via different prey selection and overlap spatially and temporally, with minor overlap in prey selection	Predator diet, temporal activity, habitat use, and spatial distribution
No evidence missing (sufficient test of interactions)	Korpimäki et al. 1996	Least weasel (*Mustela nivalis*), kestrel *(Falco tinnunculus*)	Field vole (*Microtus agresti*)	Predator interference: Voles respond more strongly to kestrals than weasels	Vole habitat shifts and mobility
No evidence missing (sufficient test of interactions)	Kunkel et al. 1999	Wolf (*Canis lupus*), cougar (*Puma concolor*)	White-tailed deer (*Odocoileus virginianus*)	Interference: Wolves and cougars kill prey of similar characteristics and in similar locations	Kill characteristics and locations
No evidence missing (sufficient test of interactions)	Nelson et al. 2007	Coyote (*Canis latrans*), San Joaquin kit fox (*Vulpes macrotis mutica*)	Kangaroo rat (*Dipodomys heermanni*)	Intraguild and interference: kit foxes partitioned habitat, space and diet with coyotes	Habitat and spatial use, diet, prey abundance, predator mortality
No evidence missing (sufficient test of interactions)	Odden et al. 2010	Tiger (*Panthera tigris*), leopard (*Panthera pardus*)	Chital (*axis axis*)	Interference: tigers display aggression towards leopards to access prey	Predator diet, predatior territorial markings, prey abundance

No evidence missing (sufficient test of interactions)	Scognamillo et al. 2003	Jaguar (*Panthera onca*), puma (*Puma concolor*)	Capybara (*Hydrochaeris hydrochaeris*), collared peccary (*Tayassu tajacu*)	Risk enhancement: Predators overlap temporally and spatially at broad-scale but differ in fine-scale habitat use and prey selection, with some prey selection overlap	Predator diet, temporal activity, habitat use, and spatial distribution
No evidence missing (sufficient test of interactions)	Steinmetz et al. 2013	Tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpinus*)	Langur (*Presbytis femoralist*, *Trachypithecus obscurus*), mouse deer (*Tragulus* spp.), wild pig (*Sus scrofa*), muntjac (*Muntiacus muntjak*), gaur (*Bos gaurus*), sambar (*Rusa unicolor*)	Substitutive: Tigers dominate prey-rich areas, leopards and dhole temporally and spatially avoid tigers to prioritize safety	Prey selection and predator and prey spatial occurrence
No evidence missing (sufficient test of interactions)	Thaker et al. 2011	Lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*), spotted hyena (*Crocuta crocuta*)	Impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), Burchell's zebra (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus africanus*), giraffe (*Giraffa camelopardalis*)	Prey selected safer habitats to avoid predators based on predator hunting mode	Predator and prey occurrence, kill locations

No evidence missing (sufficient test of interactions)	Thompson and Gese 2007	Swift fox (*Vulpes velox*), coyote (*Canis latrans*)	Northern grasshopper mice (*Onychomys leucogaster*), deer mice (*Peromyscus maniculatus*), Ord's kangaroo rat (*Dipodomys ordii*)	Interference and/or intraguild: swift foxes avoided coyote abundance towards low prey-abundance areas	Predator habitat use, prey abundance
No evidence missing (sufficient test of interactions)	Vanak et al. 2013	Lion, (*Panthera leo*), leopard (*P. pardus*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*)	Impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), Burchell's zebra (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus africanus*), giraffe (*Giraffa camelopardalis*)	Interference and intraguild interactions: Predators manage competition by balancing co-predator threats and prey selection	Predator occurrence, spatial movement and habitat selection; prey occurrence
No evidence missing (sufficient test of interactions)	Wilson et al. 2010	Bobcat (*Lynx rufus*), coyote (*Canis latrans*)	Small mammals	Intraguild predation when prey biomass decreases in bobcat range	Prey biomass, bobcat and coyote spatial movement and home range
No evidence missing (sufficient test of interactions)	Penteriani et al. 2013	Iberian lynx (*Lynx pardinus*), red fox (*Vulpes vulpes*)	Rabbit (*Oryctolagus cuniculus*)	Interference: foxes more active when lynx less active	Predator and prey movement

Predation rates and prey spatial distribution	Murray 1995	Coyote (*Canis latrans*), lynx (*Lynx canadensis*)	Snowshoe hair (*Lepus americanus*)	Predators with different hunting behavior utilize different habitats	Hunting pursuit behavior and habitat
Predator and prey relative spatial distribution	Bessey and Heithaus 2013	Pied cormorant (*Phalacrocorax varius*), nervous shark (*Carcharhinus cautus*)	Western striped trumpeter (*Pelates octolineatus*)	Subsititutive: Predators temporally segregated based on water temperature	Predation events
Predator and prey relative spatial distribution	Harmsen et al. 2011	Jaguar (*Panthera onca*), puma (*Puma concolor*)	Armadillo (*Dasypus novemcinctus*), paca (*Agouti paca*)	Risk enhancement: Diet differentiation between prey species	Prey and predator activity patterns
Predator and prey relative spatial distributions	Tambling et al. 2015	Lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*)	Buffalo (*Syncerus caffer*), warthog (*Phacochoerus africanus*), kudu (*Tragelaphus strepsiceros*) and elephant (*Loxodonta africana*)	Risk enhancement: Predators overlap temporally; when predators present in landscape, vulnerable prey shift temporal activity to avoid predators	Temporal activity; predator introduction
Predator diet and prey spatial distribution	White et al. 1994	Coyote (*Canis latrans*), kit fox (*Vulpes macrotis*)	Noctural rodents and lagomorphs (unspecified)	Interference: No spatial or temporal separation but possible diet segregation or fine-	Predator spatial distribution, home range and separation distances

				scale temporal avoidance by kit fox	
Predator diet and relative predator-prey spatial distribution	Mattisson et al. 2011	Eurasian lynx (*Lynx lynx)*, wolverine (*Gulo gulo*)	Reindeer (*Rangifer tarandus tarandus*)	Risk enhancement: predator temporal but not spatial segregation	Spatial interactions between predators
Predator diet overlap and prey spatial distribution	Melville et al. 2015	Racoon (*Procyon lotor*), coyote (*Canis latrans*), bobcat (*Lynx rufus*)	Not stated	Interference: bobcats and coyotes shared space more than raccoons did with either bobcats or coyotes	Predator home range overlap
Predator diet, spatial and temporal distribution	Lagos et al. 1995	Culpeo fox (*Pseudalopex culpaeus*), owls (*Athene cunicularia, Bubo virginianus, Tyto alba*)	Degu (*Octodon degus*)	Non-consumptive effect on prey but unexplored predator interactions: prey space use shifted in presence of predator community	Prey space use and movement
Predator interactions, spatial distribution and temporal activity	McWilliams et al. 1994	Golden eagle (*Aquila chrysaetos*), bald eagle (*Haliaeetus leucocephalus*)	Cackling Geese (*Branta canadensis minima*), Ross' geese (*Chen rossii*)	Risk enhancement or predator interference	Predators overlap spatially

Predator spatial and temporal distribution	Lovari et al. 2015	Tiger (*Panthera tigris*), leopard (*Panthera pardus*)	Various wild vertebrates (not stated)	Interference: high overlap in diet between predators	Predator diet
Predator spatial distribution	Carvalho and Gomes 2004	Red fox (*Vulpes vulpes*), wild cat (*Felis silvestris*), genet (*Genetta genetta*), stone marten (*Martes foina*)	Various rodents, rabbits, arthropods	Substitutive or interference: seasonal diet partitioning between predators	Predator diet and prey abundance
Predator spatial distribution	Duquette et al. 2014	Bobcat (*Lynx rufus*), American black bear (*Ursus americanus*), coyote (*Canis latrans*), gray wolf (*Canis lupus*)	White-tailed deer (*Odocoileus virginianus*)	Substitution or interference: Predators segregate spatially by habitat when predating fawns and dams	Predation risk; fawn and dam mortality and selection by habitat
Predator spatial distribution	Willems and Hill 2009	Crowned eagle (*Stephanoaetus coronatus*), Verreaux's eagle (*Aquila verreauxii*), Chacma baboon (*Papio cynocephalus ursinus*), leopard (*Panthera pardus*)	Vervet monkey (*Cercopithecus aethiops*)	Risk enhancement: Baboon and leopard generated spatially distinct landscapes of fear for monkeys	Prey vigilance and spatial distributions

Prey response to predator introduction	van Dyk and Slotow 2003	African wild dog (*Lycaon pictus*), lion (*Panthera leo*)	Kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*)	Substitutive: Predators spatially varied predation pressure	Predator spatial locations, kill characteristics and location
Prey spatial distribution	Garneau et al. 2007	Black bear (*Ursus americanus*), brown bear (*U. arctos*), gray wolf (*Canis lupus*)	Moose (*Alces alces*)	Substitutive: spatial and temporal partitioning between predators	Kill site locations; spatial and temporal overlap between predators
Prey spatial distribution	Garneau et al. 2008	Black bear (*Ursus americanus*), brown bear (*U. arctos*)	Moose (*Alces alces*)	Risk enhancement: temporal and spatial separation in peak of moose calf predation	Habitat at moose kills
Prey spatial distribution	Moehrenschlager et al. 2007	Swift fox (*Vulpes velox*), kit fox (*Vulpes macrotis*), coyote (*Canis latrans*), golden eagle (*Aquila chrysae*)	Various rodents, insects, birds	Interference interactions between coyotes and foxes; predation by eagles on foxes	Spatial and dietary overlap between predators; eagles (but not coyotes) consumed foxes after killing
Prey spatial distribution	Neale and Sacks 2001	Bobcat (*Lynx rufus*), coyote (*Canis latrans*)	Various rodents, lagomorphs, ungulates	Substitutive: bobcats and coyotes overlap partially in habitat and temporal activity	Predator diet and movement

Prey spatial distribution	St-Pierre et al. 2006	Ermine (*Mustela erminea*), long-tailed weasel (*M. frenata*)	Small rodents	Interference: In higher abundance of dominant guild predators, weasels increased habitat selectivity and reduced activity levels and ermines used refugia burrows	Predator habitat use, temporal activity and mortality
Prey spatial distribution	Swanson et al. 2014	Lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*)	Thomson's gazelle (*Gazella thomsoni*), wildebeest (*Connochuetes tatirim*)	Interference between lions and wild dogs; risk enhancement between lions and cheetahs	Predator density and home range
Prey spatial distribution	Thornton et al. 2004	Coyote (*Canis latrans*), bobcat (*Lynx rufus*)	Both predators: lagomorphs; coyote: ungulates, fruit; bobcat: rodents	Risk enhancement or interference: Predator spatial overlap at broad scale and segregation at fine-scale; some diet overlap	Predator diet, temporal activity, spatial distribution, habitat use
Prey spatial distribution and abundance	Cresswell and Quinn 2013	Sparrowhawk (*Accipiter nisus*), peregrine falcon (*Falco peregrinus*)	Redshank (*Tringa totanus*)	Substitutive: Predators spatially varied predation pressure	Predator attack frequency and hunting success

Relative predator and prey spatial distribution	Eccard et al. 2008	Least weasel (*Mustela nivalis nivalis*), various avian predators	Bank vole (*Myodes glareolus*)	Risk enhancement: Voles shifted activity to noctural hours to avoid weasel presence but increased owl predation	Vole giving-up densities, activity and mortality
Relative predator and prey spatial distribution	Moll et al. 2016	Lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*), spotted hyena (*Crocuta crocuta*)	Cape buffalo (*Syncerus caffer*), eland (*Tragelaphus oryx*), greater kudu (*Tragelaphus strepsiceros*), red hartebeest (*Alcelaphus buselaphus caama*), warthog (*Phacochoerus africanus*) and zebra (*Equus quagga*)	Lion kill locations and hyena occurrence affected prey aggregation	Ungulate aggregation; lion and hyena occurrence and kills
Relative predator and prey spatial distribution	van Dijk et al. 2008	Wolverine (*Gulo gulo*), wolf (*Canis lupus*), lynx (*Lynx lynx*), red fox (*Vulpes vulpes*)	Moose (*Alces alces*)	Substitutive: Wolverine spatially avoided other predators and scavenged prey carcasses	Predator foraging behavior, predator movement, diet
Relative spatial distribution of predators	Barnowe-Meyer et al. 2009	Coyote (*Canis latrans*), gray wolf (*C. lupus*), cougar (*Puma concolor*), black bear (*Ursus americanus*), brown bear (*U. arctos*), golden eagle (*Aquila chrysaetos*)	Pronghorn antelope (*Antilocapra americana*)	Substitutive interactions between coyotes and secondary predators via habitat segregation; interference interactions between coyotes and wolves	Fawn kill predators and habitat

				when wolves affect coyote behavior	
Relative spatial distribution of predators and prey	Hayward and Slotow 2009	Lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*)	Buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus scriptus*), impala (*Aepyceros melampus*), Thomson's gazelle (*Gazella thomsoni*), warthog (*Phacochoerus africanus*), blue wildebeest (*Connochaetes taurinus*)	Risk enhancement: temporal partitioning between predators	Predator and prey activity temporal patterns
Spatial distribution of predators and prey, evidence of whether wolves consumed coyotes to determine whether intraguild predation	Switalski 2003	Gray wolf (*Canis lupus*), coyote (*Canis latrans*)	Small mammals	Substitutive: Where wolves present, coyotes increasingly scavenge carcasses (likely reducing predation)	Coyote activity budgets
Spatial distribution of prey	Broekhuis et al. 2013	Cheetah (*Acinonyx jubatus*), lion (*Panthera leo*), spotted hyaena (*Crocuta crocuta*)	Not stated	Interference: cheetahs spatially avoid immediate risks from lions and spotted hyaenas	Cheetah habitat selection
Predator predation rates on prey; prey response and spatial distribution	Merkle et al. 2009	Gray wolf (*Canis lupus*), coyote (*Canis latrans*)	Elk (*Cervus elaphus*)	Interference: Wolves dominate coyotes at kill sites and increase scavenging opportunities.	Wolf-coyote interactions at ungulate carcasses

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