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A spatial theory for characterizing predator–multiprey interactions in heterogeneous landscapes

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Trophic interactions in multiprey systems can be largely determined by prey distributions. Yet, classic predator–prey models assume spatially homogeneous interactions between predators and prey. We developed a spatially informed theory that predicts how habitat heterogeneity alters the landscape-scale distribution of mortality risk of prey from predation, and hence the nature of predator interactions in multiprey systems. The theoretical model is a spatially explicit, multiprey functional response in which species-specific advection–diffusion models account for the response of individual prey to habitat edges. The model demonstrates that distinct responses of alternative prey species can alter the consequences of conspecific aggregation, from increasing safety to increasing predation risk. Observations of threatened boreal caribou, moose and grey wolf interacting over 378 181 km² of human-managed boreal forest support this principle. This empirically supported theory demonstrates how distinct responses of apparent competitors to landscape heterogeneity, including to human disturbances, can reverse density dependence in fitness correlates.

1. Introduction

Predator–prey interactions are an integral part of ecological theory because they are the basic modular building blocks for understanding the complexity and dynamics of ecological communities [1–3]. The predator functional response is a central part of this theory because it characterizes the rate at which individual predators consume prey for their own production and, reciprocally, characterizes the level of mortality that predators inflict on their prey populations [1,4]. The density and spatial distribution of prey is an important variable in the functional response because it instrumentally determines the likelihood that predators encounter, kill and consume their prey [5,6]. Classical predator–prey theory is based on the assumption that prey are well mixed across landscapes such that predator encounter rates with prey are simply a function of global prey density. This assumption often conflicts with reality

simply because the mosaic nature of the different land cover types available across landscapes creates spatial heterogeneity in resource distribution, leading prey to aggregate spatially [4,7]. Prey species may also respond to the mere threat of predation by aggregating into refuge habitat to reduce encounter rates with predators and thereby reduce predation mortality risk [8,9]. Furthermore, human agency can alter the spatial structure of landscapes, and hence the nature of predator–prey interactions, through habitat alteration or destruction consequent to resource extraction or land development [10,11]. Indeed, human agency is indubitably becoming one of the main factors controlling the distribution of animal populations, especially their aggregation patterns across landscapes [12]. These factors collectively will in turn have a decided influence on the nature of the predator consumption rate of prey [4,6,10].

Prey consumption rates by a focal predator species may also be shaped by co-occurring prey species [4]. For instance, in classic non-spatial predator–prey models, the kill rate of predators generally increases at a diminishing rate with increasing prey density (i.e. type II functional response). This leads to the prediction that *per capita* mortality risk of prey should decrease with increasing local prey density [13], a prediction that has received empirical support (e.g. [14]). However, such theory predicts that for multiprey systems it is altogether unlikely that the abundance of one prey species affects mortality risk of a rarer secondary prey [15]. This arises because the predator should spend most of its time handling the abundant prey, leaving little time to consume the secondary prey [16]. Consumption of the secondary prey largely becomes incidental and its predation rate would be essentially density independent. In such a case, the abundance of the two prey species would be uncorrelated across the landscape.

Adding considerations of spatial heterogeneity and prey species aggregation in space can change these predictions. Variation in the spatial abundance and juxtaposition of one prey species can alter predation mortality risk on a second species, via a process known as apparent competition [17–20]. This mechanism causes prey species densities to be negatively correlated across landscapes. Spatial heterogeneity in prey distribution can enhance the strength of apparent competition [20] by influencing the encounter rate between the predator and its multiple prey species [21], and subsequently, the time spent handling each species [16,22,23]. Thus, in areas where one prey species is highly aggregated, its encounter rates with predators could be locally relatively high, leading to a relatively high rate of consumption. This can spill over and influence the *per capita* mortality risk for the second prey species, but it will depend on that species' spatial distribution in relation to the first prey species, its own population size, as well as the predator's movement tactics and prey preference [22,24].

Developing quantitative approaches to understand how heterogeneity drives predator–multiprey interactions can provide a strong spatially informed basis for anticipating how ecological communities may become structured in heterogeneous landscapes. This information becomes especially relevant as human use of landscapes exacerbate landscape-scale heterogeneity by fragmenting habitats and creating edges. Understanding the potential impact of these animal aggregations on the mortality risk that predators inflict on their prey is, therefore, key to developing conservation and

management that facilitates coexistence of humans and wildlife species, especially in the face of increasing human modification of landscapes [4]. Developing such a quantitative approach involves blending mathematical modelling of species interactions with quantitative analyses of species movement in different environmental contexts that create spatial heterogeneity across landscapes [1].

We present here such a modelling approach that characterizes a predator feeding in a spatially heterogeneous, multiprey system. We use this model to illustrate how differences in movement patterns of prey species, and hence their spatial distribution in response to spatial heterogeneity, shapes mortality risks to the prey species within the landscape. We then apply the model to an extensive dataset collected to evaluate how human alteration of a landscape in eastern Canadian boreal forest shapes winter interactions among grey wolves (*Canis lupus*), woodland caribou (*Rangifer tarandus*) and moose (*Alces alces*) prey in a 378 181 km² area. We show how landscape heterogeneity predictably alters the distribution of mortality risk from predation and hence the nature of predator interactions with those prey species. We do this by accounting for the effects of animal distribution across landscapes on the functional response in a predator–multiprey system.

The model is explicitly designed to predict how prey spatial movement in response to landscape level heterogeneity determines their *per capita* mortality risk to predation. While this is a key component of prey population dynamics [4,5], we do not explicitly scale up mortality risk to predict temporal dynamics *per se*. Rather, we assume predator and prey species have fixed global densities. We then explore how landscape alteration rearranges the spatial concentrations of predator and prey across a landscape, and how that influences mortality risk. As such, we advance principles about spatial dependency in predator–prey interactions. These principles offer a key step towards developing mechanistically informed next-generation models that do characterize spatio-temporal dynamics of predator and prey populations [1].

2. The model

We envision a landscape comprised a mosaic of land cover types (e.g. cutblocks in a forest landscape) with sharp edges between them. In such a landscape, edge effects become pervasive across space. We assume that animal movement and spatial aggregation is sensitive to edges between land cover types, but that the nature of the movement and aggregation varies by species. Some species, for instance, may be most abundant directly at the edge, whereas others are least abundant at the edge, and gradually increase in number with distance from the relatively poor-quality land cover [25]. Species may even display intermediate responses to edges. For example, the abundance of woodland caribou is higher at about 4.5 km from forest cuts than closer to or farther away from these features [26].

The predator's consumption rate is fundamentally determined by its preference for different prey species that, in turn, determines the proportion of each prey species that is included in the diet. Consumption rate is further determined by predator search rate for prey, and predator handling time of prey (time spent chasing and consuming prey). Classic

population dynamic formalisms, which assume homogeneous spatial structure and mass action encounter between a predator and its prey, typically characterize such a consumption process using a multiple-prey type II functional response [22]. We adapt this functional response to our purposes here by developing a spatially explicit formalism that mechanistically infuses considerations of how prey aggregation due to spatially heterogeneous landscapes alters predator–prey encounter and hence the prey search and handling processes. That process will inherently be dependent on the distance between a predator and an edge, the type of land cover in which it is foraging and how edge effects influence prey aggregation that in turn influences search and handling processes. Although we focus on a single predator feeding on two prey species, the principles nonetheless generalize to greater than two prey species.

(a) Characterization of the landscape for a spatially explicit analysis

We consider predators and prey interacting within domains Ω that represent two-dimensional landscape spaces where at least one boundary is an edge. These edges could involve any land cover type, as long as it influences the movement of at least one prey species. As such, the model takes the prey-centric perspective to predict species-specific, steady-state pattern of space-use. The ensuing consumption of prey by a predator is then assessed, given the steady-state solutions. We tailor our modelling to accommodate a representation of domain that allows for a continuous spatial representation of prey locations. The spatial locations of prey within a domain Ω are described as a function of distance $s > 0$ from the nearest edge. We denote by C_s the curve of points located at distance s from the nearest edge and let $m(s)$ be the arc-length of C_s . We denote by u_s the arc-length parametrization of C_s , i.e. the location of points \mathbf{x} on C_s are identified by their distance along the curve. This allows each location $\mathbf{x} \in \Omega$ to be expressed using curvilinear coordinates (s, u_s) with $u_s \in [0, m(s)]$. This principle is illustrated in figure 1 using parametrization for two different landscape domains, where the arc-lengths for C_{s1} and C_{s2} differ within each kind of domain. In particular, the area of Ω is given by computing the double integral of the constant function 1:

$$\int_0^L \int_0^{m(s)} du_s ds,$$

or also LM , where L is the maximal distance from the edge and M is the average width of the domain

$$M = \frac{1}{L} \int_0^L m(s) ds.$$

We adopt this representation for spatial coordinates, rather than using a more conventional Cartesian approach, because it allows for greater flexibility in the range of natural or human-created shapes of landscape domains that can be considered. That is, our approach is designed to allow consideration of a wider range of landscape configurations than the square or rectangular domains such as those used in classical models of spatially explicit dynamical systems [1]. For example, our approach allows for fine-scale assessments of the behavioural response of animals to non-regular

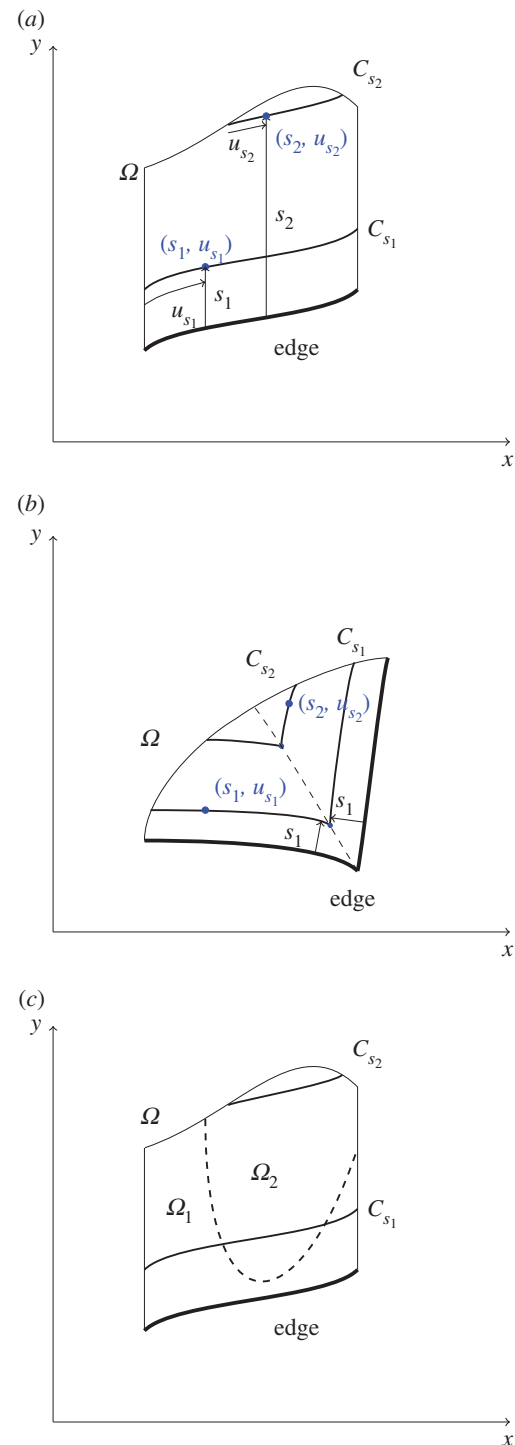


Figure 1. (a) Domain Ω with coordinates described using curves C_s of locations at a fixed distance s from the edge along with the distance u_s along C_s (here from the starting point chosen on the left). In (b), the dashed line represents points in Ω at equal distance from two pieces of edge, those points can be safely neglected from the domain as the probability of an individual from the population being on this curve is zero. (c) Domain Ω containing distinct land covers Ω_1 and Ω_2 with the dashed curve being the boundary between the land covers. C_{s1} has a component in both land covers while C_{s2} is entirely in Ω_2 . Note that the portion of C_{s1} in Ω_1 is the union of two disjoint portions of curve. The length $m_i(s)$ of $C_{s1} \cap \Omega_1$ is the sum of the length of the two portions. (Online version in colour.)

habitat edges resulting from natural disturbances due to extreme weather events or fire, or human activities [27].

Our approach allows for the entire landscape domain Ω to be subdivided into i different land cover or land use

types Ω_i such that Ω becomes a disjoint union (i.e. heterogeneous patchwork) of the i different land cover types. We consider the intersection $C_s \cap \Omega_i$ and denote by $m_i(s)$ its length. Note that $C_s \cap \Omega_i$ can be the union of disjoint portions of C_s . For instance, in figure 1c, the land cover Ω_1 intersects C_{s1} and yields two disjoint intervals separated by the intersection of the land cover Ω_2 with C_{s1} while C_{s2} is contained entirely in Ω_2 .

(b) A spatially explicit functional response for multiprey systems

The above characterization of the landscape enables us to modify a classic non-spatial functional response to allow consideration of spatially explicit predator–prey interactions. We do this by expressing the key foraging parameters of the consumer functional response in terms of spatial coordinate s (i.e. distance from edge). We begin with a classic multiple predator Type II functional response [22], denoted E_x , that describes a predator's intake rate of prey species X in a system comprised of two prey species (1 and 2) as:

$$E_X(s) = \frac{\sum_j a_j N_{Xj}(s) U_{Pj}(s) \alpha_{Xj}(s)}{1 + h_1 \sum_j a_j N_{1j}(s) U_{Pj}(s) \alpha_{1j}(s) + h_2 \sum_j a_j N_{2j}(s) U_{Pj}(s) \alpha_{2j}(s)}, \quad (2.1)$$

where a_j is the search rate (area/time) within patch type j , $\alpha_{Xj}(s)$ is the proportion (range: 0–1) of prey X included in the diet, which reflects the predator's preference between prey species 1 and 2 (i.e. $\alpha_{1j}(s) + \alpha_{2j}(s) = 1$) at distance s within patch type j . $N_{Xj}(s)$ describes the distance-dependent prey density in patch j and is defined below. We let h_X (time/prey) be the time spent handling (i.e. chasing and consuming) prey species 1 and 2, respectively.

In this model, effects of landscape heterogeneity are embedded in the search rate $a_j(s)$ and prey species density $N_{Xj}(s)$ within a land cover j , that, because of aggregative behaviour of prey in response to habitat edges, will vary with distance s from the edge of that land cover type. A spatially informed model of such aggregative effects must then specify how the spatial domain of the land cover types and prey spatial movement within them influences search rate and prey density.

We denote the relative use of land cover j by prey X or predator P at distance s as

$$U_{Xj}(s) = \frac{w_{Xj}(s)m_j(s)}{\sum_i w_{Xi}(s)m_i(s)} \quad \text{or} \quad U_{Pj}(s) = \frac{w_{Pj}(s)m_j(s)}{\sum_i w_{Pi}(s)m_i(s)}$$

where w_{Xj} are the selection coefficients associated with land covers of type j among the i types available for prey species $X = (1, 2)$, and w_{Pj} is the coefficient for the predator. The selection coefficients reflect the relative probability of occurrence of a predator or prey species at a given location, and they can be determined from resource selection functions [28]. This formalism then allows a spatially explicit determination of $a_j(s)$ where $a_j(s) := a_j \times U_{Pj}(s)$.

We characterize the edge effects on prey density $N_{Xj}(s)$ by specifying how densities of prey species 1 and 2 vary as a function of the distance to the nearest edge of interest, assuming that prey actively move away from the edge, with the distance moved depending on the species-specific repulsion of the edge effect, where high repulsion implies that prey have strong avoidance of the edge. Following [26], we

estimate the steady-state solutions of this landscape-scale movement for prey species X , $v_X(\mathbf{x})$, using the following advection–diffusion model:

$$\frac{\partial v_X(\mathbf{x}, t)}{\partial t} = \nabla \cdot \left(\frac{\rho_0^2}{2} \nabla v_X \right) - \nabla \cdot \left(\frac{\rho_0^2}{2} b \mathbf{V}_\Phi(\mathbf{x}) v_X \right), \quad (2.2)$$

where $v_X(\mathbf{x}, t)$ is the probability of being at location $\mathbf{x} = (x, y)$ in the domain Ω at time t , ρ_0 is the mean move length, b is the directional bias per unit length travelled, $\mathbf{V}_\Phi(\mathbf{x})$ is a vector field of location data points that describe the prey species orientation in relation to the edge and its displacement from the edge. The parameter Φ is the distance at which the repulsive effect of the edge vanishes (more details in [26]). Because v_X are (continuous) probability density functions, they can be integrated so that

$$\int_{\Omega} v_X(\mathbf{x}) d\mathbf{x} = 1,$$

for each prey species $X = (1, 2)$. Given that Ω can be parameterized using (s, u_s) , we can calculate $v_X(s)$, the relative probability that prey species X is at a distance s from an edge within any land cover type using

$$v_X(s) = \int_0^{m(s)} v_X(s, u_s) du_s.$$

Now, we suppose that the density of species X (N_X , number of individuals X /unit area within the two-dimensional domain Ω) at some x in Ω only depends on the distance s . To formulate this, we define the density distribution factor as $\tilde{v}_X(s) = v_X(s)L$. Therefore, the density at distance s is defined as:

$$N_X(s) = \tilde{v}_X(s) N_X$$

and we call $N_X(s)$ the density distribution of species X , with domain $[0, L]$. $N_X(s)$ is indeed well defined because

$$\int_0^L N_X(s) ds$$

is the total number of individuals of species X in the domain Ω . Using $N_X(s)$, we can define the density distribution of species X at distance s on land cover j as

$$N_{Xj}(s) = N_X(s) \frac{w_{Xj}(s) \sum_i m_i(s)}{\sum_i w_{Xi}(s) m_i(s)}.$$

Substituting this spatial formalism for prey density into equation (2.1) allows for the spatial representation of the overall predator intake rate of prey X at distance s given the proportion of time spent in the i land cover types. Given this formalism, we can then calculate the *per capita* mortality risk ($D_X(s)$) for prey species X given the presence of other prey species within the landscape domain as:

$$D_X(s) = \frac{E_X(s)}{N_X(s)}. \quad (2.3)$$

Our approach assumes that animal spatial distribution has reached a steady state. We further assume that this state is reached faster than other potentially important changes in the populations and landscape structure.

3. Application of spatial functional response to empirical analysis

We illustrate the utility of this theory using (i) a hypothetical case example of a predator feeding on two prey in a landscape with edge effects and (ii) a real-world case example involving wolves preying on caribou and moose in a boreal forest landscape in which the spatial coordinates of each of these species was measured in a landscape impacted by forest harvesting. The hypothetical case illustrates key properties of the model by assessing the consequences of prey aggregation on its consumption by predators in a simple predator–multiprey system. The real-world case shows that these effects can indeed be manifest in a more complex landscape impacted by human activities, and for which those human impacts are raising important conservation concerns [4].

(a) Hypothetical case

We examine the case where the predator has no preference for either prey (i.e. $\alpha_X = N_X/[N_C + N_M]$). Prey species C and prey species M are, therefore, equally vulnerable. The case involves the condition in which predator and prey species can select among three land cover types, i.e. Ω_i , $i = 1, 2, 3$, one of which is created by habitat disturbance (e.g. fire or logged forest stand). All prey display distance-dependent movement bias with respect to habitat disturbances. We consider that only one prey species displays non-monotonic edge effects that result in conspecific density being highest at intermediate distances from the disturbance's edge. We assume that the other species displays a classic avoidance response to the edge in which its density rises monotonically with increasing distance from the edge. We determine the steady-state use patterns of the two prey given their movement response within a rectangular spatial domain Ω ($\Omega_i \in \Omega$) of length 15 with boundary disturbance along only one width (figure 2a) to the habitat edge. We embedded this information into the functional response to determine expected patterns in kill rates.

We illustrate the effect of increasing the relative density of the alternative prey (e.g. species introduction or invasion), by simulating a predator hunting in a simple landscape comprised of three land cover types available in the same proportion (i.e. $A_1 = A_2 = A_3$), but randomly distributed in space (i.e. equal proportions at any distance from the disturbance). Among the three land cover types, prey species 1 and 2 display the selection coefficient: $w_{11} = w_{21} = w_{P1} = 1$; $w_{12} = w_{23} = w_{P3} = 2$; $w_{13} = w_{22} = w_{P2} = 3$. The predator has a general attack rate: $a_i = 1$, and handling times: $h_1 = 0.1$ and $h_2 = 0.1$. When prey species 1 lives at a density of 1 in a single prey-species system, the aggregation resulting from edge effects to habitat disturbance yield positive density dependence with *per capita* mortality (figure 2b). As prey 2 invades the system, however, the benefit of grouping that prey species 1 experienced when alone is gradually replaced by an increase in *per capita* predation risk consequent to being near prey species co-occurring on the landscape. Habitat disturbance thus increases predator-induced mortality risk as the alternative prey becomes abundant. Meanwhile, prey 2 consistently benefits from the grouping of prey 1 by experiencing reduced mortality risk where they aggregate (electronic supplementary material, appendix S2 and figure S3).

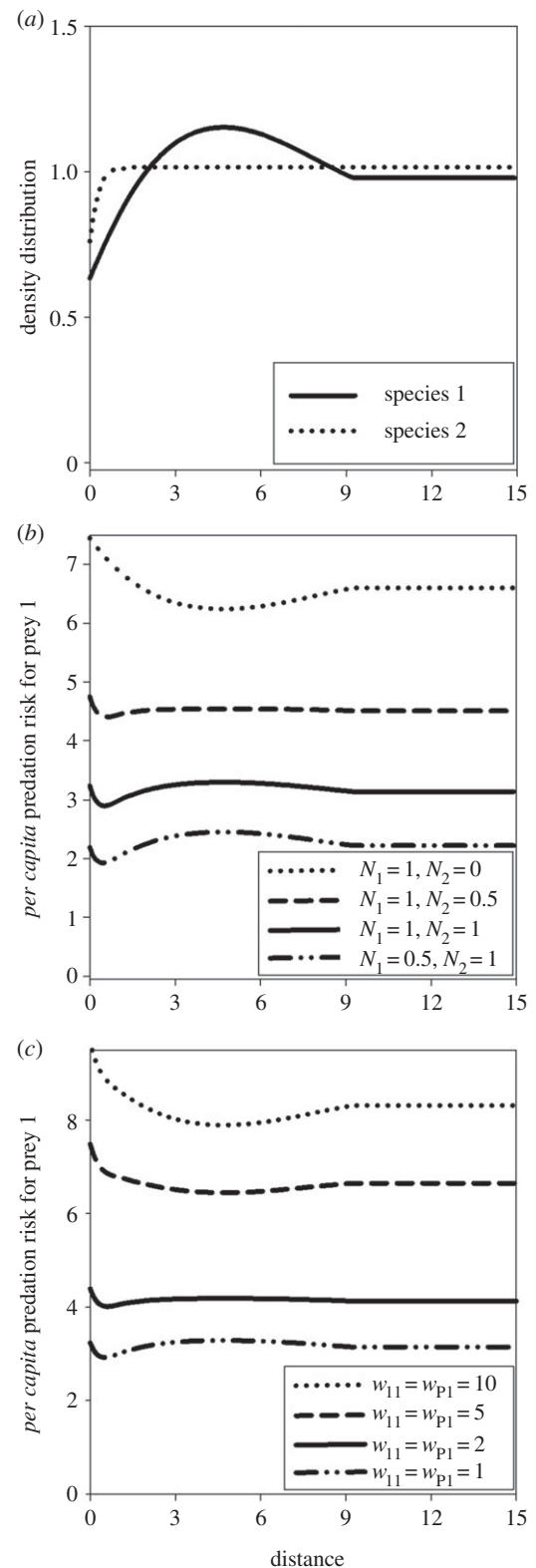


Figure 2. (a) Density distribution function of prey species 1 (\tilde{v}_1) and 2 (\tilde{v}_2) over the spatial domain $L = 15$ from the nearest edge, with the resulting consequences on (b) *per capita* predation risk for species 1 given its overall density and the density of species 2, and (c) *per capita* predation risk for species 1 in a two-prey system, given the changes in its selection (w_{11}) and the predator's selection (w_{P1}) for land cover type 1, assuming that the other parameter values remain at $w_{21} = 1$; $w_{12} = w_{23} = w_{P3} = 2$; $w_{13} = w_{22} = w_{P2} = 3$.

An increase in habitat selection by the predator and differences in habitat selection by the prey can have a similar impact. We illustrate this by keeping model parameters the

same, except that we now assume that $N_1 = N_2 = 1$, and habitat selection of prey 1 and the predator varies. When the predator and prey 1 are generalists, disturbance-induced aggregation increases *per capita* predation risk for that prey (figure 2c). As the predator focuses on the land cover type selected by prey 1, grouping has the same consequences as increasing local density of prey 1 and decreasing local density of prey 2. Indeed, grouping decreases *per capita* predation risk and we observe positive density dependence (figure 2c). A strong selection for a cover type by the predator associated with a moderate selection by one prey (e.g. $w_{21} = 2$) would have the same outcome, but less pronounced. Under these changing conditions, prey 2 consistently experiences reduced mortality risk from the grouping of prey 1 (electronic supplementary material, appendix S2 and figure S4).

(b) Real-world case example: caribou, moose and wolf in managed boreal forests

This case example concerns the role of wolf predation on caribou and moose that is influenced by forest harvesting in boreal ecosystems. Interactions among these three species are gaining increasing conservation concern because it is postulated that moose have an indirect negative effect on caribou via a wolf mediated-apparent competition interaction, especially as moose are better able to thrive in landscapes that are altered by humans via forest harvesting [4,23,24]. What remains uncertain, however, is whether it is universally true that forest operations lead to this outcome for the wolf–caribou–moose system. Our analysis shows how the theory can help to address this uncertainty through monitoring of animal spatial movement as well as quantification of model parameters across landscapes in which forest harvesting has been the major source of anthropogenic disturbance for the past decade [26]. We focused on distance-dependent responses of caribou, moose and wolves to habitat edges created by road construction and forest cutovers.

(i) Methods

The quantification of the spatially explicit, mechanistic functional response requires values for the parameters N_C , N_M , h_M , h_C , a_i , α_C , w_{Ci} and v_C , where subscripts C and M represent caribou and moose, respectively. All these parameters came from the literature (electronic supplementary material, appendix S1). We also estimated parameters w_M , v_M and w_P , which were quantified from the analysis of moose track networks detected from extensive aerial surveys, as well as locations from 15 GPS-collared moose and nine GPS-collared wolves from four packs followed in the Côte-Nord region of Québec (electronic supplementary material, appendix S1). The study area is a typical boreal forest characterized by a mosaic of conifer forests, lichen-heath communities, peatlands, mixed and deciduous forests, burned areas and water bodies.

Once the spatially explicit, mechanistic functional response has been quantified, we tested its predictions based on 145 radio-collared (Argos/GPS or GPS collar) female caribou followed during winter over a 378 181 km² area located across Québec's boreal forest. Individuals were relocated at least twice a day, and 11 170 locations were recorded, on average, for each individual. We used logistic regression to evaluate the relationship between the

probability of mortality of female caribou (individuals that died were scored 1, and the others 0) and their average distance to the nearest cut or road.

(ii) Results

Given their fine-scale movements, caribou and moose were expected to be distributed differently with respect to cuts and roads, a prediction that received strong empirical support (figure 3 and see also electronic supplementary material, appendix S1 for details). On this basis, we determined that, if caribou were the only prey for wolves on the landscape, then caribou should experience their lower *per capita* risk of predation where their density is highest (figure 4a, Caribou (one-prey system)), i.e. at approximately 4 km from human disturbances (figure 3). By contrast, in the case where caribou and moose are both available as prey for wolves in the northern Québec landscape, the model predicts that caribou aggregation due to human disturbances should increase *per capita* predation risk (figure 4a). Predation risk should vary non-monotonically with distance from cuts or roads, a prediction that should hold across a variety of environmental conditions (see electronic supplementary material, appendix S1: sensitivity of *per capita* mortality risk predictions for caribou). Of the 145 female caribou that we followed up in winter, 46 died and 99 survived. The LOESS analysis of data (Proc LOESS, [29]) indicated that the probability of mortality of radio-collared female caribou covaried non-monotonically with distance from a road or a recent cut (figure 4b). Females located approximately 10 km from the nearest road or recent cut had the highest risk of mortality. A polynomial logistic regression confirmed the trend and the peak location: $\text{Logit}(s) = -1.68 + 0.35s + -0.018s^2$; $p < 0.02$ for each parameter; $n = 145$ (electronic supplementary material, appendix S2 and figure S5).

While the direction of the observed non-monotonic trend was qualitatively consistent with the model predictions, the quantitative increase in mortality risk extended farther away from the edge than predicted. Nevertheless, given the spatial complexity of the modelling, our coarse approximation of the distance depended effect, based simply on how caribou and moose move with respect to cuts and roads, is encouraging; especially so, given that the prediction is altogether different than expectations for caribou in a one-prey system in the same kind of harvested landscape (figure 4a).

4. Discussion

Predator–prey theory has been extremely useful in developing modern conceptualizations of how ecological communities are structured and how they function [1,3]. This body of theory also increasingly has practical implications by helping to inform how looming human impacts that create heterogeneous landscapes through habitat exploitation or destruction might alter interactions and viability of predator and prey species [4]. Our advancement here of a spatially informed theory of predator–multiprey interactions responds to calls [1,4] to operationalize spatial predator–prey theory in ways that can include quantitative measures of species movement and spatial aggregation.

The growing interest in analysing the spatial distributions of species has certainly lead to increasingly sophisticated means to gather information on their spatial locations

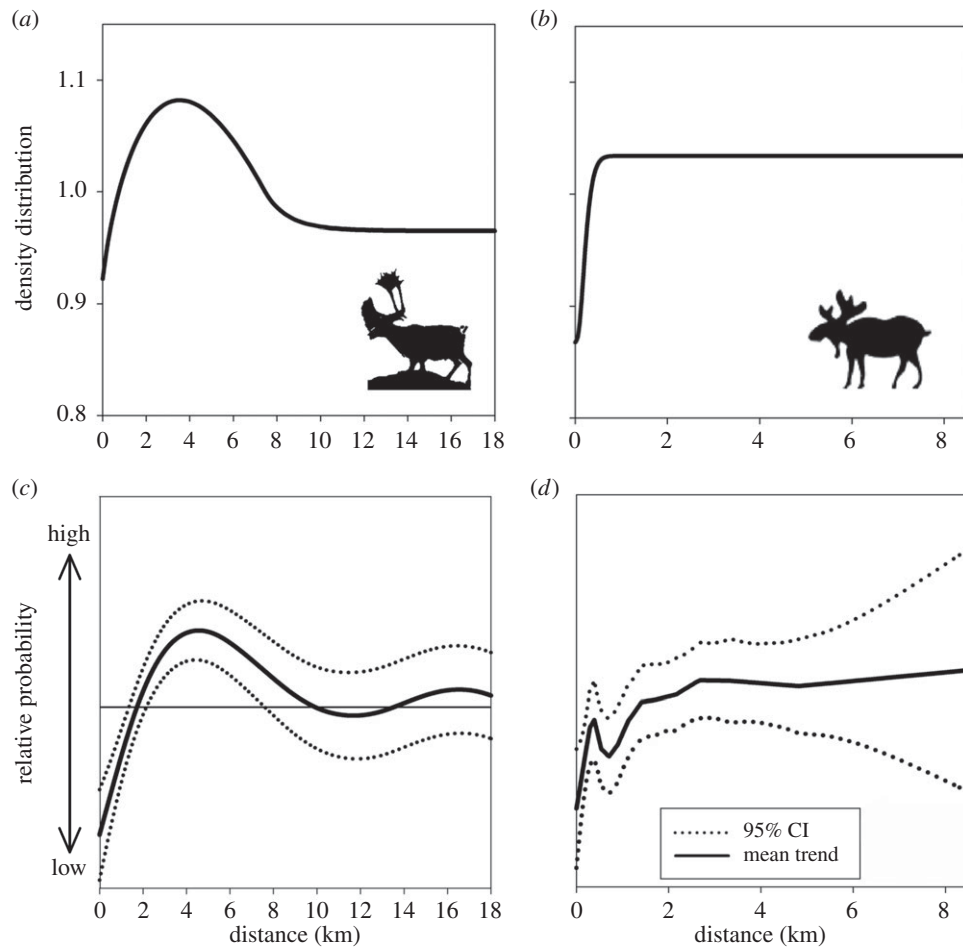


Figure 3. Expected distribution of (a) caribou and (b) moose with respect to the distance from the nearest anthropogenic disturbances (\bar{v}_M), as predicted from an advection–diffusion movement model developed from radio-collared individuals followed in the boreal forest of the Côte-Nord region of Québec, Canada. (c) Relative probability of occurrence of track networks of (c) caribou or (d) moose in winter, as a function of the distance from the nearest road. Information on caribou came from the analysis conducted by [26], and published by © 2013 The University of Chicago Press.

(e.g. satellite telemetry) as well as the development of statistically sophisticated analysis approaches that help to characterize the environmental features with which species associate across landscapes [28,30,31]. Our approach lends itself to enlist these methods of information gathering to characterize species distributions and interactions using real-time data gathered across broad landscapes.

Our model is tailored to explore the cases in which the relative risk of predation for a prey population depends not only on its distribution but also on the distribution of other co-occurring prey species. Such effects can arise in systems involving intraguild predation, predator-mediated competition between prey and apparent competition. Classic dynamical systems models that characterize these kinds of interactions assume that each species is homogeneously distributed in space and so encounter each other randomly. But, such an assumption of encounter is often not consistent with conditions experienced across natural landscapes that are quite heterogeneous due to a mosaic patchwork of land cover types. In such cases, species tend to aggregate in preferred habitats or alter their degree of aggregation when predators and co-occurring prey species are present or when humans alter those cover types [4,10,11].

Our modelling focuses on how spatial aggregation of prey influences parameters of the predator functional response by quantifying movement responses to habitat edges. The model demonstrates that distinct responses of alternative prey

species to environmental heterogeneity can alter the consequences of conspecific aggregation, from increasing safety to increasing predation risk. The model outlines the conditions under which spatial heterogeneity drives predator–prey interactions in either direction. In a single predator–prey system, the increase in local conspecific density often results in positive density dependence through predator-mediated Allee effects [16,32]. Our theoretical model supports this observation for predators with a type II functional response. Furthermore, we demonstrate that a species could also benefit from grouping in a two-prey system if its predator displays a similarly strong selection for the same cover type. In this case, the prey population would face a relatively high predation rate, but individuals that aggregate in certain areas would experience the lowest *per capita* risk of predation. Safety in numbers would also emerge in multi-prey systems occupied by generalist predators if all prey species have the same spatial distribution. This situation appears rather unlikely however. Different animal species on the same trophic level commonly display distinct movement responses [21,27,33] and spatial organization with respect to the same habitat features [25,26,34]. In fact, a basic ecological principle is that adaptive evolution should promote differences in the reaction of individual species to environmental heterogeneity (e.g. [35–37]). Our findings that spatial structure in predator–prey interactions in multi-prey systems could jeopardize the potential advantages of

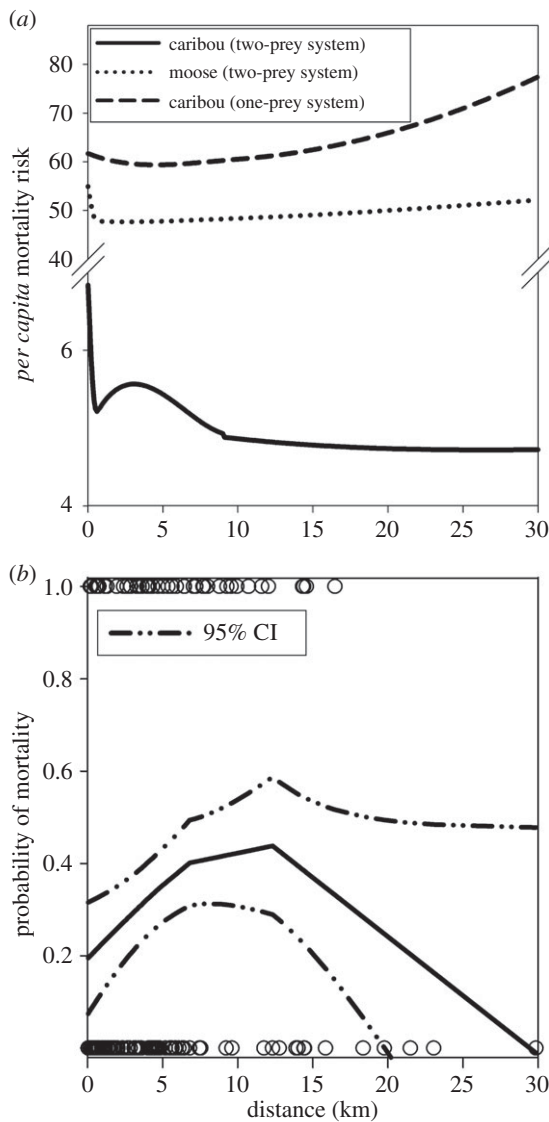


Figure 4. (a) *Per capita* probability of mortality of forest-dwelling caribou, as predicted from equation (2.3) for a single predator–prey system, and *per capita* risk of mortality for members of sympatric caribou or moose populations, as a function of their distance from the nearest anthropogenic feature, and (b) probability of mortality of 145 radio-collar caribou as a function of their distance from the nearest road of cut. White circles are the raw observations, whereas the solid line is the average trend (with its 95% confidence interval, CI) predicted from a logistic regression based on locally weighted scatterplot smoothing (LOESS).

aggregating should, therefore, be pervasive to a broad range of ecological systems.

The case study of caribou, moose and wolves provides empirical support for the prediction that grouping can increase *per capita* risk in multiprey systems. The model made predictions that were congruent with observations, at least as a coarse, first approximation. Like similar tests of coarse spatial approximations (e.g. [38]), this boosts confidence that the model captured the key spatial processes needed to explain how spatial heterogeneity can fundamentally alter predator–multiprey interactions, relative to aspatial conditions.

Both caribou and moose had a relatively low probability of occurrence in cuts or on roads. Their relative probability of occurrence gradually increased with the distance from these anthropogenic features, but differently for the two prey species. For caribou, the probability reached a maximum at approximately 4 km; whereas for moose, the probability increased

towards a plateau that was reached within 3 km (electronic supplementary material, appendix S1). The caribou aggregation near 4 km should reduce predation risk in a one-prey system or in a two-prey system whenever moose display the same distance-dependent response to cuts and roads. But, moose respond differently to anthropogenic features, which in turn alters the expected density dependence in mortality risk for caribou. In this case, caribou aggregation near human-induced edges should increase instead of decrease their risk, while providing a local relief in predation risk for moose populations.

Our spatially explicit functional response assumes that the predators do not strongly switch their preference between prey species, an assumption that appears appropriate for the caribou–moose–wolf system [22]. If predators were to display a strong positive density-dependence in preference for a prey species, the increased *per capita* risk of predation associated with grouping should become even stronger because predators would increase their focus on the abundant prey even more strongly in those areas. The trend should still hold even if we were to account for the fact that an increase in prey density should result in a numerical response by wolves [39,40]. Indeed, wolf density (or wolf utilization distribution) should then be higher in areas of relatively high local prey density. Adding a mechanistic numerical response to our model would be a first step to expand our spatial model to predict spatio-temporal predator–prey population dynamics [1].

Our findings have important conservation implications. Forest-dwelling caribou are threatened in Canada [41], and the decline of their populations are closely linked to human disturbances, especially to logging activities [42–44]. Caribou generally experience higher predation risk in areas comprising a relatively large proportion of cutblocks [43]. A mechanism generally put forward to explain the increased mortality is that timber harvest brings mature conifer forests back to an early-seral-stage that, once invaded by deciduous vegetation, attracts moose. The local increase in moose density then triggers a numerical response from wolf populations, which leads to more frequent interactions with caribou [38,45,46]. Our study outlines an additional mechanism that does not rely on a numerical response from moose or wolf. Moose and caribou react differently to logging-induced edges, and these differences are directly responsible for an increase in the rate of interaction between caribou and wolves at an intermediate distance from cuts or roads. In other words, the skewed distribution of caribou caused by their behavioural response to human disturbances induces spatial structure in hunting patterns of wolves, and some caribou end up paying the price of living in a bad neighbourhood. Our empirical test conducted on 145 female caribou distributed over 378 181 km² of boreal forest provided qualitative support to this prediction, because risk does not simply decrease monotonically with distance from cuts and roads, but displayed a non-monotonic relationship (figure 4). This additional mechanism that we outline might, therefore, exacerbate the pathway of apparent competition between caribou and moose that has been previously proposed [24,46,47]. While our model can explain the nature of increase in *per capita* mortality risk that caribou experienced where they occur at relatively high density, we recognize quantitative differences between our predictions and observations remain. This suggests further empirical and modelling effort to better capture nuances in spatial movement and interactions for this particular system. The model, nevertheless, provides a

framework for steering research towards resolving the mechanisms and kinds of refined spatial data needed to fully characterize the caribou–moose–wolf system.

Our study illustrates that species-dependent responses to spatial heterogeneity can have a fundamental impact on food web interactions and ecosystem functioning. The risk faced by prey does not only depend on their overall density, but also on their spatial distribution, the distribution of alternative prey and the movements of predators in complex landscapes. Food web dynamics thus cannot be adequately understood without accounting for spatial patterns in the distribution of animals from different trophic levels.

Ethics. All capture and handling of animals was approved by an Institutional Animal Care and Use Committee—Comité de protection des animaux of the Université Laval.

Data accessibility. The datasets supporting this article are available at <http://dx.doi.org/10.5061/dryad.bf771>.

Authors' contributions. D.F. designed the study and developed the model; P.-L.B. contributed to the model and solved the PDE equation; D.F. and N.C. conducted the statistical analyses; N.C. and C.L. extracted the GIS information; D.F., S.H., C.D., J.M., V.B., M.-H.S.-L. and P.D. were in charge of the fieldwork; O.S., D.F. and P.-L.B. wrote the manuscript; and P.D., M.-H.S.-L., C.L., S.H., C.D., V.B. J.M. edited the manuscript.

Competing interests. We declare we have no competing interests.

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