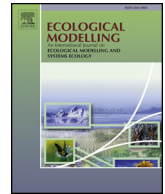




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Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Community consequences of foraging under fear

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ARTICLE INFO

Keywords:

Predator-prey interactions
Individual-based model
Landscape of fear
Home range
Biodiversity
Foraging

ABSTRACT

Non-consumptive effects of predators within ecosystems can alter the behavior of individual prey species, and have cascading effects on other trophic levels. In this context, an understanding of non-consumptive predator effects on the whole prey community is crucial for predicting community structure and composition, hence biodiversity patterns. We used an individual-based, spatially-explicit modelling approach to investigate the consequences of landscapes of fear on prey community metrics. The model spans multiple hierarchical levels from individual home range formation based on food availability and perceived predation risk to consequences on prey community structure and composition. This mechanistic approach allowed us to explore how important factors such as refuge availability and foraging strategy under fear affect prey community metrics. Fear of predators affected prey space use, such as home range formation. These adaptations had broader consequences for the community leading to changes in community structure and composition. The strength of community responses to perceived predation risk was driven by refuge availability in the landscape and the foraging strategy of prey animals. Low refuge availability in the landscape strongly decreased diversity and total biomass of prey communities. Additionally, body mass distributions in prey communities facing high predation risk were shifted towards small prey animals. With increasing refuge availability the consequences of non-consumptive predator effects were reduced, diversity and total biomass of the prey community increased. Prey foraging strategies affected community composition. Under medium refuge availability, risk-averse prey communities consisted of many small animals while risk-taking prey communities showed a more even body mass distribution. Our findings reveal that non-consumptive predator effects can have important implications for prey community diversity and should therefore be considered in the context of conservation and nature management.

1. Introduction

Predators affect prey populations in two different ways: directly by consuming and indirectly by evoking fear (Brown et al., 1999; Lima, 1998). While it is clear that consumption has negative consequences for prey populations, the impact of fear is not that obvious. Prey individuals sensing the presence of a predator may respond with morphological changes, for example, the development of spines against being eaten in *Daphnia pulex* (Krueger and Dodson, 1981) or behavioral adjustments, such as increased vigilance behavior (Hunter and Skinner, 1998), alterations in group size (Creel and Winnie, 2005) or diurnal vertical migration (Stich and Lampert, 1981) in order to minimize predation risk. Additionally, fear effects can have profound consequences on ecosystem functioning due to cascading impacts on other species (Ripple and Beschta, 2004; Schmitz et al., 2004; Werner and

Peacor, 2003). Due to the frequently reported losses of apex predators in many ecosystems (Estes et al., 2011), an understanding of indirect effects of predators on prey is of high importance to better understand and predict consequences for biodiversity and ecosystems.

Common behavioral adjustments of animals perceiving predation risk are modifications in space use during foraging. In order to understand these modifications the “landscape of fear” concept has been developed, consisting of visual maps that quantify the spatial distribution of predation risk (Laundré et al., 2010, 2001). Predation risk perception can be measured by using established methods such as giving-up densities (Brown, 1988) or vigilance patterns (Altendorf et al., 2001). In combination with information about food availability and locomotion costs landscapes of fear can help to decipher and predict animal movement decision (Gallagher et al., 2017). Furthermore, landscapes of fear can be integrated in basic ecological concepts, such

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as the link between bottom-up and top-down control (Laundré et al., 2014).

Adaptations in prey behavior due to perceived predation risk can have cascading effects on other species. These effects have been summarized under the term ‘behavior-mediated indirect interactions’ (Dill et al., 2003; Werner and Peacor, 2003). Behavior-mediated indirect interactions occur in manifold ecological communities with quantitatively significant effects on community dynamics, often exceeding the impact of density-mediated effects (reviewed in Werner and Peacor, 2003). Experimental analysis of behavior-mediated effects is often challenging due to difficulties of disentangling direct and indirect effects. Nevertheless, by using playbacks from a predator, the domestic dog, Suraci et al. (2016) could show that increases in fear reduce raccoon foraging on marine biota leading to cascading effects across multiple trophic levels in the intertidal food web. Thereby, fear of predators can act as an important ecosystem service that can structure communities and ecosystems (Ripple and Beschta, 2004).

To date, most studies on behavior-mediated effects of predators on their prey either focused on specific behavioral adaptations on the level of single individuals (e.g. Lima and Dill, 1990; Kotler et al., 1991; Jacob and Brown, 2000) or on consequences for other trophic levels (e.g. Beckerman et al., 1997; Dill et al., 2003). However, consequences of fear at the prey community level are largely unknown, despite their potential implications for conservation and management. Non-consumptive effects have been shown to have strong negative impacts on reproduction of the prey (Zanette et al., 2011) e.g. via maternal effects (Boonstra et al., 1998; Sheriff et al., 2010). Furthermore, non-consumptive effects can exist in prey communities even if direct predation is low or not present (Creel and Christianson, 2008). An understanding of community responses to predation risk and the underlying mechanisms behind them is therefore important to predict how changing predator abundance affects prey community structures.

In this study, we assessed the consequences of non-consumptive predator effects on prey community structure and composition. Given the challenge to scale up from the behavior of individuals to the whole community structure, we applied an individual-based mechanistic model of home range formation in a mammalian prey community where individual space use is based on the trade-off between food availability and predation risk. It extends a modelling approach by Buchmann et al. (2011) which has been successfully applied to explain community responses to habitat loss and fragmentation (Buchmann et al., 2013), the importance of individual foraging movement for community structure (Buchmann et al., 2012) and to generate realistic landscape patterns of biodiversity in the context of matrix suitability (Prevedello et al., 2016). The incorporation of fear in the model advances our understanding of the impact of predator-prey interactions on home range formation and the consequences for community structure and composition.

A key concept in our model is the premise that behavioral strategies of animals under predation risk can be expected to have consequences on prey community structure. Animals adjust the time they spend in local foraging patches and the amount of food they exploit from them in response to perceived predation risk. Animals can adopt different foraging strategies in order to minimize predation risk. Animals that use a risk-averse strategy reduce foraging in risky patches to decrease the probability of encountering a predator. To compensate for the reduced food intake in risky patches, animals increase foraging activities in safe patches. This adaptation in foraging activities represents a commonly observed pattern in many animals such as fish (Rozas and Odum, 1988; Werner et al., 1983) and small mammals (Jacob and Brown, 2000; Simonetti, 1989). For example, under the presence of owls several gerbil species increase their food intake in bush microhabitats in contrast to open habitats since they offer shelter from avian predators (Kotler et al., 1991). In contrast to the risk-averse foraging strategy, animals with a risk-taking foraging strategy utilize food resources both in risky and safe patches. Risk-taking animals reduce the probability of

predation in dangerous patches by using shorter foraging bouts. These animals frequently use refuges or return to their den in order to escape from a predator. An example for this strategy are birds that directly fly to cover when detecting a predator (Schneider, 1984). By implementing contrasting foraging strategies of prey animals (risk-averse and risk-taking) in the model we assessed a possible spectrum of consequences of different strategies on the prey community in concert with landscape of fear effects.

Additionally to the foraging strategy of prey animals under predation risk, refuge availability in the landscape plays an important role. If available, prey animals frequently use refuges in order to reduce predation risk (Lima and Dill, 1990). In aquatic systems, refuges are known to alter the impact of predation risk and can affect prey population dynamics and coexistence (Orrock et al., 2013). By varying the amount of refuges in the landscape we assessed how prey community structures are affected by refuge availability.

Based on these premises, we specifically aim to assess the following hypotheses: (1) Perceived predation risk in the landscape impacting individual space use in prey species can shape prey community structures. (2) The interplay between the availability of high-quality refuges and foraging strategies of prey animals is a driving mechanism of prey community responses to predation risk.

2. Methods

2.1. Model overview

The model simulates home range formation in a mammalian prey community based on food availability and perceived predation risk. It aims to gain a mechanistic understanding about space use behavior under fear and its consequences for community structure and composition. As our model focuses on the indirect effects of predation on space use, it does not include the direct effects of predator-induced mortality on individuals or communities over time. The model predicts how individual changes in behavior can affect the structure and composition of prey communities, in turn allowing us to predict how non-consumptive predator effects can alter prey community metrics. It extends a successfully validated modelling approach developed by Buchmann et al. (2011) by integrating landscapes of fear and different foraging strategies of animals under predation risk. A detailed model description following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2010, 2006) is provided in the Supplementary material, Appendix A. Here we only give an overview of the general model structure and processes.

The individual-based and spatially-explicit model includes two entities: (1) Landscape cells, which are described by their location, the amount of food resources they contain and the predation risk that animals perceive in this cell, and (2) prey individuals, which are characterized by their body mass and their foraging strategy under predation risk (Table 1). The body mass is used to calculate physiological traits such as energy requirements per day and movement costs of prey individuals via allometric relationships. In this study we focus on small, herbivorous mammals with a body mass ranging from 10 g to 1000 g. Predators are not modelled explicitly, but are represented by the predation risk in the landscape cells i. e. the landscape of fear. We assume generalist predators such as eagles, buzzards, foxes or lynxes.

2.2. Landscape design

The landscape is characterized by the distribution of food resources and predation risk. The whole landscape comprises 100×100 cells with each cell representing 4 m^2 . Landscape cells can be either productive, i.e. they contain food that can be consumed by animals or they are non-productive and do not contain food resources. We assume that 30% of the landscape cells contain food. Productive food cells are distributed randomly in the landscape. Each productive cell initially

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