Understanding predator-prey interactions: The role of fear in structuring prey communities

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Univ.-Diss.
zur Erlangung des akademischen Grades
"doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin "Ökologie"

eingereicht als publikationsbasierte Dissertation an der
Mathematisch-Naturwissenschaftlichen Fakultät
Institut für Biochemie und Biologie
der Universität Potsdam

Ort und Tag der Disputation: Potsdam, 28. Mai 2019
Hauptbetreuer/in: Prof. Dr. Florian Jeltsch
weitere Gutachter: Prof. Dr. Dries Bonte, Jun.Prof. Dr. Juliano Sarmento Cabral

Abstract

Predators can have numerical and behavioral effects on prey animals. While numerical effects are well explored, the impact of behavioral effects is unclear. Furthermore, behavioral effects are generally either analyzed with a focus on single individuals or with a focus on consequences for other trophic levels. Thereby, the impact of fear on the level of prey communities is overlooked, despite potential consequences for conservation and nature management. In order to improve our understanding of predator-prey interactions, an assessment of the consequences of fear in shaping prey community structures is crucial.

In this thesis, I evaluated how fear alters prey space use, community structure and composition, focusing on terrestrial mammals. By integrating landscapes of fear in an existing individual-based and spatially-explicit model, I simulated community assembly of prey animals via individual home range formation. The model comprises multiple hierarchical levels from individual home range behavior to patterns of prey community structure and composition. The mechanistic approach of the model allowed for the identification of underlying mechanism driving prey community responses under fear.

My results show that fear modified prey space use and community patterns. Under fear, prey animals shifted their home ranges towards safer areas of the landscape. Furthermore, fear decreased the total biomass and the diversity of the prey community and reinforced shifts in community composition towards smaller animals. These effects could be mediated by an increasing availability of refuges in the landscape. Under landscape changes, such as habitat loss and fragmentation, fear intensified negative effects on prey communities. Prey communities in risky environments were subject to a non-proportional diversity loss of up to 30% if fear was taken into account. Regarding habitat properties, I found that well-connected, large safe patches can reduce the negative consequences of habitat loss and fragmentation on prey communities. Including variation in risk perception between prey animals had consequences on prey space use. Animals with a high risk perception predominantly used safe areas of the landscape, while animals with a low risk perception preferred areas with a high food availability. On the community level, prey diversity was higher in heterogeneous landscapes of fear if individuals varied in their risk perception compared to scenarios in which all individuals had the same risk perception.

Overall, my findings give a first, comprehensive assessment of the role of fear in shaping prey communities. The linkage between individual home range behavior and patterns at the community level allows for a mechanistic understanding of the underlying processes. My results underline the importance of the structure of the landscape of fear as a key driver of prey community responses, especially if the habitat is threatened by landscape changes. Furthermore, I show that individual landscapes of fear can improve our understanding of the consequences of trait variation on community structures. Regarding conservation and nature management, my results support calls for modern conservation approaches that go beyond single species and address the protection of biotic interactions.

Zusammenfassung

Raubtiere beeinflussen ihre Beute durch die Verringerung der Anzahl (numerische Effekte) und durch das Hervorrufen von Verhaltensänderungen (Verhaltenseffekte). Während die Auswirkungen von numerischen Effekten gut erforscht sind, sind die Auswirkungen von Verhaltenseffekten unklar. Außerdem werden bei Verhaltensänderungen selten die Auswirkungen auf die Beutetiergemeinschaft betrachtet, sondern nur die Effekte auf einzelne Individuen bzw. Arten oder auf andere Stufen der Nahrungskette. Eine Betrachtung auf der Stufe der Beutetiergemeinschaft ist jedoch sehr wichtig, da nur so ein umfassendes Verständnis von Räuber-Beute-Gemeinschaften möglich ist.

In der vorliegenden Arbeit habe ich die Auswirkungen von Verhaltenseffekten auf die Raumnutzung und die Struktur von Beutetiergemeinschaften untersucht. Dazu habe ich ein räumliches Modell benutzt, welches die Bildung von Beutetiergemeinschaften über den individuellen Aufbau von Aktionsräumen der Beutetiere simuliert. Die Einrichtung von Aktionsräumen basiert dabei auf der Nahrungsverfügbarkeit in der Landschaft und auf dem vom Beutetier wahrgenommenen Risiko von einem Räuber gefressen zu werden. Die räumliche Verteilung des wahrgenommenen Risikos wird auch als Landschaft der Angst bezeichnet.

Meine Ergebnisse zeigen, dass sich die Raumnutzung und die Struktur der Beutetiergemeinschaft durch Verhaltenseffekte verändern. Unter dem Einfluss von Angst haben die Beutetiere ihre Aktionsräume in sicherere Bereiche der Landschaft verlegt. Außerdem hat sich in risikoreichen Landschaften die Vielfalt der Beutetiere verringert und die Zusammensetzung zu Arten mit einem geringen Körpergewicht verschoben. Wenn die Beutetiergemeinschaft Landschaftsveränderungen wie z.B. dem Verlust oder der Zerschneidung von Lebensraum ausgesetzt war, haben sich die Auswirkungen von Verhaltenseffekten weiter verstärkt. Durch eine Erhöhung der Größe und Anzahl von Rückzugsräumen, die nicht von Räubern erreicht werden können, sowie deren Verbindung in der Landschaft, kann die Stärke dieser Effekte jedoch begrenzt werden. In einem weiteren Schritt habe ich die Auswirkungen von Unterschieden in der Risikowahrnehmung zwischen Individuen untersucht. Diese Unterschiede haben dazu geführt, dass Tiere mit einer hohen Risikowahrnehmung sich ihren Aktionsraum vornehmlich in sicheren Bereichen gesucht haben, während Tiere mit einer geringen Risikowahrnehmung Bereiche mit einer hohen Nahrungsverfügbarkeit genutzt haben. Dadurch konnten sich in Landschaften mit unterschiedlichen Risiken, vielfältigere Beutetiergemeinschaften etablieren, als in Landschaften mit gleichmäßigem Risiko.

Insgesamt geben meine Ergebnisse einen guten Überblick über die Auswirkungen von Verhaltenseffekten auf Beutetiergemeinschaften. Die Verknüpfung von individuellem Verhalten mit Mustern auf der Gemeinschaftsebene erlaubt es die zugrundeliegenden Mechanismen zu identifizieren und zu verstehen. In Bezug auf den Naturschutz unterstützen meine Ergebnisse den Ruf nach modernen Schutzmaßnahmen, die über den Erhalt von einzelnen Arten hinausgehen und den Schutz von Beziehungen zwischen Arten einbeziehen.

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CHAPTER 1

General introduction

1.1 Community ecology and predator-prey interactions

The goal of community ecology is to understand the patterns in the coexistence of species in space and time and the underlying processes (Vellend, 2010). A key driver of community structures are biotic interactions, especially predator-prey interactions (Tylianakis et al., 2008; Tylianakis et al., 2010; Valiente-Banuet et al., 2015). Predator-prey interactions are ubiquitous in ecosystems and have important consequences on all scales, from individual behavior and population cycles to community dynamics, trophic cascades and ecosystem functioning (Barbosa and Castellanos, 2005). An understanding of predator-prey interactions is also crucial for conservation and nature management due to their key role in sustaining biodiversity and potential utility in ecosystem restoration, for example by mitigating negative effects of invasive species (Ritchie and Johnson, 2009; Ritchie et al., 2012).

A major focus has been on the effects of predators on other species. They can be divided into two categories, numerical and behavioral effects (Fig. 1.1). Numerical effects describe the direct killing of the prey by the predator, decreasing prey abundance. These changes in prey demographics can have further, indirect consequences for other species which are called density-mediated indirect effects (Wootton, 1994). In comparison, behavioral effects do not directly change prey abundance but modify the traits of the prey (Brown et al., 1999; Lima, 1998). Examples for such effects are alterations in vigilance behavior (Childress and Lung, 2003; Hunter and Skinner, 1998), movement patterns (Fortin et al., 2005; Sih and McCarthy, 2002; Stich and Lampert, 1981) or group size (Barta et al., 2004; Creel and Winnie,

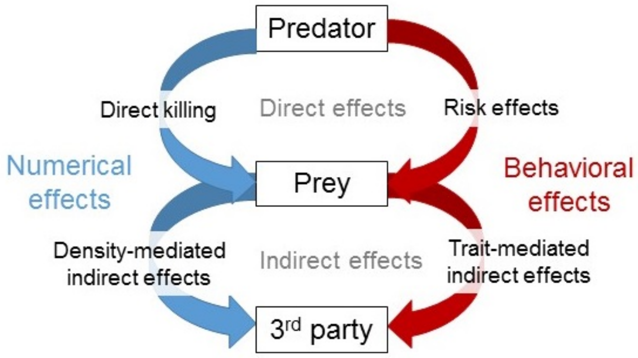

Fig. 1.1. Classification of predation effects. Numerical effects (left) operate through changes in prey abundance, behavioral effects (right) through changes in prey behavior. Direct effects of the predator on the prey can indirectly affect other third party species. The figure was modified from Creel and Christianson (2008)

2005). Even though these risk effects do not directly impact prey abundance, the costs of antipredatory behavior reduce prey fitness with consequences on prey demographics (Creel and Christianson, 2008; Zanette et al., 2011). Similar to numerical effects, behavioral effects can influence other species via trait-mediated indirect effects (Werner and Peacor, 2003).

Traditionally, research has focused on numerical effects of predators on prey. However, more recent studies have shown that behavioral effects are a significant driver of community dynamics, probably being more dominant than numerical effects in driving trophic interactions (Peacor and Werner, 2001; Preisser et al., 2005; Werner and Peacor, 2003). Due to their importance in shaping community structures, behavioral effects have been studied in various fields of animal ecology, from antipredatory decision-making to trophic cascades.

1.2 Behavioral effects of predators

1.2.1 Risk effects

The presence of predators poses a predation risk to the prey. This predation risk is not homogeneous but differs in space and time because predators have specific activity phases and prefer specific areas for predation (Lima, 1998). Thus, the prey animal can reduce its predation risk by avoiding areas or times of high risk. This antipredatory decision-making has mostly been investigated in the context of foraging (Lima and Dill, 1990). When foraging under predation risk, animals often face the dilemma that high-quality food is mostly available in risky areas while safe areas only offer low-quality food (McArthur et al., 2014). Therefore, animals need to tradeoff between food and shelter (Brown et al., 1999).

For temporal variation in risk, the risk allocation hypothesis states that the highest antipredatory effort of animals should be exhibited in short and infrequent high-risk situations and that foraging activities should be shifted to pulses of low risk (Lima and Bednekoff, 1999). However, if the prey faces a situation with continuously high risk, antipredatory behaviour should decrease as other activities cannot be postponed infinitely (Lima and Bednekoff, 1999). This hypothesis has been tested in numerous empirical studies, but most of them only partially support the hypothesis (reviewed in Ferrari et al., 2009). For example, roe deer show an increased vigilance during pulses of high risk, but do not decrease their antipredatory behavior under continuously elevated predation risk (Eccard et al., 2017). Possible reasons for differences in the outcome could be variation in the energetic state of the prey or imperfect information about the presence of the predator (Luttbeg, 2017).

Regarding spatial variation in predation risk, the concept of the "landscape of fear" has been used to improve our understanding of prey space use (Laundré et al., 2001; Laundré et al., 2010). The landscape of fear is a map that visualizes the spatial distribution of predation risk that prey animals perceive (Laundré et al., 2001; Laundré et al., 2010). Such maps have been quantified for various taxa such as ungulates (Iribarren and Kotler, 2012), rodents (van der Merwe and Brown, 2008), monkeys (Willems and Hill, 2009) and marine mammals (Wirsing et al., 2008). In combination with energy landscapes, which visualize movement costs, landscapes of fear support a mechanistic understanding and allow for a prediction of animal movement decisions (Gallagher et al., 2017). Furthermore, landscapes of fear can help to understand the role of bottom-up and top-down effects on prey population dynamics (Laundré et al., 2014)

1.2.2 Trait-mediated indirect effects

Trait-mediated indirect effects describe the interaction between three species: One species alters its phenotype due to the presence of another species and this change has consequences on a third species (definition following Abrams, 1995). A subgroup of trait-mediated indirect interactions are behavior-mediated indirect interactions where alterations in the behavior of the responding species due to the presence of another species affect the interaction with a third species (Dill et al., 2003). Since many prey species respond with behavioral adaptations to the presence of a predator, I will here focus on behavior-mediated indirect interactions.

Behavior-mediated indirect interactions are commonly found in ecological communities (Dill et al., 2003; Werner and Peacor, 2003). For example, Turner et al. (2000) experimentally tested the consequences of predatory fish on freshwater snails and their periphyton resources. Fish were caged in order to exclude any numerical effects of the predator. The presence of fish led to an increased use of covered areas by freshwater snails. Thus, periphyton abundance decreased in the covered areas, while it increased in areas that were avoided by snails. Similar interactions were reported for other systems, e.g. for fish, mayflies and algae (McIntosh and Townsend, 1996) or spiders, grasshoppers and grass (Schmitz et al., 1997). Although these studies demonstrate the existence of behavior-mediated indirect interactions, the studied systems are biased towards aquatic systems and invertebrates (Schmitz et al., 2004), probably due to easier manipulation of these systems.

Nevertheless, the role of behavior-mediated indirect interactions has also been acknowledged for terrestrial systems with large carnivores (Ripple and Beschta, 2004). Observations from systems where large carnivores have been extirpated have underlined the importance of top predators in structuring ecosystems and sustaining biodiversity as well as their potential to induce trophic cascades (Estes et al., 2011). One of the most famous examples for a trophic cascade induced by behavior-mediated indirect interactions is the system of wolves and elk in the Yellowstone National Park (Ripple and Beschta, 2004). When wolves were absent, elk foraging movement was not restricted by predation risk and led to a strong reduction in the vegetation. These changes in the vegetation modified the habitat for many species, especially in riparian habitat and have been correlated to a reduction in beaver abundance (Ripple and Beschta, 2012). With the reintroduction of wolves, elk restricted their movement to areas with high cover, allowing for an increased recruitment of woody species in the now unused risky areas (Fortin et al., 2005; Laundré et al., 2010; Ripple et al., 2001). This example shows that the presence of the predator and the landscape of fear they induce can structure an ecosystem and sustain diversity.

However, due to the observational character of the study and the lack of a control, it is often questioned whether fear really is the reason for the changes in the Yellowstone ecosystem, as alternative hypotheses might explain the alterations in ecosystem structure (e.g. Kauffman et al., 2010). To overcome these deficiencies, Suraci et al. (2016) developed an experiment in which they manipulated fear by using playbacks of large predators. They showed that these playbacks led to changes in the foraging behavior of a mesopredator, the raccoon. These changes in the foraging behavior of raccoons had further consequences on raccoon prey species, increasing their abundance and modifying interactions of prey species with other competitive species. Thereby, the study by Suraci et al. (2016) provided an experimental evidence for the key role of large carnivores in structuring ecosystems, controlling mesopredators and sustaining biodiversity. Additionally, it supports calls for the conservation of apex predators in ecosystems around the world (Doherty et al., 2015; Estes et al., 2011; Ripple et al., 2014; Ritchie et al., 2012).

1.3 Factors influencing behavioral effects

1.3.1 External factors

Behavioral responses of prey towards predation risk are strongly affected by habitat heterogeneity (Gorini et al., 2012). An important driver is the availability of safe places, i.e. refuges in which the risk of predation is reduced (Lima, 1998). For example, the survival of juvenile perch strongly increased with the availability of refuges in their habitat (Persson and Eklöv, 1995). Beside the availability, the quality of refuges plays an important role, since it drives the strength of competition between prey animals that use the refuge (Donelan et al., 2017; Orrock et al., 2013). For instance, tissue growth of snails increased with refuge quality as competition for food with other snails decreased (Donelan et al., 2017). Overall, refuge use has been shown to affect prey behavior (Stankowich and Blumstein, 2005), population dynamics (Cooper et al., 2007) and the strength of trophic cascades (Grabowski, 2004).

The availability and quality of refuges in many habitats is threatened by habitat loss and fragmentation. Such landscape changes are known to be one of the main reasons for biodiversity loss (e.g. Newbold et al., 2015; Schipper et al., 2008) but also affect species interactions such as the interactions between predator and prey (Tylianakis et al., 2010; Valiente-Banuet et al., 2015). The direction of the impact of habitat loss and fragmentation on predator-prey interactions strongly depends on the specialization of the predator (Ryall and Fahrig, 2006). For example, generalist and omnivorous predator species are expected to be less affected by landscape changes compared to the focal prey species, thus habitat loss and fragmentation lead to an increased predation risk for the prey (Swihart et al., 2001). In contrast, specialist predators are supposed to be more vulnerable to extinction and will therefore decrease when facing landscape changes, releasing prey species from predation pressure (Crooks and Soulé, 1999). In case of mesopredators, such a release from predation pressure can have strong consequences on the survival of their prey species (Crooks and Soulé, 1999; Elmhagen and Rushton, 2007).

Additionally to landscape changes, humans can impact prey behavioral responses more directly by inducing their own landscape of fear. Besides the predation risk of natural predators, many large mammals face the risk of hunting by humans (Darimont et al., 2015; Dorresteijn et al., 2015). For example, during hunting season, wild boars shifted their home ranges closer to a reserve where hunting was forbidden to reduce their hunting risk (Tolon et al., 2009). Another study on roe deer showed that prey animals often need to balance contrasting patterns of predation risk induced by natural predators and humans (Lone et al., 2014). Additionally, humans can impact the animal's landscape of fear via other activities such as hiking, traffic and land-use (Ciuti et al., 2012; Kays et al., 2016). Such examples underline that multiple threats need to be investigated to understand behavioral responses of prey facing risk from natural predators and human activities.

1.3.2 Internal factors

Additional to external factors, internal factors can influence the behavioral responses of prey animals towards predation risk. An important driver for animal movement decisions is the internal state of the animal (Nathan et al., 2008). For foraging under predation risk, numerous studies have shown that the level of hunger is a key driver of the animal's risk-taking behavior (e.g. Kohler and McPeek, 1989; Murray, 2002; Pettersson and Brönmark, 1993). For example, threespine sticklebacks (*Gasterosteus aculeatus*) expose themselves to a higher predation risk when they are hungry compared to well-fed sticklebacks. Further drivers of differences in behavioral responses are age (e.g. Réale and Festa-Bianchet, 2003), sex (e.g. Fitzgibbon, 1990) or the body size of the animal (e.g. Preisser and Orrock, 2012; Urban, 2007a).

Another source of variation in risk behavior is animal personality. Many animals show consistent individual differences in their response towards predation risk as part of their behavioral type (Sih, 2004; Wolf and Weissing, 2012). For instance, bold lizards used refuges only shortly while shy lizards spent longer times in the refuge after a predatory approach (López et al., 2005). Specialization of animals to specific risk environments can help to reduce competition with conspecifics (Wilson, 1998). Moreover, consistent individual differences are supposed to have ecological implications influencing population growth, species interactions and community dynamics (Wolf and Weissing, 2012).

1.4 Consequences of behavioral effects on prey communities

When Brown et al. (1999) introduced the concept of the "ecology of fear", their focus was on the population- and community-level consequences of prey and predator's optimal behavior. However, behavioral effects of predators have mostly been investigated on the level of prey individuals (see section 1.2.1) or on the consequences of behavioral responses on other species (see section 1.2.2). Consequences of fear on the level of prey community are largely unknown, although they have important implications for conservation and management (Creel and Christianson, 2008).

One explanation for the lack of studies on the community level could be the higher effort of experimental testing of several species at the same time compared to the testing of single species. Furthermore, experimental conditions might need to be adapted to the specific traits of animals. For example, when measuring the giving-up density, species differ in their preferences regarding food quality, physical characteristics and substrate types (Bedoya-Perez et al., 2013). Thus, food types would need to be adapted to different species.

One solution to solve these experimental challenges is the usage of theoretical models. Theoretical models have formed the basis of research in predator-prey interactions, yielding influential models such as the Lotka-Volterra equations and allowed to gain new insights (Berryman, 1992). In the context of fear, individual-based models are especially useful, since they allow for a mechanistic understanding of community patterns based on individual-level behavior (Grimm et al., 2017). Furthermore, a model addressing the consequences of fear on prey communities should include a spatial component as habitat heterogeneity can be a key driver of prey behavior (Gorini et al., 2012).

1.4.1 Model structure

In order to assess the consequences of fear on prey community structure, I used an established model by Buchmann et al. (2011). The original individual-based and spatially-explicit model simulates animal community structure and composition via individual home range formation based on food resource availability. It has been successfully validated to yield realistic community structures of terrestrial mammals (Buchmann et al., 2011). Furthermore, it has been used to explain community responses to habitat loss and fragmentation (Buchmann et al., 2012), the role of individual foraging movement in shaping community structures (Buchmann et al., 2013) and to generate realistic patterns of biodiversity in the context of matrix suitability (Prevedello et al., 2016).

I made use of the modeling approach by Buchmann et al. (2011) and extended it by incorporating landscapes of fear. Landscapes of fear affect animal behavior during home range formation. Animals need to balance their often contrasting demands for food and safety, leading to modifications in home range establishment. These behavioral effects can then result in changes in prey community structure and composition.

In general, the model consists of three steps (Fig. 1.2):

(1) After the generation of the landscape, a prey individual is drawn from the regional species pool. Thereby, the animal gets assigned an individiual body mass. Based on this body mass, further allometric traits such as feeding rate and movement costs are calculated. Depending on the focus of the study, further traits can be assigned, such as foraging strategy (Chapter 2) or magnitude of risk perception (Chapter 4).

(2) The newly drawn prey individual consequently searches for a home range in the landscape. The home range has to fulfill the daily energy requirements of the animal. For the addition of cells to the home range, the animal tradeoffs the potential food gain

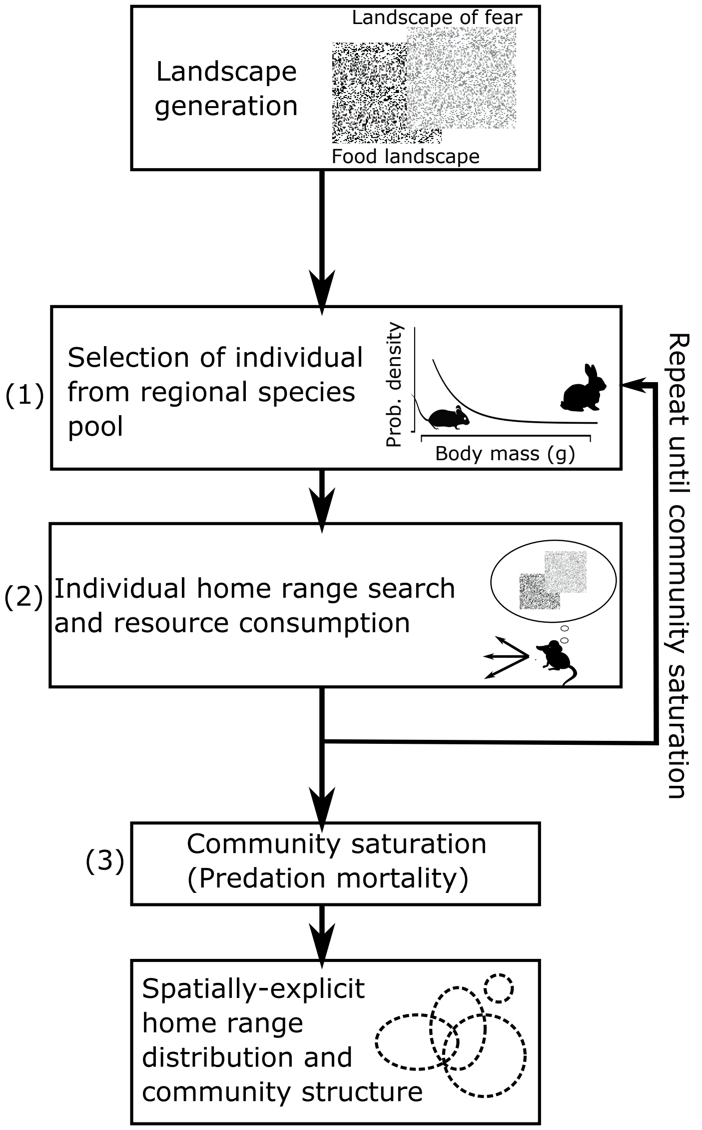

Fig. 1.2. Overview of the main elements of the model that was applied to assess the consequences of fear on prey communities. See the referring numbers in the text for further explanation of the processes. This figure was modified from Buchmann et al. (2011).

with the perceived predation risk and movement costs. This tradeoff can be influenced by the animal's traits such as its individual risk perception (Chapter 4). If the animal found a suitable home range in the landscape, it settles down and consumes the resources within the home range. If the home range search was not successful, the animal is excluded from the community.

(3) The first and second step are repeated until the community is saturated, i.e. a specific number of animals consecutively failed to establish a home range in the landscape. Optionally, the process predation mortality (Chapter 4) can be executed after community saturation. In this process, animals are killed by a predator based on the safety of their home range.

After community saturation, the simulation is terminated and the spatial structure and composition of the prey community can be evaluated.

With the model, numerous parameters can easily be varied. For example, prey community structures for different configurations of the landscape of fear can be assessed. Furthermore, individual traits of prey animals can be manipulated. Thereby, the model offers a unique opportunity to assess the complex consequences of risk effects on prey community structure.

1.5 Research objectives and structure of this thesis

The goal of this thesis is to assess the role of fear in shaping prey communities. By using the model described in paragraph 1.4.1, I evaluated the consequences of fear on prey home range formation and on prey community patterns. I assessed these consequences in two steps. Firstly, I evaluated the general consequences of fear on the prey community and identified two major drivers of prey community responses. Secondly, I further investigated these drivers.

My findings are summarized in three independently readable research articles (Chapter 2-4). In all articles, I was the lead author. I was predominantly responsible for the development of the study design, implementation and extension of the modelling approach by Buchmann et al. (2011), conducting of the simulation, data analysis and manuscript writing. All articles contain suggestions from the co-authors. The first article (Chapter 2) additionally contains suggestions from two independent reviewers of the journal. All articles are written in first-person plural due to the involvement of co-authors.

My first article entitled "Community consequences of foraging under fear" was published in the journal *Ecological Modelling* 383, 80-90 in 2018. In this article (Chapter 2), I assessed the general consequences of fear on prey space use and prey community structure. Prey animals adapted their home range formation under fear resulting in changes in prey community structure and composition. Prey community responses to fear were mainly driven by two mechanisms: refuge availability and foraging strategy of the animal. Increasing refuge availability allowed the animals to use larger parts of the landscape and had positive effects on prey diversity and total biomass of the prey community. Furthermore, the number of large animals that was able to establish a home range and persist in the community increased with refuge availability. Prey foraging strategies affected community composition with regard to the evenness. Under medium refuge availability, risk-averse prey communities showed an uneven distribution that was shifted towards smaller animals. In contrast, risk-taking prey communities showed a more even body mass distribution. Overall, this study revealed that fear has important implications for prey space use and community structure including diversity and should be considered in regard to conservation and nature management.

My second article entitled "The risk of ignoring fear: Underestimating habitat loss effects on biodiversity" is currently under review at *Ecography*. In this article (Chapter 3), I investigated the consequences of landscape structure on prey community responses to fear. Since my first study showed that refuge availability can be an important driver of prey community structure, I assessed this in more detail in the second article. The focus was on the effects of landscape changes such as fragmentation and habitat loss. I used different combinations of food landscapes and landscapes of fear with varying degree of habitat loss and fragmentation and evaluated prey community responses to these landscape changes. The results revealed that negative effects of habitat loss and fragmentation on prey communities are intensified by fear, resulting in a non-proportional diversity loss of up to 30% and reinforcing shifts in community composition from large to small animals. Regarding habitat properties, the highest diversity was supported in landscapes with a high food and shelter availability and low fragmentation degree. Furthermore, the availability of shelter promoted a higher stability in species diversity to changes in habitat quality. The findings highlight the importance of fear in shaping prey community structures under conditions of landscape change and reveal the key role played by the spatial distribution of safe patches in mitigating the negative effects of landscape changes. In the context of nature management, the results support modern conservation efforts that go beyond single-species approaches by taking impending changes in species interactions into account.

My third article entitled "Individual landscapes of fear: Intra- and interspecific differences in risk perception modify space use, survival probability and prey community structure" is ready for submission. In this article (Chapter 4), I focused on the consequences of intra- and interspecific variation in the landscape of fear on prey community structure. While I assumed the same landscape of fear for all animals in the prey community in my previous articles, I included now individual variation in risk perception in the model which leads to different landscapes of fear for individual prey animals. I assessed how different distributions of risk perception in the prey community affected prey space use and community structure by using varying configurations of the landscape of fear. I compared these community responses to prey communities without variation in risk perception. In prey communities with individual variation I found an adaptation in space use leading to a spatial segregation between animals with different degrees of risk perception. In these communities, animals with a high risk perception used safer home ranges and had a higher survival probability compared to animals with a low risk perception and to animals in communities without variation in risk perception. On the community level, communities with variation in risk perception showed an increased diversity compared to communities without variation for heterogeneous landscapes of fear. In risky and safe landscapes of fear, the proportion of animals with a risk perception that was adapted to the conditions in the landscape was the main driver of diversity. In risky landscapes diversity of the prey community increased with the proportion of animals with a low risk perception in the prey community, while in safe landscapes diversity increased with the proportion of animals with a high risk perception. These findings provide a first assessment of the consequences of intra- and interspecific differences in risk perception on prey community structure. Thereby, they offer new insights in the consequences of predator-prey interactions and underline the importance of including individual trait variation in community ecology.

The thesis concludes with a general discussion of my findings (Chapter 5). I synthesize my findings, integrate them into existing concepts and frameworks and compare them to empirical findings. Furthermore, I discuss the implications of my findings regarding nature conservation and management and give an outlook on future directions in predator-prey research.

CHAPTER 2

Prey community responses to fear

Title	Community consequences of foraging under fear
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Journal	*Ecological Modelling* 383, 80-90
Date of submission	Received 6 March 2018; Revised 15 May 2018; Accepted 15 May 2018; Published 10 September 2018
Status	Published
Keywords	Predator-prey interactions, Individual-based model, Landscape of fear, Home range, Biodiversity, Foraging

2.1 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.

2.2 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., 2001; Laundré et al., 2010). 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 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. Jacob and Brown, 2000; Kotler et al., 1991; Lima and Dill, 1990) 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.

2.3 Methods

2.3.1 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., 2006; Grimm et al., 2010) is provided in the Supplementary material, Appendix A.1. 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 2.1). 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.

TABLE 2.1: Entities and their state variables

Entity *State variable*	Unit	Description
Landscape cells		
p-food	Dry biomass, $g/(\text{cell} \cdot \text{day})$	Food resource availability in cell
p-safety	-	Safety of a cell, inverse to predation risk
Individuals		
i-bodymass	g	Body mass of individual
i-feartype	-	Foraging strategy of individual under predation risk
Allometric traits:		
i-feedrate	Dry biomass, g/day	Amount of food resources that need at least be contained in the home range
i-lococost	Dry biomass, g/cell	Locomotion costs for moving one cell forward
i-maxhr	cells	Maximum home range size
i-foodshare	-	Defines magnitude of food resource exploitation

2.3.2 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 $4\,\text{m}^2$. 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 contains food resources reflecting the average daily productivity in grass- and shrublands ($0.685\,\text{g}/(\text{m}^2 \cdot \text{day})$ Whittaker, 1975). From these food resources, we assume that 80% of the food resources are lost to other taxonomic groups or not suitable for animal consumption so that only 20% of the average daily productivity can be used by prey animals (see Buchmann et al., 2011, for further discussion on this value). Food resources are exploited by animals during the simulation and do not refill. Besides food resources, cells either have a high perceived predation risk (*p-safety*=0.1) or a low perceived predation risk (*p-safety*=0.9). All non-productive cells have a high perceived predation risk because we assume that a lack of vegetation corresponds with high perceived predation risk. This corresponds to landscapes in which animals have to cope with areas of hostile matrix in their home ranges which is typical for human-dominated landscapes such as clear-cuts in forests.

Productive cells can have a high or a low perceived risk of predation. In the following, we use the term "risky habitat" for productive cells with a high perceived predation risk and "refuge" for productive cells with a low perceived predation risk. The proportion of refuges is a systematically tested model parameter. The distribution of perceived predation risk in the landscape represents the landscape of fear for the prey animals. We assume that the landscape of fear is static, i.e. the predation risk in the cells does not change during the simulation.

2.3.3 Foraging strategies

In the model we implemented two highly contrasting foraging strategies in separate model runs to explore a possible spectrum of consequences of different strategies on the prey community. We assume that individuals of both foraging strategies are central place foragers frequently returning to a central place, their den. The den is an absolute refuge where individuals do not face predation risk. Foraging strategies were tested separately, i.e. all individuals in a community had the same strategy. Moreover, we compared the two contrasting foraging strategies to a control foraging strategy in which animals do not respond to predation risk in the landscape, i.e. their food intake only depends on food availability and physiological constraints. The rationale of these two strategies is described in the following; their implementation is described below, in the process home range formation.

The foraging strategy of risk-averse individuals focuses on adaptations in food intake between patches with different predation risk. Risk-averse animals show a reduced food intake in risky habitat to minimize the time they are exposed to this high risk. To compensate the lower food intake under high risk, they forage more intensively in refuges and show an increased food intake in these patches compared to control individuals. These animals are facing indirect costs of their antipredatory behavior via the costs of missed opportunities. Risk-taking individuals deal with predation risk by adapting their activity patterns. In risky habitat, risk-taking animals show short foraging bouts with frequent returns to the den and hiding in refuges in order to minimize encounters with a predator. This behavior increases the energy costs of risk-taking animals in risky habitat. To cover the increased movement costs, they need to exploit more food resources to fulfill their daily energy requirements. In refuges, risk-taking individuals have the same activity patterns as animals of the control.

The two foraging strategies represent simplified behavioral strategies of animals foraging under predation risk. The risk-averse foraging strategy allows to explore the consequences of adaptations in food intake under perceived predation risk on prey communities while the risk-taking strategy focuses on consequences of increased movement costs due to perceived predation risk. By using these extreme and contrasting examples, we intend to gain a first overview of the spectrum of consequences that different foraging strategies have on prey community structures.

2.3.4 Process scheduling

Each simulation starts with the generation of a new landscape with a specific distribution of food and perceived predation risk. After the generation of the landscape, in each step of the model one additional new prey individual characterized by its body mass and foraging strategy searches for a home range in the landscape. The home range has to contain enough food resources to fulfill the animal's energy requirements. If the individual finds a suitable home range, it exploits the food resources within the home range. Otherwise, the individual is excluded from the community, we assume that the individual disperses to another area outside the simulated landscape or dies. Existing individuals in the landscape are not affected by newly added individuals. The simulation continues until the community is saturated, i.e. 100 individuals (parameter "nfail", see Supplementary material, Appendix A.1, Table A.2) have consecutively not been able to establish a home range in the landscape because they could not reach their energy requirements. In the following, we briefly describe the processes within the model (see Fig. 2.1 for an overview of processes in the model).

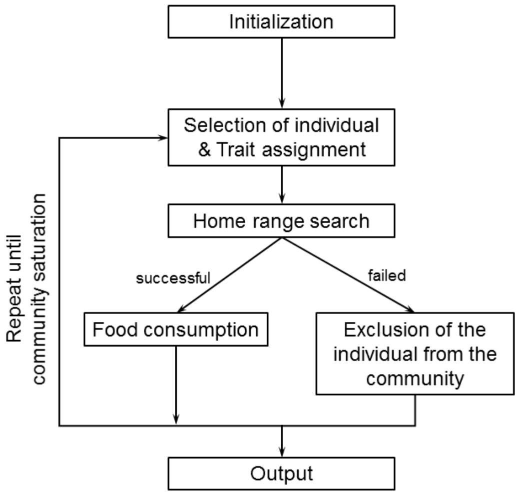

Fig. 2.1. Schematic overview of processes in the model. After initialization, a new individual is created and gets assigned certain traits. This individual searches for a home range in the landscape that fulfills its daily energy requirements. The addition of cells to the home range is based on food availability and perceived predation risk in cells. If the home range search is successful, the individual consumes the food resources within, otherwise it is excluded from the community. These steps are repeated until the community is saturated.

2.3.5 Trait assignment

In each model step a new prey individual characterized by its body mass and foraging strategy is created. The body mass of the new individual is drawn from a "body mass input distribution", a truncated power-law distribution with an exponent of -1.5 (see Supplementary material, Appendix A.1, Table A.2). This specific exponent was chosen since it yields realistic community structures (Buchmann et al., 2011; Buchmann et al., 2012). On the basis of the body mass further traits of the animal are calculated by using allometric relationships, namely the feeding rate, locomotion costs, maximum home range size and the share of food resources that is available to an animal per grid cell (see Supplementary material, Appendix A.1, Table A.3). In addition to body mass, individuals are attributed a foraging strategy: either risk-averse, risk-taking, or control.

2.3.6 Home range search and food consumption

The key process of the model is the home range search of the newly created prey individual. The home range needs to contain enough food resources to cover the individual's daily feeding rate and movement costs for foraging within the home range. Individuals are central place foragers frequently returning to a central place, their den, within their home range. This is implicitly represented in the model by calculating the movement costs for the distance to a cell and the return.

The home range search starts with the choice of a core cell, the central place of the home range where the den of the individual is located. This cell is chosen randomly from the pool of productive cells. The addition of a cell to the home range consists of two steps, the choice of which cell is added and the calculation of the food gain from the cell. The cell that is added next to the home range is chosen from the neighboring cells of the cell that was added last to the home range. We assume that the animal has a perceptual range of one cell, i.e. it can sense the food availability and the predation risk in the eight neighboring cells. For the decision, which of these cells is added to the home range the suitability of a cell is calculated by the product of food availability and predation risk:

$$\text{Suitability} = \textit{p-food} \cdot \textit{p-safety} \tag{2.1}$$

The cell with the highest suitability is added to the home range. For the control, only the food availability is taken into account (Suitability = *p-food*). If several cells have the same suitability, the cell with the minimum distance to the core is chosen. After the decision for a cell, the food gain from this cell is calculated. The food gain is the difference between the exploited food and the movement costs:

$$\text{Food gain} = \text{Exploited food} - \text{Movement costs} \tag{2.2}$$

For the control and the risk-taking individuals the amount of exploited food is the arithmetic product of food availability in the cell (*p-food*) and the allometric magnitude of food exploitation (*i-foodshare*).

$$\text{Exploited food} = \textit{p-food} \cdot \textit{i-foodshare} \tag{2.3}$$

For risk-averse individuals predation risk (*p-safety*) additionally affects food intake.

$$\text{Exploited food} = \textit{p-food} \cdot \textit{i-foodshare} \cdot 2 \cdot \textit{p-safety} \tag{2.4}$$

The factor 2 was chosen so that the food intake at a medium predation risk ($\textit{p-safety} = 0.5$) equals the food intake of the control. In safe cells ($\textit{p-safety} > 0.5$), risk-averse animals have a higher food intake than risk-taking and control animals whereas their food intake is reduced in dangerous cells ($\textit{p-safety} < 0.5$). The factor *i-foodshare* leads to different feeding efficiencies in mammals depending on their body size.

For control and risk-averse individuals movement costs are the product of the allometric costs (*i-lococost*) and twice the distance to the core cell ($distance_{core}$) as the individual has to move to the foraging cell and back to the central place.

$$\text{Movement costs} = 2 \cdot \textit{i-lococost} \cdot distance_{core} \tag{2.5}$$

Risk-taking individuals have the same movement costs when predation risk is low (i.e. $\textit{p-safety} \geq 0.5$). However, high predation risk ($\textit{p-safety} < 0.5$) causes additional movement costs for risk-taking individuals:

$$\text{Movement costs} = 2 \cdot \textit{i-lococost} \cdot distance_{core} + \textit{p-food} \cdot \textit{i-foodshare} \cdot (1 - 2 \cdot \textit{p-safety}) \tag{2.6}$$

Movement costs in risk-taking individuals thus increase depending on the amount of food in the cell. We assume that the higher the food intake the more often the individual interrupts foraging to return to the den. Furthermore, movement costs in this case can also include costs of other adapted behavior not related to movement such as increased vigilance. Exemplary calculations for the different foraging types during home range search are shown in Supplementary material, Appendix A.1, Table A.4.

If after adding a cell the food gain from the home range meets the daily energy requirements of the animal and the movement costs, the home range search was considered successful and the individual establishes its home range in these cells. If the amount of cells exceeds the maximum home range size before the energy requirements are achieved, the individual fails to find a home range and is excluded from the community, i.e. we assume that it disperses to another area outside the simulated landscape or dies. If the home range search was successful, food resources (*p-food*) of cells within the home range are reduced by the amount of exploited food calculated during the home range search. Due to fractal characteristics of food resources, animals only exploit a share of the available food resources in a grid cell and do not deplete food resources completely. Therefore, the individuals entering subsequently are able to include cells that already have been exploited, leading to overlapping home ranges. A visual representation of exemplary home ranges for animals with different foraging strategies is shown in Fig. 2.2.

2.3.7 Community saturation

As the simulation progresses, an increasing number of individuals establish home ranges and deplete food resources within the landscape. This reduction in available food means that new individuals are less likely to establish home ranges. Thus, the community becomes saturated. Simulations were stopped if 100 individuals have consecutively not been able to find a home range. The sequential failure of individuals indicates that most accessible food resources in the landscape have been exploited and a further establishment of home ranges was not possible.

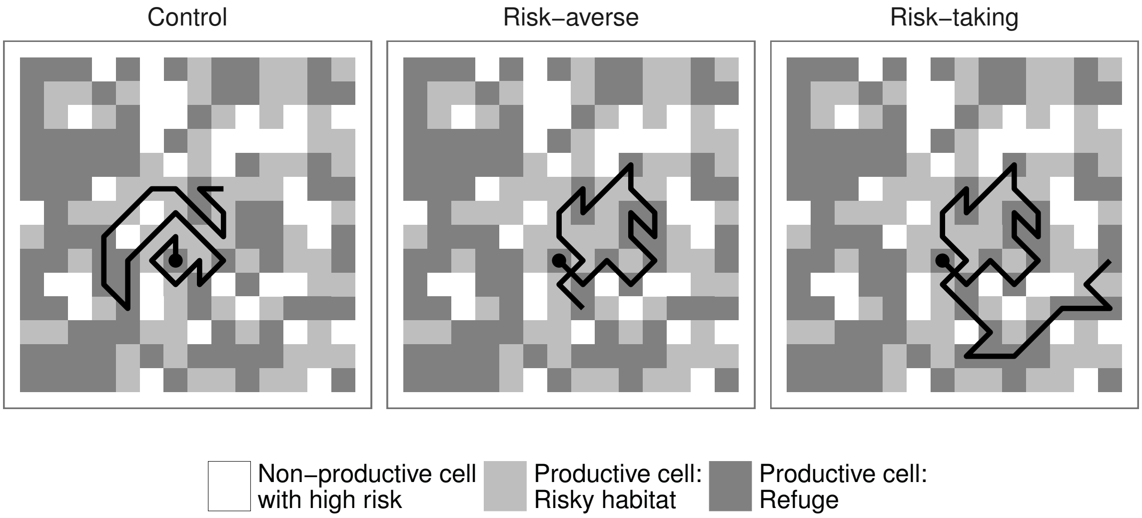

Fig. 2.2. Example of individuals with a body mass of 50 g accumulating cells to their home range. The black dot marks the home range center, the line marks the cells that the individual one after the other adds to its home range. Risk-averse and risk-taking animals both prefer refuges but differ in the food intake and movement costs per cell, resulting in the addition of more cells to the home range for risk-taking animals. For the landscape a proportion of 50% refuges was chosen. All productive cells contained the same amount of food resources, 0.548 g dry biomass per cell.

2.3.8 Design and analyses of simulation experiments

All simulations were conducted in Netlogo 5.3.1 (Wilensky, 1999). To compare the effect of different foraging strategies with a control foraging strategy we performed simulations for risk-averse, risk-taking and control prey communities. All individuals in one simulation had the same foraging strategy. Furthermore, we varied the proportion of refuges in the landscape (from 0 to 1, with an interval of 0.1). 30 repetitions were performed for each combination of foraging strategy and landscape configuration. Model output included body mass, size and location of individuals that successfully established a home range in the landscape and food availability in the landscape cells at the end of the simulation. To analyze the effect of body mass, initial food availability in the landscape and the proportion of refuges on the home range size we made additional simulations where only one individual established a home range in the landscape. We varied the body mass of the individual (from 10 g to 1000 g), the initial food availability in the landscape (by reducing the default food availability from 100 to 10% of the initial food availability) and the proportion of refuges in the landscape (from 0 to 100%). While varying one of these parameters, the others were kept constant, the body mass at 50 g, the reduction in food resource availability at 0% and the proportion of refuges at 50%. For each combination 30 replicate simulations were conducted. Statistical analyses were conducted in R version 3.3.2 (R Core Team, 2017). To calculate Shannon diversity, species richness and evenness the package vegan (Oksanen et al., 2017) was used. For the calculation of these community metrics prey individuals were categorized into species depending on their body mass. We used a total number of 100 species. The right border of the body mass interval (in g) representing a species was defined by

$10 + S^{1.5}$ with S as the species number from 0 to 100. The left border of the interval was the right border of the previous species. The exponent 1.5 was chosen in order to cover the range of possible body masses in the model. Additionally, we calculated community metrics for evenly spaced body mass intervals and for 10 species. All body mass intervals and species numbers yielded similar results (see Supplementary material, Appendix A.2, Fig. A.2 for a comparison of community metrics of different body mass intervals and species numbers).

2.4 Results

2.4.1 Space use patterns

To gain a better understanding of individual home range formation we compared the addition of cells to the home range between control, risk-averse and risk-taking individuals (Fig. 2.2). Results show that all individuals avoided including non-productive cells in their home range since they could not gain food resources from these. Individuals of the control consecutively added productive cells closest to the home range core, often resulting in circular home ranges. Risk-averse and risk-taking individuals preferred refuges, although possibly located further away from the home range center. From refuges, individuals could gain more food (risk-averse) or had lower movement costs (risk-taking) than in risky habitat. If the home range contained risky habitat, risk-taking individuals needed to add more cells to their home range than risk-averse individuals to cover the increased movement costs in this habitat.

The individual's home range size was the result of the interplay between its traits and the landscape configuration (Fig. 2.3). Traits influencing the home range size were the daily energy requirements, the movement costs per distance unit and the foraging strategy under predation risk. The first two traits were determined by the body mass due to allometric relationships. Home range size increased with body mass as the individuals had higher energy requirements and movement costs (Fig. 2.3a). Risk-taking individuals had larger home ranges than risk-averse individuals and individuals of the control.

Additionally, the landscape configuration affected the home range size. An important factor determining home range size was food resource availability in the landscape. Simulations always started with the same food resource availability but due to the depletion of food resources by animals that already established a home range, individuals that were chosen later in the simulation found a lower food resource availability in the landscape. Since the depletion by animals varied across simulations we reduced the initial overall food resource availability in the landscape to analyze the effect of food availability on individual home range size and compare between different foraging strategies (Fig. 2.3b). The reduction in food resource availability led to an increase in home range size. Again, home range sizes of risk-taking individuals were generally higher than for risk-averse and control individuals. Concerning individuals of the risk-averse and the risk-taking behavioral type, the proportion of refuges also had an effect on the home range size. With increasing proportions of

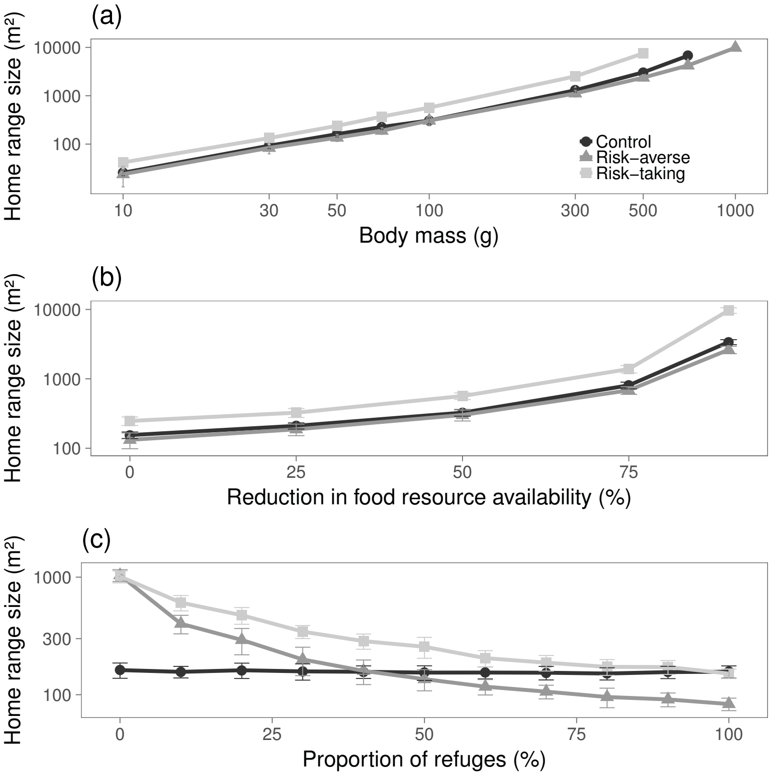

Fig. 2.3. Effect of body mass (a), resource availability (b), and the proportion of refuges (c) on home range size. The home range size of individuals is affected by the interplay of multiple parameters. To show these effects we analyzed the influence of single parameters on the home range of a single individual while keeping the others constant. The following constant values were chosen: Body mass of the individual: 50 g (plot b, c); Food resource reduction: 0% (plot a, c); Proportion of refuges: 50% (plot a, b). Note the logarithmic scale on the y-axes and on the x-axis of plot (a).

refuges home range size decreased (Fig. 2.3c). Risk-averse individuals showed a larger decrease in home range size than risk-taking individuals.

Beside effects on home range formation, the behavioral response of animals to risk had consequences for the landscape usage by prey animals (Fig. 2.4). The overlap of home ranges per grid cell in low-risk and high-risk areas differed between foraging strategies (Fig. 2.4a). Risk-averse communities showed a higher overlap of home ranges in risky habitat compared to refuges. The high food intake of risk-averse individuals in refuges caused a strong depletion of these resources. Consequently, these cells were occupied by few individuals (low density) profiting from the good resource conditions. Other individuals had to use risky habitat which could, due to the low food intake in these, be utilized by many individuals, resulting in a high overlap of home ranges in this area.

The reverse pattern was found in risk-taking communities although the difference between risky habitat and refuges was much smaller here. Risk-taking individuals had the same food intake in risky habitat and refuges. Due to the preference for refuges, which bear lower movement costs, the home range overlap was higher in these than in the risky habitat.

Furthermore, modified space use patterns of individuals due to the fear distribution had consequences for the exploitation of food resources in the landscape. The preference for refuges led to an unequal use of food resources in the landscape (Fig. 2.4b). Due to the increased foraging pressure in refuges, food resources were depleted to a higher degree (i.e. lower giving-up density) than food resources in risky habitat which had a higher giving-up density. This difference in depletion was more distinct for risk-averse individuals.

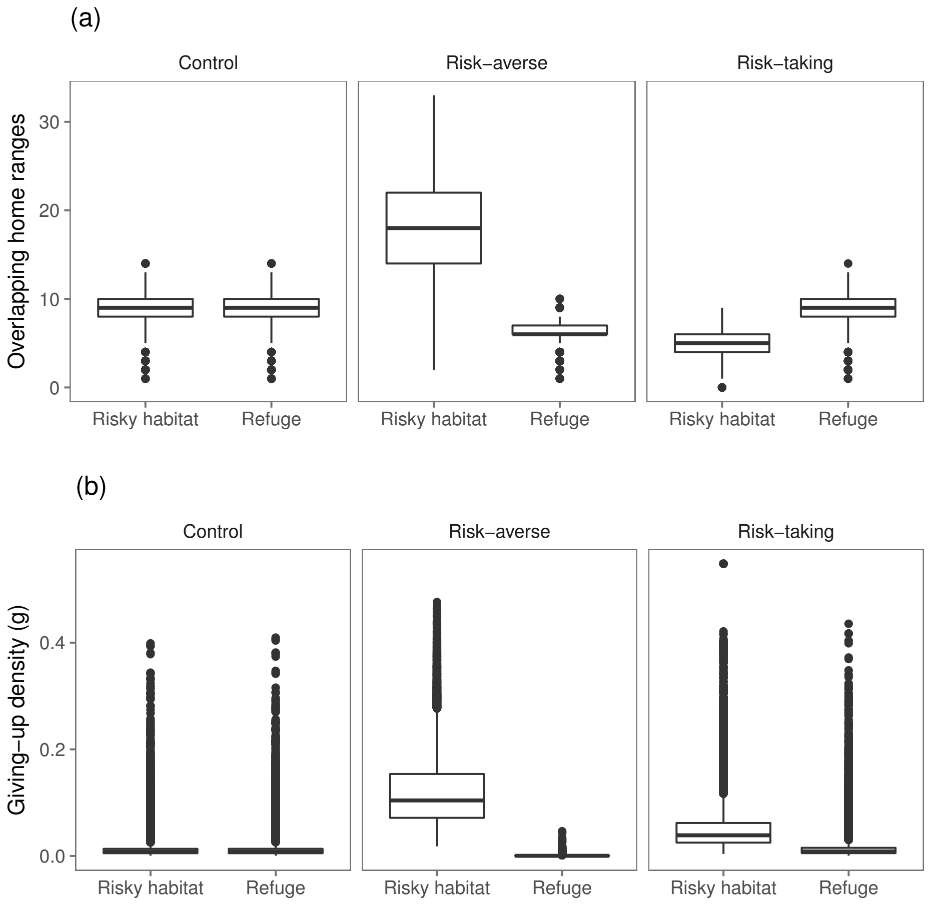

Fig. 2.4. Comparison between landscape usage in risky habitat and refuges. Panel (a) compares the number of overlapping home ranges per grid cell in risky habitat and refuges for the three different foraging strategies. Panel (b) shows the amount of food resources that are left in risky habitat respectively refuges at the end of the simulation. This represents the food density at which individuals cease including cells in their home range since it is not efficient anymore and is similar to the giving-up density which is often used in field experiments. A proportion of 50% refuges in the landscape was used. Boxplots show the pooled distribution of the number of overlapping home ranges (a) or giving-up density (b) for all 30 repetitions. Black dots represent outliers of the distribution.

2.4.2 Community effects

The median body mass increased for both risk-averse and risk-taking individuals with the proportion of refuges indicating a shift in the community structure towards animals with a larger body mass (Fig. 2.5a). The increase was steeper in the community with risk-taking individuals than in the risk-averse for low proportions of refuges. For high proportions of refuges, the pattern was inverted, with a higher increase in median body mass of the risk-averse community compared to the risk-taking community. Furthermore, risk-averse communities reached a higher median body mass under high proportions of refuges compared to risk-taking and control communities.

Regarding the number of individuals in the community, risk-averse and risk-taking showed different patterns to increasing proportions of refuges (Fig. 2.5b). For the risk-averse community the number of individuals decreased with an increasing proportion of refuges, whereas

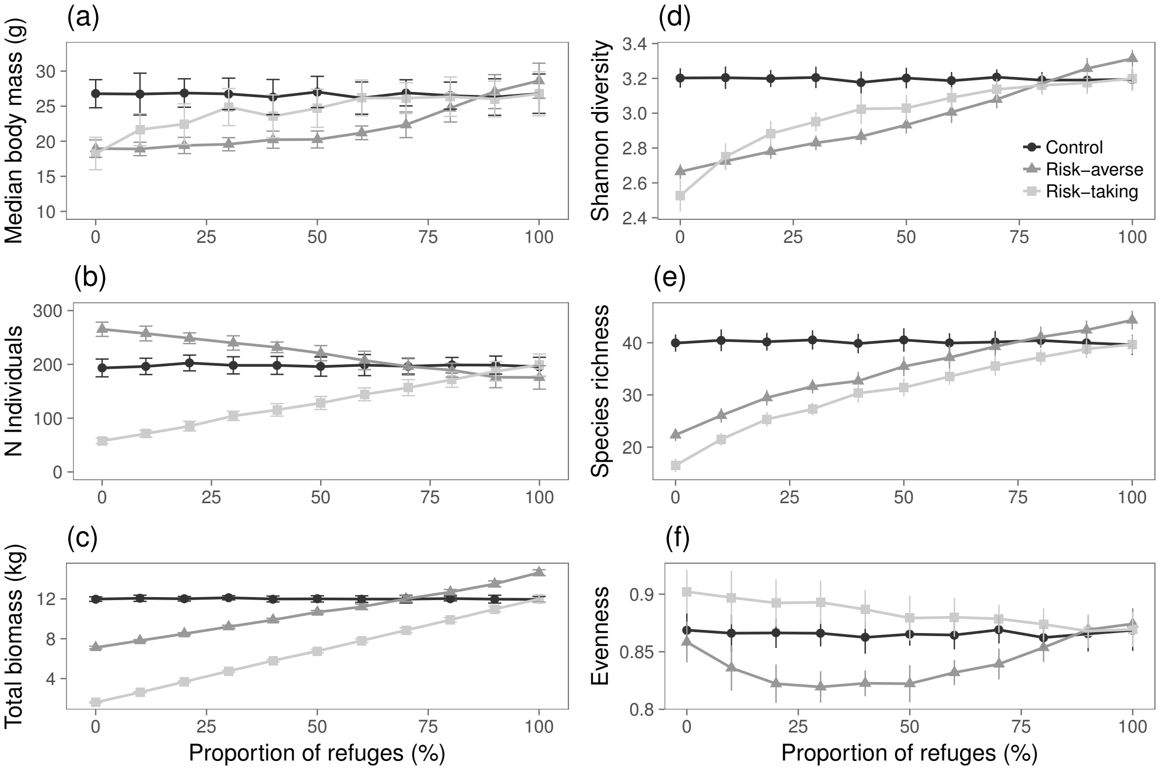

Fig. 2.5. Changes in general community metrics over the proportion of refuges in the landscape. Results show the effect on the median body mass (a), the abundance (b), the total biomass of the community (c), Shannon diversity (d), species richness (e) and evenness (f) for different proportions of refuges in the landscape.

it increased in the community of risk-taking individuals. The total biomass of the community represents the sum of the body mass of all individuals in the community. For the community of risk-taking and risk-averse individuals the total biomass increased with the proportion of refuges and in case of the risk-averse individuals even exceeded the total biomass of the control (Fig. 2.5c).

Similar to the total biomass and the mean body mass, Shannon diversity and species richness increased with the proportion of refuges (Fig. 2.5d, e). Risk-taking prey communities showed a higher diversity for medium proportions of refuges than risk-averse prey communities. If no refuges were present in the landscape, risk-averse prey communities had a higher diversity than risk-taking communities. For high proportions of refuges the diversity and species richness of risk-averse communities were higher than the control. The evenness of the risk-taking community decreased with the proportion of refuges and was generally higher than the evenness of the control (Fig. 2.5f). In contrast, the evenness of the risk-averse prey communities showed a U-shaped pattern with the smallest evenness at medium proportions of refuges.

In order to get further insights into the community structure we compared the distribution of body masses within the community for exemplary proportions of refuges (Fig. 2.6). The risk-averse and the risk-taking communities both showed a clear shift to smaller individuals accompanied by a loss of large individuals for low proportions of refuges (Fig. 2.6a). In these scenarios, the body mass distribution is similar to the body mass distribution of control communities that are facing a reduced initial food availability of 20% of the default availability. With increasing proportion of refuges the body mass distributions of the communities approximated each other. For a proportion of 50% of refuges the risk-taking community was nearly equal to the control while the risk-averse community still showed a shift towards animals with smaller body masses (Fig. 2.6b). If all cells were refuges, the body mass distribution in the control, the risk-averse and the risk-taking community was approximately the same (Fig. 2.6c).

2.5 Discussion

In this study we investigated the consequences of non-consumptive predator effects on prey community metrics by using a mechanistic model of individual home range formation. The results support our hypothesis that perceived predation risk shapes prey community structure due to modifications in prey space use. Furthermore, the model gives insights into the role of refuges and foraging strategies of prey animals for prey community structure. The availability of refuges increased general community metrics such as total biomass, mean body mass, species richness and Shannon diversity. Foraging strategies of prey individuals affected the composition of the prey community by shifting the body mass distribution towards smaller individuals occurring in high abundances. This shift was more pronounced in risk-averse than in risk-taking prey communities especially for a medium proportion of refuges.

2.5.1 Foraging strategies under predation risk

We compared the performance of prey communities using two contrasting foraging strategies under predation risk. Risk-taking animals have increased movement costs in areas with risky habitat since they return more often to refuges in order to escape from predators. To cover the increased movement costs, risk-taking animals need to exploit more food to fulfill their daily energy requirements which results in larger home ranges. Home range overlap of risk-taking animals is slightly higher in refuges since they bear lower movement costs. Due to the higher food requirements of risk-taking animals, fewer individuals could be supported by the available food resources in the landscape resulting in decreased biomass and species richness at the community level compared to risk-averse communities and the control.

In contrast to risk-taking prey, risk-averse animals face indirect costs of their antipredatory behavior via the costs of missed opportunities. Risk-averse individuals reduce their foraging in risky habitat and thus miss exploiting food resources in these parts of the landscape. Individuals balance the reduced food intake in risky habitat with intensive foraging in refuges. This behavior caused strong competition for food resources in refuges and a fast depletion of these by only a few animals. Therefore, risk-averse communities show a low overlap of home ranges in refuges. In risky habitat, low food exploitation by risk-averse

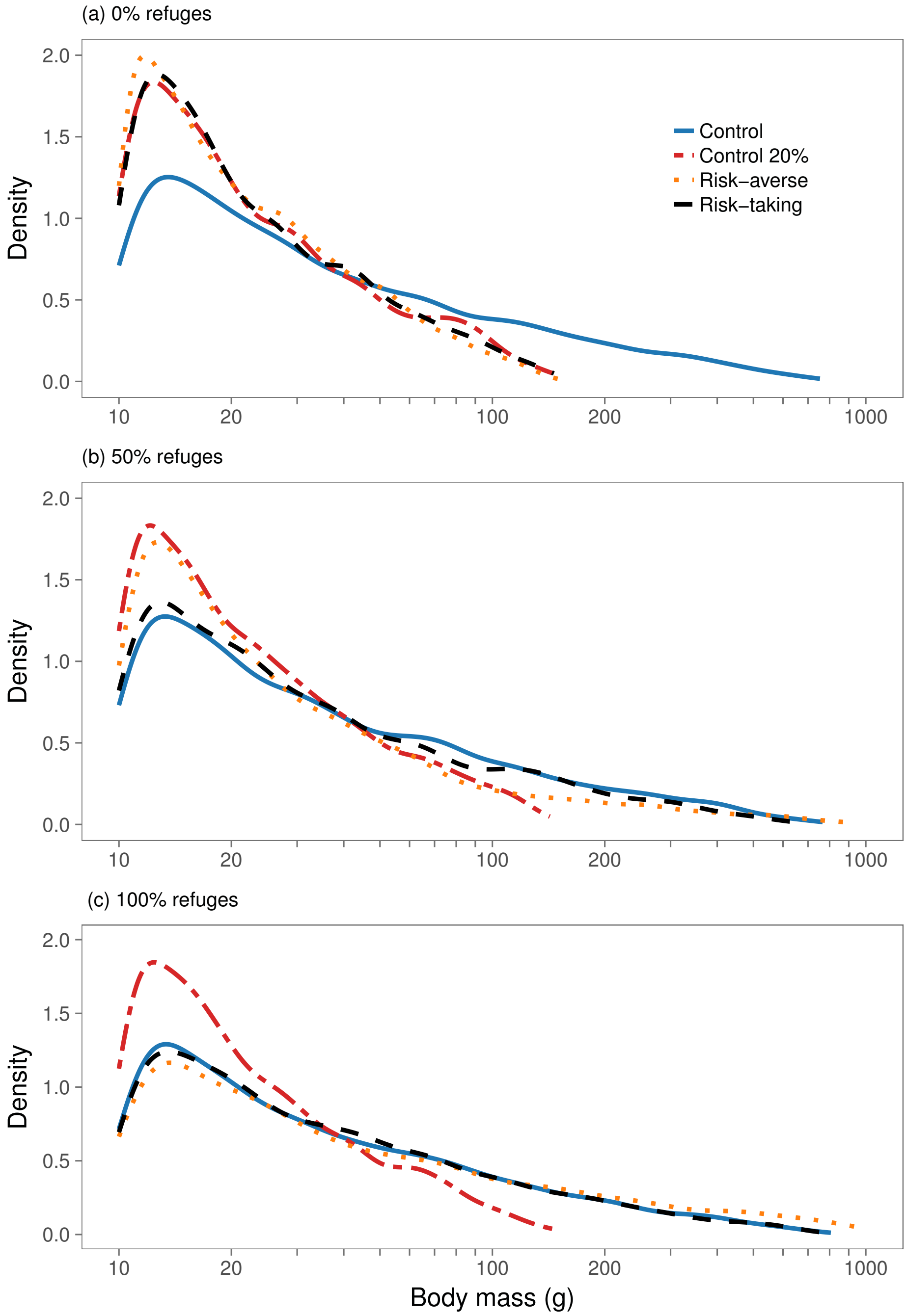

Fig. 2.6. Body mass distribution in the community for different proportions of refuges. To estimate the effects of overall habitat productivity on body mass distribution an additional control was added with a reduced initial food availability of 20% of the default food availability. Density plots show the relative occurrence of body masses in the community to compare distributions with different absolute body masses. Note the logarithmic scale on the x-axis.

animals results in a high overlap of home ranges. In comparison to risk-taking prey communities, risk-averse communities showed a higher biomass and species richness since their antipredatory behavior only reduced the access to food resources but did not lead to additional energy costs.

Foraging strategies could be considered to be the result of different personality traits between individuals. The impact of individual differences in traits such as boldness and exploratory behavior on animal space use has been confirmed for many species (reviewed in Spiegel et al., 2017). For example, starlings that spend more time on the ground have larger home ranges compared to starlings that spend more time on perches (Minderman et al., 2010). This is similar to larger home ranges of risk-taking individuals in the model. Nevertheless, empirical studies have shown that animals often adapt their foraging decisions according to specific conditions (Lima, 1998). For example, hungry animals are more likely to use risky areas than well-fed animals (Gotceitas and Godin, 1991; Kohler and McPeek, 1989; Pettersson and Brönmark, 1993), i.e. they switch between a risk-averse and a risk-taking strategy depending on their internal state. Obviously, the implemented foraging strategies in the model do not allow for such an adaptive foraging behavior but they can give an initial overview about the spectrum of consequences that differences in foraging behavior can have. Further studies should refine the implemented foraging strategies by integrating more sophisticated trade-offs such as a direct feedback of perceived predation risk on the fitness of the animal and the possibility of adaptations in the behavior depending on the internal state and external conditions. Additionally, future studies could incorporate communities in which individuals follow different foraging strategies representing for example differences in personalities between individuals. This would allow to investigate which foraging strategies are favored under varying environmental conditions.

Regarding community composition, risk-taking communities consisted of animals with larger body mass and a more even body mass distribution but lower number of individuals compared to risk-averse communities. Risk-averse communities were more shifted towards small individuals occurring at high abundance. The high number of individuals in risk-averse communities caused a high species richness while the uneven distribution of body masses resulted in lower evenness and Shannon diversity compared to risk-taking communities. Differences in community composition of risk-taking and risk-averse communities shed first light on the question which foraging strategy prey animals should use to maximize their fitness. Under low refuge availability a risk-averse strategy is preferable for small animals since their low energy requirements allow them to forage only in the refuges. Large animals with high energy requirements should follow a risk-taking strategy since it allows them to use additional food resources from risky habitat patches.

2.5.2 Refuge availability

Changes in prey community structure emerged from modified home range formation on the individual level. Individuals integrated areas with the maximum food availability and the lowest predation risk in their home ranges. In the model we used landscapes of fear varying in the proportion of refuges to risky habitat in order to investigate the role of refuge availability for prey communities. On the individual level, prey home range sizes decreased with increasing availability of refuges (Fig. 2.3c). Within refuges, food gain of prey individuals was higher compared to risky habitat since they could exploit more food (risk-averse strategy) or had lower movement costs (risk-taking strategy). Therefore, the integration of refuges in the home range allowed animals to fulfill their food requirements by foraging in a smaller area.

The use of refuges is a common strategy among animals in order to minimize predation risk (Lima and Dill, 1990). Many animals show modifications in their space use due to changes in the landscape of fear, either on the scale of shifting their home ranges to other areas or by adapting the space use within the home range. For example, wild boars respond to variation in predation risk during the hunting season by shifting their home ranges towards protected areas where hunting is not allowed (Tolon et al., 2009). Deer and black bears respond to increased predation risk with adaptations within the home range e.g. by decreasing the usage of ecotones and roads, respectively (Padié et al., 2015; Stillfried et al., 2015), the distance traveled and exploratory behavior (Marantz et al., 2016). Furthermore, refuge use leads to a heterogeneous distribution of food resources in the landscape. Due to the lower giving-up density in refuges food resources are depleted to a lower level compared to food resources in risky habitat (Fig. 2.4b). These differences in food resource exploitation can induce trophic cascades (Werner and Peacor, 2003).

On the community level, modifications in space use due to increased refuge availability had positive effects on prey community metrics, leading to higher species richness, diversity and total biomass. These results are in good agreement with empirical patterns found in coral reef fish assemblages showing increased species abundance and richness with refuge availability in reefs (Caley and St John, 1996; Hixon and Beets, 1993). Additionally, these results support the habitat heterogeneity hypothesis stating that environmental heterogeneity increases species diversity (Bazzaz, 1975). Increasing availability of refuges causes a heterogeneous distribution of fear in the landscape and therefore allows more species to coexist.

Moreover, refuge availability drives community composition in risk-averse and risk-taking animal communities. While there is a large difference in the number of individuals between risk-averse and risk-taking animals under low refuge availability, both communities show similar numbers of individuals under high refuge availability.

In risk-averse communities low food availability in risky habitat allows only small animals the establishment of a home range while large animals are not able to find enough food to cover their food requirements. With increasing refuge availability, more food becomes available. As a result, large animals can establish home ranges and replace small animals. Due to higher food requirements of large animals the number of individuals in the community decreases while median body mass increases.

By contrast, risk-taking animals face increased movement costs in risky habitat. Under low refuge availability these movement costs strongly increase the food requirements of the animals. Therefore, food resources in the landscape are depleted by fewer animals compared to risk-averse communities. With increasing refuge availability, movement costs decrease and more and larger animals can establish a home range in the landscape. Therefore, the number of individuals and the median body mass increase.

For high levels of refuge availability, biomass, diversity and species richness of risk-averse prey communities even exceeded the values of the control. The high availability of refuges allows risk-averse animals to use nearly the whole landscape so that competition for refuges is reduced. Due to the intensive foraging in refuges, risk-averse animals can exploit even more food than animals of the control. However, the consumption of food resources at such a high rate would in reality only be possible if food resources refill very quickly, otherwise it would soon lead to a breakdown of food resources. Cases of mesopredator release have shown strong increases in the population of mesopredators under the absence of predation risk from top predators accompanied by increased consumption of prey animals which can lead to the breakdown of prey populations (Elmhagen and Rushton, 2007; Ritchie and Johnson, 2009).

Low levels of refuge availability led to a reduction of large animals and an increase of smaller animals in risk-averse and risk-taking communities compared to control communities. This shift towards animals with smaller body mass is similar to the shift that can be observed in control communities facing a decreased initial food availability. Similarities arise because the reduced food gain of risk-aware individuals in risky habitat is comparable to the food gain of control individuals in cells with a decreased food availability.

2.5.3 Scaling up from the individual level to the community level

Linking different hierarchical levels the model bridges the gap between behavioral and community ecology. In our model, patterns emerge from underlying processes, which is crucial to understand complex interactions in ecosystems (Cabral et al., 2017) and to tease apart effects of bottom-up vs. top-down control on biodiversity.

One reason why models often cover only one hierarchical level is the increasing complexity when integrating more levels (Grimm et al., 2017). Nevertheless, several examples show that it is possible to develop individual-based community models (e.g. for forests: Köhler and Huth, 1998, for fish communities: Giacomini et al., 2009). The crucial point to reduce the complexity in such models is to find a way to represent all species in a community, and their interactions, with the same basic approach. In forest ecology, gap models (Botkin et al., 1972; Bugmann, 2001) have used this approach for decades. Animal community ecology has made progress in this direction, the key being a trait-based approach where species differ only in their parameterization, but not in their representation (Jeltsch et al., 2013b). In the presented model we further reduced complexity by using allometric relationships to calculate several physiological traits; again, this approach has been used in forest modelling for a long time. Thus, individuals can be described only by their body mass and their specific foraging strategy under predation risk.

2.5.4 Possible extension of the model: temporal variation in predation risk

The model predicts possible consequences of different landscapes of fear and foraging strategies on prey community structure emerging from adaptations in space use. However, the model focuses on spatial variation in predation risk and does not include temporal variation of that risk. The occurrence of temporal variation in risk is common in nature due to seasonal changes, varying light intensity during the lunar cycle or within a day (Dodson, 1990; Kotler et al., 1994; Werner, 1986). The risk allocation hypothesis states that animals should increase antipredator behavior during pulses of high risk and allocate foraging activities to pulses of low-risk (Lima and Bednekoff, 1999). Several studies have shown temporal adaptations in animals to minimize predation risk, e.g. gerbils that show the highest foraging activities during the darkest hours of the night (Kotler et al., 1994) or elk that shift from diurnal to nocturnal activity to avoid hunters (Visscher et al., 2017). It can be expected that such temporal adaptations have effects on the community level since they can affect competition between prey animals arising from changes in activity times. For the integration of temporal variation in predation risk in the model it would be necessary to explicitly include time and allow modifications of home ranges after an individual has settled at a specific location, including the displacement of individuals with an established home range by other individuals. Depending on the time scale, it might also be necessary to include further processes such as reproduction, mortality and dispersal. Nevertheless, it has been shown that the static approach developed by Buchmann et al. (2011) that we used here can capture realistic features of community composition and structure (Buchmann et al., 2011; Prevedello et al., 2016).

2.5.5 Implications for empirical research and nature management

Our results reveal that perceived predation risk can shape prey community structures. Although adaptations in behavior and cascading effects on ecosystem functioning are widely known, risk effects on prey communities remain poorly studied (Creel and Christianson, 2008). A study on songbirds highlights the strong impact of perceived predation risk on reproduction (Zanette et al., 2011). Furthermore, landscapes of fear are expected to control the extent of bottom-up and top-down processes in prey populations (Laundré et al., 2014). Additionally, the concept of landscapes of fear can also be applied to apex predators. For example, a study by Mech (1977) showed that wolves are afraid of hunting close to the territories of neighboring packs. Thereby, they create buffer zones in which prey animals, such as deer can browse safely which can have cascading effects on the vegetation.

Since risk effects are difficult to assess empirically, a combination of empirical and modelling studies might prove useful to investigate the consequences of fear in different prey communities (Jeltsch et al., 2013a). Empirical studies can provide information about the basic principles from which differences in community structure emerge, such as the configuration of the landscape of fear or the foraging behavior of prey animals concerning their decisions on which locations they choose for their home range. By integrating this information, the model can be applied to specific prey communities and allows the prediction of community structures and composition. Vice versa, the model provides mechanisms that are important for shaping community structure that could then be tested in empirical studies.

The prediction of prey community structure under different conditions can prove useful since in many areas landscapes of fear are changing. Firstly, ecosystems face a loss of apex predators resulting in the loss of top-down control (Estes et al., 2011). Secondly, predators are reintroduced in ecosystems where they have been formerly present, leading to changes in the spatial distribution of prey animals which can affect other trophic levels (Kuijper et al., 2013). Thirdly, human activities affect the predation risk that animals perceive. These can be direct risk effects on hunted species (Bonnot et al., 2013; Tolon et al., 2009) or indirect effects on non-target species (Mori, 2017). Furthermore, human activities and disturbances create landscapes of fear for predators and prey, which can decrease the strength of non-consumptive effects on prey animals due to adaptive behavior of predators (Oriol-Cotterill et al., 2015) and in case of the prey often exceed the predation risk perceived from natural predators (Ciuti et al., 2012). Further research on the consequences for prey communities is necessary to estimate the effect of large predators on biodiversity.

2.6 Conclusions

The consequences of non-consumptive predator effects on prey communities are until now largely unknown since research focuses either on behavioral adaptations on the individual level (e.g. Altendorf et al., 2001; Martin et al., 2003) or on possible effects for other trophic levels and ecosystem functioning (Schmitz et al., 2004; Werner and Peacor, 2003). The presented model integrates behavior on the individual level with effects on the level of the prey community. This approach allows to link patterns at the community level with mechanistic processes on the individual level which is a central goal in ecology (Cabral et al., 2017). Our findings show that modifications in home range formation due to perceived predation risk shape prey community structures with important implications for biodiversity of the whole prey community. An understanding of the consequences of non-consumptive predator effects on prey communities is crucial under the current loss of apex predators in many ecosystems (Estes et al., 2011). Furthermore, anthropogenic land use and hunting modify existing landscapes of fear with potentially extensive consequences for animal communities (Kuijper et al., 2016). The model presented in this study helps to understand and evaluate the magnitude of general mechanisms such as refuge availability and foraging strategy affecting prey community responses under predation risk. Based on these results, further studies combining simulation models and empirical studies can be designed to evaluate the impact of non-consumptive predator effects on prey communities.

2.7 Declaration of interest

None.

2.8 Acknowledgements

This work was supported by Deutsche Forschungsgemeinschaft in the framework of the BioMove Research Training Group (DFG-GRK 2118/1).

2.9 Supplementary material

Appendix A.1: ODD-protocol
Appendix A.2: Comparison of community metrics

CHAPTER 3

Consequences of fear on prey communities facing landscape changes

Title	The risk of ignoring fear: Underestimating habitat loss effects on biodiversity
Authors	Lisa Teckentrup, Stephanie Kramer-Schadt, Florian Jeltsch
Journal	*Landscape Ecology*, LAND-D-10-00090
Date of submission	Received 06 March 2019
Status	under review; initially submitted to *Ecography* (ECOG-04300) on 24 September 2018, rejected on 26 January 2019
Keywords	Predator-prey interactions, fragmentation, habitat loss, landscape of fear, perceived predation risk, home range, biodiversity, community

3.1 Abstract

Habitat loss and fragmentation threaten species not only through structural landscape changes and resource reduction, but also through modifications to species' interactions. In particular, the observed consequences of landscape changes for predator-prey interactions often lack a clear pattern, indicating a range of complex behavioral adaptations and interactions. One potentially important contributing factor shaping these consequences is perceived predation risk and hence fear, which is rarely explicitly addressed in studies on habitat loss and fragmentation. We used an individual-based model to assess the role of fear in altering animal community responses to habitat loss and fragmentation. Moreover, we identified habitat properties driving these changes. The model simulates home range formation of an herbivorous, mammalian prey community based on food availability and fear and predicts realistic community structures under different landscape scenarios. We found that fear intensified the negative effects of habitat loss and fragmentation on prey communities, causing a non-proportional diversity loss of up to 30%. Moreover, shifts in community composition from large to small animals were reinforced. Regarding habitat properties, we could show that the highest diversity is supported in landscapes with non-fragmented safe areas. Our findings highlight the importance of fear in shaping prey community structures under conditions of landscape change. Our generic modelling approach allows us to address the mechanisms that link individual space use with community structure and reveals the key role played

by the spatial distribution of safe patches in mitigating the negative effects of landscape changes. Thereby, our approach and results support modern conservation efforts that go beyond single-species approaches by taking impending changes in species interactions into account.

3.2 Introduction

Habitat loss and fragmentation are major threats to biodiversity (Laurance et al., 2012; Newbold et al., 2015; Schipper et al., 2008) and have been the focus of ecological research for decades (Fardila et al., 2017). Besides direct causes, such as reduced availability and connectivity of habitats (reviewed in Ewers and Didham, 2006), biodiversity is affected by alterations and losses in species interactions, such as predator-prey interactions (Tylianakis et al., 2008; Tylianakis et al., 2010; Valiente-Banuet et al., 2015), and can accelerate species loss and lead to the collapse of ecosystem services (Díaz et al., 2013).

The consequences of habitat loss and fragmentation on predator-prey interactions have been investigated in both theoretical (e.g. Schneider 2001; Swihart et al. 2001, reviewed in Ryall and Fahrig 2006) and empirical studies (e.g. Chalfoun et al., 2002; Lahti, 2001; Paton, 1994). Nevertheless, the direction and strength of alterations in predator-prey interactions due to landscape changes often remains unclear (Ryall and Fahrig, 2006). For example, fragmentation can increase or decrease predator abundance at edges or have no significant effect at all (Chalfoun et al., 2002). Such divergent results are often explained as being taxon-specific and context-dependent (Chalfoun et al., 2002). However, most studies focus on the lethal effects of predators, while non-lethal effects are either ignored or only implicitly considered. Nevertheless, non-lethal effects can be even stronger than lethal effects (Werner and Peacor, 2003). For example, fear in terms of perceived predation risk can affect many prey species even if the actual predation rate is low. This can have detrimental effects on species diversity beyond mere predation (Preisser et al., 2005). Therefore, an evaluation of non-lethal effects on prey communities can improve our understanding of the consequences of changes in predator-prey interaction on prey communities facing landscape change.

In contrast to lethal effects that directly decrease prey abundance, non-lethal effects act on the behavioral level (Lima, 1998). Prey species alter their behavior due to the perceived presence of a predator and thereby aim at minimizing their predation risk (Brown, 1988; Lima, 1998). Non-lethal effects are driven by the predation risk that an animal perceives in dependence on specific landscape features. In particular, habitat quality, including the availability and quality of refuges and shelter, is a key factor determining the magnitude and direction of non-lethal effects (Donelan et al., 2017; Gorini et al., 2012; Orrock et al., 2013). In the presence of landscape changes, habitat quality is likely to be altered, for example through the occurrence of edge effects (Ries et al., 2004).

The aim of this study was to explore the role of fear in terms of perceived predation risk in shaping prey communities facing landscape changes and to identify habitat properties that support prey diversity. As the effects of perceived predation risk are often difficult to disentangle from lethal effects in experimental studies, we applied an individual-based and spatially-explicit model simulating prey community assembly via home range formation based on a trade-off between food availability and perceived predation risk (Teckentrup et al., 2018). With a spatially-explicit approach, landscape changes can easily be implemented and the consequences for animals' space use can be investigated. The individual-based design of the model allowed us to investigate the consequences of individual alterations in space use on community structure while disentangling the effects of habitat loss from habitat lost due to fear effects. The modelling approach has been proven to predict realistic community structures (Buchmann et al., 2011) and diversity patterns in the context of matrix suitability (Prevedello et al., 2016).

Specifically, we assessed the following research questions in this study: 1) To what extent does perceived predation risk affect prey community responses to habitat loss and fragmentation? 2) Which habitat properties drive changes in prey community structure facing landscape changes?

3.3 Material and Methods

We used an individual-based, spatially-explicit model to simulate home range formation of risk-aware and risk-unaware (control) herbivorous, mammalian prey communities. It is based on a model by Teckentrup et al. (2018) using a modelling approach by Buchmann et al. (2011). Here, we only provide a brief description of the model, while a detailed documentation following the ODD protocol (Grimm et al., 2006; Grimm et al., 2010) is given in the Supplementary Material, Appendix B.1.

3.3.1 Landscape scenarios and landscape changes

Realistic fractal landscapes with a size of 129 × 129 cells were generated with the well-established midpoint-displacement algorithm (Hargrove et al., 2002; Körner and Jeltsch, 2008; Saupe, 1988). Each cell represented $4\,\mathrm{m}^2$. The z-values of the landscape grid were used to represent food resource availability (*p-food*). Food resources were scaled to an average resource availability of $2.74\,\mathrm{g}$ dry biomass $\cdot$ grid cell^{-1} $\cdot$ day^{-1}, a typical value for shrub- and grasslands (Whittaker, 1975). Only 20% of these food resources were available to prey animals, while the rest was lost to other taxa or was not consumable (Buchmann et al., 2011). The configuration of the landscapes was controlled by σ^2, determining the variance in displacement of points, and the Hurst-Factor H, determining the spatial autocorrelation of points. We used a moderate variance (σ^2=30) in all landscapes. For spatial autocorrelation, we used three different values representing varying degrees of fragmentation of the landscape (H=0.1 for low, H=0.5 for medium and H=0.9 for high fragmentation, Fig. 3.1b). We assumed that all prey individuals were herbivorous and competing for the same single resource. Food resources were exploited by animals during the simulation and not replenished, leading to a decrease in food resource availability during the simulation.

Besides food resources, all landscape cells had a specific perceived predation risk (*p-safety*). This represents the landscape of fear that prey animals perceive. Landscapes of fear were static, i.e. the perceived predation risk in cells did not change during the simulation. In order to test different conditions that animals might encounter in nature, the perceived predation risk in habitat cells was either positively or negatively correlated with food resource availability in the landscape.

For habitat loss, food resource availability in specific cells (depending on the landscape scenario, see explanation below) was set to 0 until only a certain proportion of cells containing food resources was left (Fig. 3.1b). Cells with food resources are hereafter called "habitat cells", since we assume that the availability of food corresponds to conditions that allow animals to survive and reproduce, and cells that have been set to 0 due to habitat loss are called "matrix cells". We assumed a high perceived predation risk in matrix cells (*p-safety*=0), as their lack of vegetation corresponds to a high predation risk. This hostile matrix represents typical human-dominated landscapes, such as clear-cuts in forests. We tested landscapes with a habitat loss ranging from 0% to 90% in intervals of 10%.

The consequences of habitat loss on animal communities depend not only on the quantity and configuration of the habitat that is lost, but also on the quality (Bragagnolo et al., 2007; Fleishman et al., 2002; Summerville and Crist, 2004). Therefore, we used four different landscape scenarios, representing a gradient of habitat quality in the remaining habitat (Fig. 3.1a). The scenario F^+S^+ ('high food, high safety') represents a landscape scenario in which habitat cells of high quality remained after habitat loss, i.e. cells with low food availability and safety were lost first. By contrast, in the scenario F^-S^-, cells with a high food availability and high safety were lost first, resulting in a landscape with low habitat quality. Furthermore, we simulated two intermediate scenarios, F^+S^-, where habitat cells with a high food availability and low safety remained, and F^-S^+, where habitat cells with a low food availability and high safety remained.

In specific scenarios, edge effects were included. We defined edge effects as an alteration of perceived predation risk at the edges of the habitat. Food resource availability was not affected by edge effects. To implement edge effects, we defined all cells within a certain distance (5 m, 10 m, 20 m) from the matrix as edge cells. In edge cells, the perceived predation risk was modified to the average perceived predation risk of all cells in the radius of the edge effect distance (Fig. 3.1c). To allow for an easier comparison between simulations with different landscape scenarios and edge effects and to disentangle the effects of fear and habitat loss due to fear, we calculated the overall "habitat quality" of each simulation. Habitat quality was calculated as the sum of food availability and safety in habitat patches, encompassing habitat loss scenarios as well as habitat loss due to fear (S^+, S^-, edge effects). By comparing communities' responses to habitat quality with their responses to the single factors of landscape scenarios and the distance range of edge effects, we estimated the impact of different habitat properties on prey communities. That is, the effects of fear also result in effective habitat loss, and we wanted to separate fear effects from the general effects of habitat loss in order to avoid trivial findings.

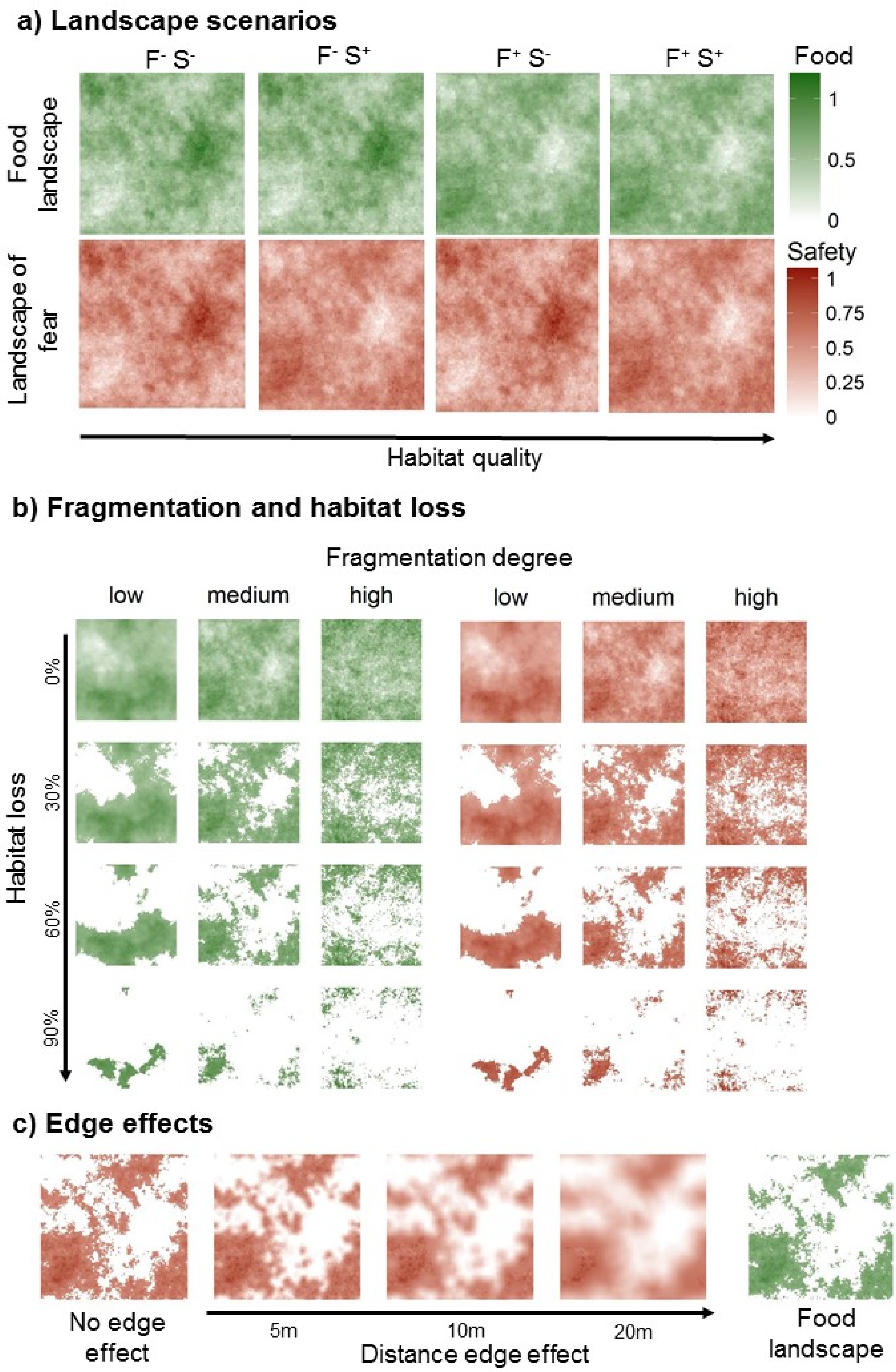

Fig. 3.1. Overview of exemplary landscapes used in the model. Landscape scenarios (a) show the different combinations of food and landscapes of fear for 0% habitat loss. Plot b) shows exemplary food and fear landscapes for different degrees of fragmentation and habitat loss in a landscape scenario of F^+S^+. Plot c) shows changes in the landscape of fear under the consideration of edge effects for medium fragmentation and 50% habitat loss. The food landscape is not affected by edge effects.

3.3.2 Home range model

The model simulates home range formation of prey individuals based on food availability and perceived predation risk. It does not include any direct predation effects but focuses on indirect, non-lethal effects of predators. Therefore, predators are not explicitly modelled but are represented by the landscape of fear. Prey individuals are characterized by their body mass and were drawn from a truncated power law distribution with an exponent of -1.5 (Buchmann et al., 2011; Buchmann et al., 2012). This distribution represents the regional species pool of an herbivorous, small mammal community and ranges from body masses of 10 g (e.g. mice and voles) to 1 kg (e.g. rabbits). Based on the body mass, additional traits of the animal, namely daily feeding rate, movement costs, maximum home range size and the resolution at which it can exploit food resources, were calculated using allometric relationships (see Supplementary Material, Appendix B.1, Table B.3 for details).

Furthermore, we differentiated between risk-aware and risk-unaware (control) communities. Animals from control communities do not perceive predation risk in landscape cells and therefore do not change their foraging behavior, i.e. these animals do not suffer from non-lethal predator effects. In contrast, risk-aware communities perceive predation risk and adapt their foraging behavior accordingly. By using risk-aware and control communities in separate model runs, the consequences of perceived predation risk on prey community structure could be evaluated.

In each step of the model, a new prey individual is drawn from the regional species pool. This animal then searches for a home range in the landscape, which has to contain enough food to fulfill the animal's daily energy requirements. We assume animals to be central place foragers, frequently returning to their den within the home range. Home range search starts at a randomly chosen habitat cell where the individual establishes its den. We assume that this core cell represents an absolute refuge for the prey animal (*p-safety*=1).

Starting from the core cell, the animal adds cells to its home range until its energy requirements are fulfilled. The cell to be added next is chosen from the neighboring cells of the cell that was previously added to the home range. We assumed that the animal has a perceptual range of one cell, i.e. it can sense food availability and predation risk in neighboring cells. To decide which of these cells is added to the home range, the suitability of a cell is calculated using the "μ/f-rule" (death per unit energy, Gilliam and Fraser, 1987), which relates perceived predation risk to food availability:

$$\text{Suitability} = (1 - \textit{p-safety})/\text{Food gain} \tag{3.1}$$

The cell with the lowest ratio of predation risk and food gain is added to the home range, i.e. the animal chooses the minimum predation risk per unit energy. For the control, the suitability of a cell is only defined by food gain (Suitability = Food gain), and the cell with the highest suitability is chosen. If several cells are equally suitable, one of the cells with the minimum distance to the core is chosen randomly.

Food gain is the amount of energy that an animal can gain from a certain cell while accounting for the movement costs of foraging in this cell. It is calculated by:

$$\text{Food gain} = \text{Food intake} - \text{Movement costs} \tag{3.2}$$

The amount of food intake is the arithmetic product of food availability in the cell (*p-food*) and the individual magnitude of food exploitation (*i-foodshare*) depending on body mass:

$$\text{Control:} \qquad \text{Food intake} = \textit{p-food} \cdot \textit{i-foodshare} \tag{3.3a}$$

The parameter *i-foodshare* is used to distinguish the different consumption levels of local food resources by prey individuals of different body masses. For risk-aware individuals, perceived predation risk additionally affects food intake:

$$\text{Risk-aware:} \qquad \text{Food intake} = \textit{p-food} \cdot \textit{i-foodshare} \cdot 2 \cdot \textit{p-safety} \tag{3.3b}$$

The factor 2 in eq. 3.3b was chosen so that the food intake at a medium predation risk (*p-safety*=0.5) equals the food intake of the control. Movement costs are the product of the allometric costs (with increasing costs for large animals) and twice the distance to the core cell, as the individual has to move to the foraging cell and back to the central place.

$$\text{Movement costs} = \textit{i-lococost} \cdot 2 \cdot \text{distance}_{\text{core}} \tag{3.4}$$

Movement costs are the same for risk-aware and control animals.

After the addition of a cell to the home range, the food gain from all cells in the home range is compared with the daily energy requirements of the animal. If the food gain covers the daily energy requirements, the home range search is successful. The individual establishes its home range in these cells and consumes the resources within them. Otherwise, more cells are added to the home range. If the number of cells exceeds the maximum home range size before the energy requirements are met, the individual fails to find a home range and is excluded from the community, i.e. we assume that it relocates to another part of the landscape or dies.

3.3.3 Community assembly

The consumption of food resources within the home range reduces food availability within the landscape. As food resources become scarcer, more and more individuals fail to find a suitable home range. We stopped the simulations if 100 animals consecutively failed to find a home range. At this point, the accessible food resources were exploited and further home range establishment was not possible (Buchmann et al., 2011; Teckentrup et al., 2018).

3.3.4 Simulation design and statistical analyses

All simulations were conducted in NetLogo 6.0.2 (Wilensky, 1999). We performed 20 repetitions for each scenario. Statistical analyses were conducted in R, version 3.4.2 (R Core Team, 2017). Diversity indices were calculated with the package "vegan", version 2.4-4 (Oksanen et al., 2017). In order to calculate diversity indices, we assigned individuals to species based on their body mass. We therefore divided the body mass input distribution into 50 body mass classes, i.e. the regional species pool consisted of 50 species. Body mass classes were defined by body mass intervals. The right border of the body mass interval (in g) representing a species was defined by $10 + N^{1.77}$, with N as the species number from 1 to 50. The left border of the interval was the right border of the previous species. The exponent 1.77 was chosen in order to cover the range of possible body masses in the model.

We used linear mixed-effects models (R package "lme4", version 1.1.17, Bates et al., 2015) to separate the general effects of reduced habitat quality due to habitat loss from fear effects. We compared two models, with one model containing the explanatory variables 'habitat quality' and fragmentation, while the other model contained fragmentation as well as the single explanatory variables constituting habitat quality, namely food availability in the landscape (F^+/F^-), fear effects (S^+/S^-) and edge effects. For both models, a habitat loss of 90% was assumed. We used Shannon diversity as a response variable. As a random factor, we used the repetition number of the model run. Three-way interactions were excluded, as they had no significant impact on the results. We selected models based on the information theoretic approach and chose the model with the lowest AIC score. The package "metafor", version 2.0 (Viechtbauer 2010), was used to create the forest plot (Fig. 3.4) ranking the single variable contributions. For the 3D plot (Fig. 3.5), we used a general additive model with Gaussian link function (package "mgcv", version 1.8.20 Wood, 2011; Wood, 2017) and total biomass as a response variable and Shannon diversity and habitat quality as explanatory variables. All other plots were plotted with the package "ggplot2", version 3.0 (Wickham, 2016).

3.4 Results

3.4.1 General effects of habitat loss and fragmentation on control animal communities

As expected, habitat loss decreased the total biomass of control animal communities due to the reduction in overall food availability (Fig. 3.2a). The effects of habitat loss were stronger in F^--scenarios, where food patches of lower productivity remained. The diversity of control communities decreased strongly with increasing habitat loss in F^--scenarios and slightly in F^+-scenarios, where food patches of high productivity remained (Fig. 3.2b). This reduction was especially marked if habitat loss was higher than 50%. The 95% quantile of body mass represents the largest animals in the community and allows for an overview of changes in community composition (Fig. 3.2c). In F^+-scenarios, the 95% quantile of body mass remained constant for all degrees of habitat loss. By contrast, it decreased in F^--scenarios, indicating a reduction of large animals in the community. Regarding space use, animals in the control communities responded with an increase in home range size to rising habitat loss (Fig. 3.2d). In F^--scenarios, the median home range size dramatically increased, with home ranges growing up to 4 times larger for 90% habitat loss compared to home range sizes without habitat loss. For F^+-scenarios (i.e. high-productive food patches remained), the median home range size showed a moderate increase for high degrees of habitat loss (> 70%). Additionally, the median home range size increased with fragmentation in control communities under high habitat loss.

3.4.2 Effects of fear on prey communities facing landscape changes (without edge effects)

Landscape changes modified the properties of risk-aware prey communities depending on the risk scenario they faced (Fig. 3.3). For risk-aware communities in S^--scenarios (i.e. risky patches remain while safe patches are lost), prey diversity was lower compared to control communities, with differences becoming larger with increasing habitat loss. By contrast, the prey diversity of risk-aware communities in S^+-scenarios (i.e. safe patches remain while risky patches are lost) was similar to that of control communities for low and medium habitat loss and slightly higher under high habitat loss (Fig. 3.3a). Fragmentation had no effect on prey diversity. For the different food scenarios F^+ and F^-, community metrics of risk-aware prey communities followed the trends in control communities. Therefore, the deviation plot to the control showed no effect of the food scenario (Fig. 3.3a). Regarding the total biomass, the responses of risk-aware prey communities were comparable to the patterns found for Shannon diversity (Supplementary Material, Appendix B.2, Fig. B.2a). Changes in prey diversity were driven by alterations in community composition. In risky landscapes (S^-), prey communities consisted of animals with a smaller body mass compared to the control, while safe landscapes (S^+) supported larger animals (Fig. 3.3b). On the spatial scale, fear increased the home range sizes of prey animals in S^--scenarios, especially under high habitat loss (Supplementary Material, Appendix B.2, Fig. B.2b). Moreover, differences in home range size between control communities and prey communities in S^--scenarios were stronger for low degrees of fragmentation than for high. In S^+-scenarios, home range sizes of risk-aware animals decreased with increasing habitat loss. This decrease was more pronounced in F^+-scenarios and under low fragmentation. Additionally, animals altered their foraging patterns when experiencing fear, resulting in a more heterogeneous food resource exploitation (Supplementary Material, Appendix B.2, Fig. B.3).

3.4.3 Habitat properties driving prey community responses

The diversity of risk-aware prey communities was better explained by the specific habitat properties (model comparison; landscape scenario, distance range of edge effect and fragmentation, AIC: -1659.3, df: 32) than by the overall habitat quality and fragmentation (AIC:

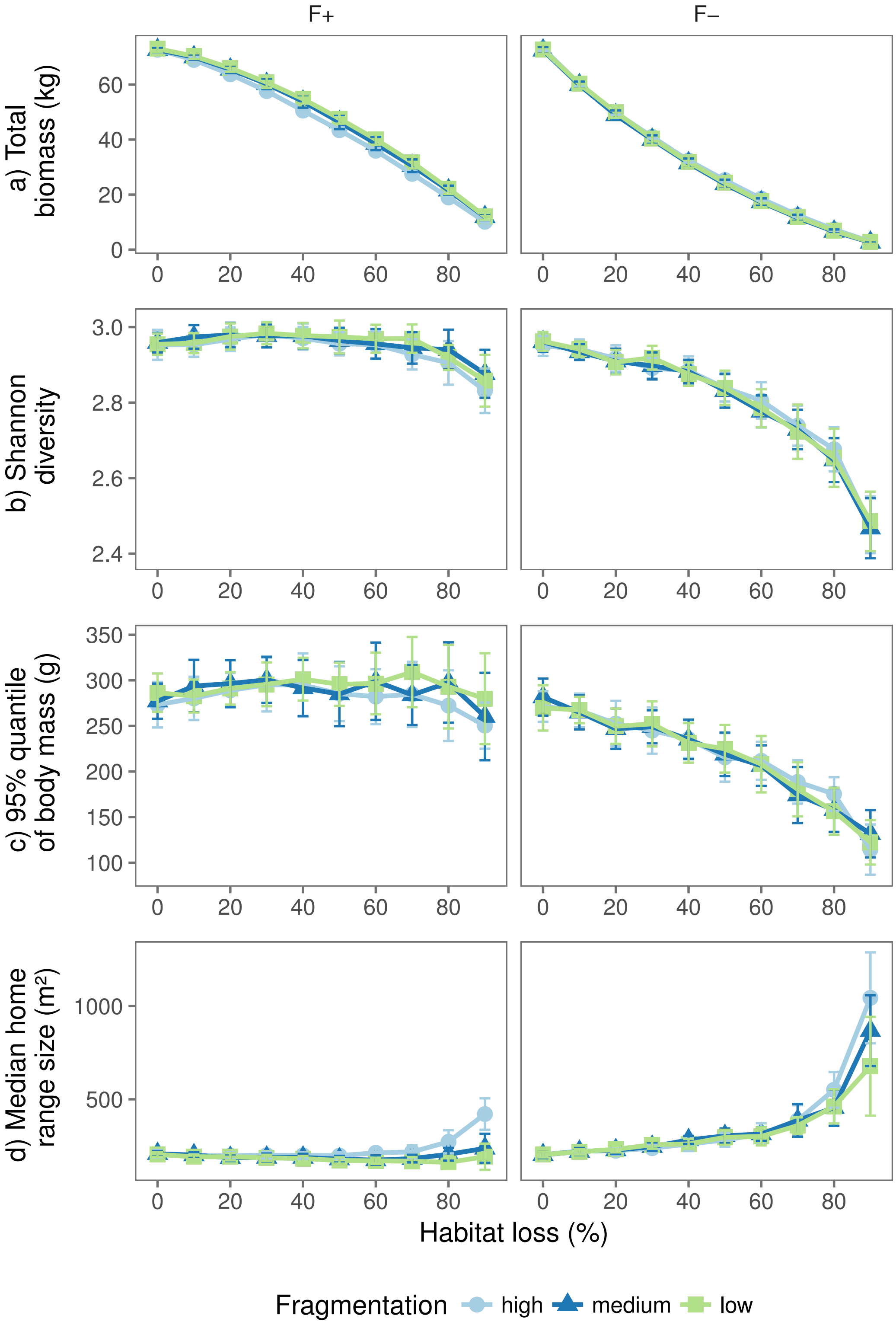

Fig. 3.2. Response of control animal communities (unaware of predation risk) to habitat loss and fragmentation. Panels on the left show results for F^+-scenarios in which food cells with a high productivity remained; panels on the right show results for F^--scenarios in which food cells with a low productivity remained. Total biomass is the sum of all body masses of individuals in the community. 95% quantile of body mass represents the body mass of 5% of the largest animals in the community. Error bars represent the standard deviation.

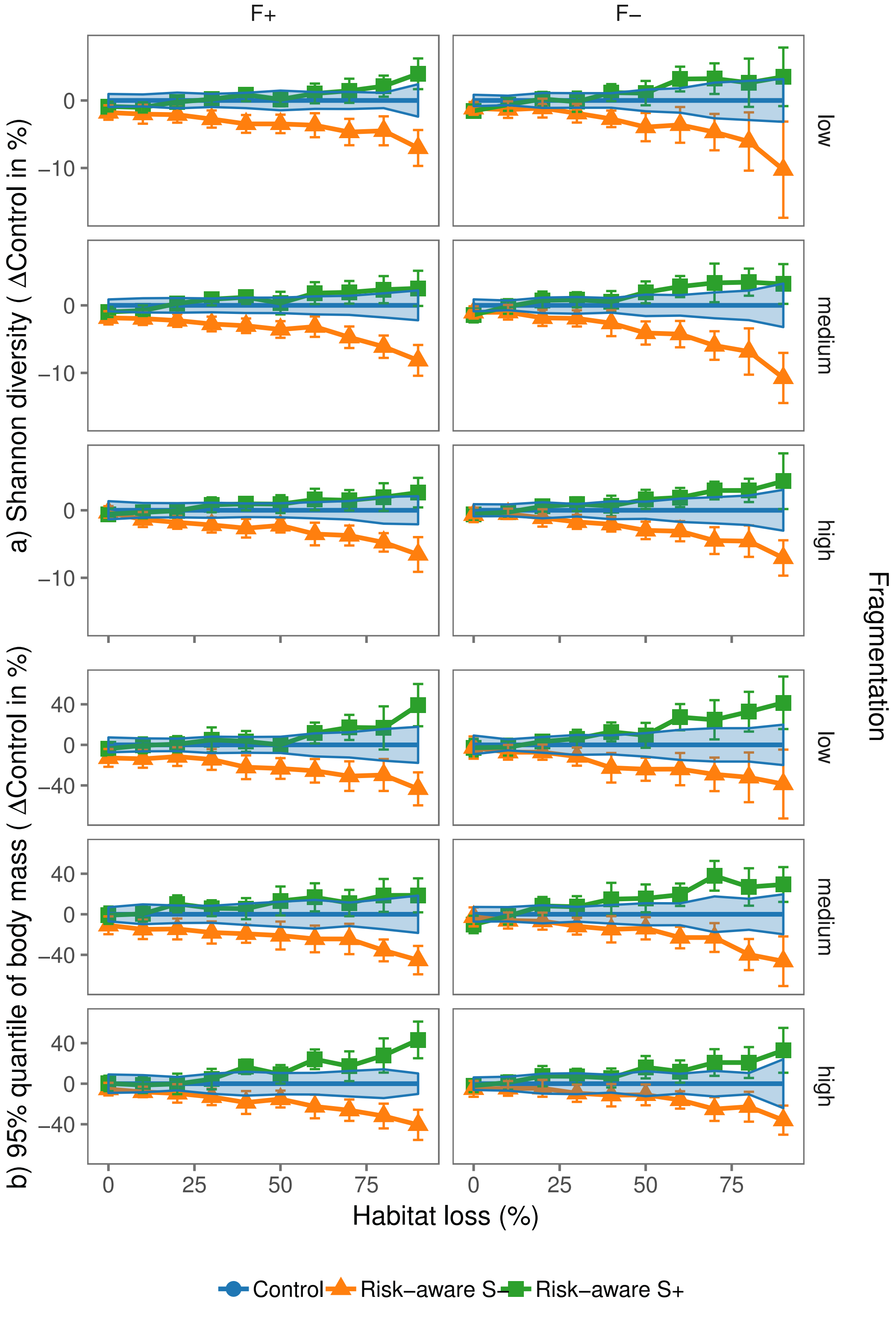

Fig. 3.3. Deviation of diversity and 95% quantile of body mass of risk-aware communities facing habitat loss and fragmentation for the two different food scenarios in comparison to the control community. Plots show the deviation in diversity and median home range size of the risk-aware community (orange triangles and green rectangles) from the control (blue circles). For risk-aware communities, two different landscapes of fear were assumed. In S^{-}-scenarios (orange triangles) risky patches remain, in S^{+}-scenarios (green rectangles) safe patches remain. No edge effects were present in these simulations.

-1504.2, df: 8). Ranking the effects of different habitat properties on the diversity of the prey community showed that the landscape scenario and the interaction between a high degree of fragmentation and the distance range of the edge effect were the main drivers of prey diversity (Fig. 3.4). Overall, fragmentation shaped the interaction between the total biomass and Shannon diversity of the prey community (Fig. 3.5). Under low fragmentation, high diversity levels could be reached in high and low habitat quality, while under high fragmentation only lower levels of diversity were reached. Focusing on landscapes with the same habitat quality but different landscape scenarios, prey communities had a higher total biomass in landscapes where habitat patches with a high food availability remained (F^+, Fig. 3.6a). Regarding safety, total biomass was higher in landscapes with low fragmentation where risky habitat patches (S^-) remained. Shannon diversity of prey communities increased with habitat quality (Fig. 3.6b). In scenarios where risky habitat patches remained (S^-), the increase in diversity along with habitat quality was steeper than in scenarios where safe habitat patches remained (S^+), especially under high fragmentation.

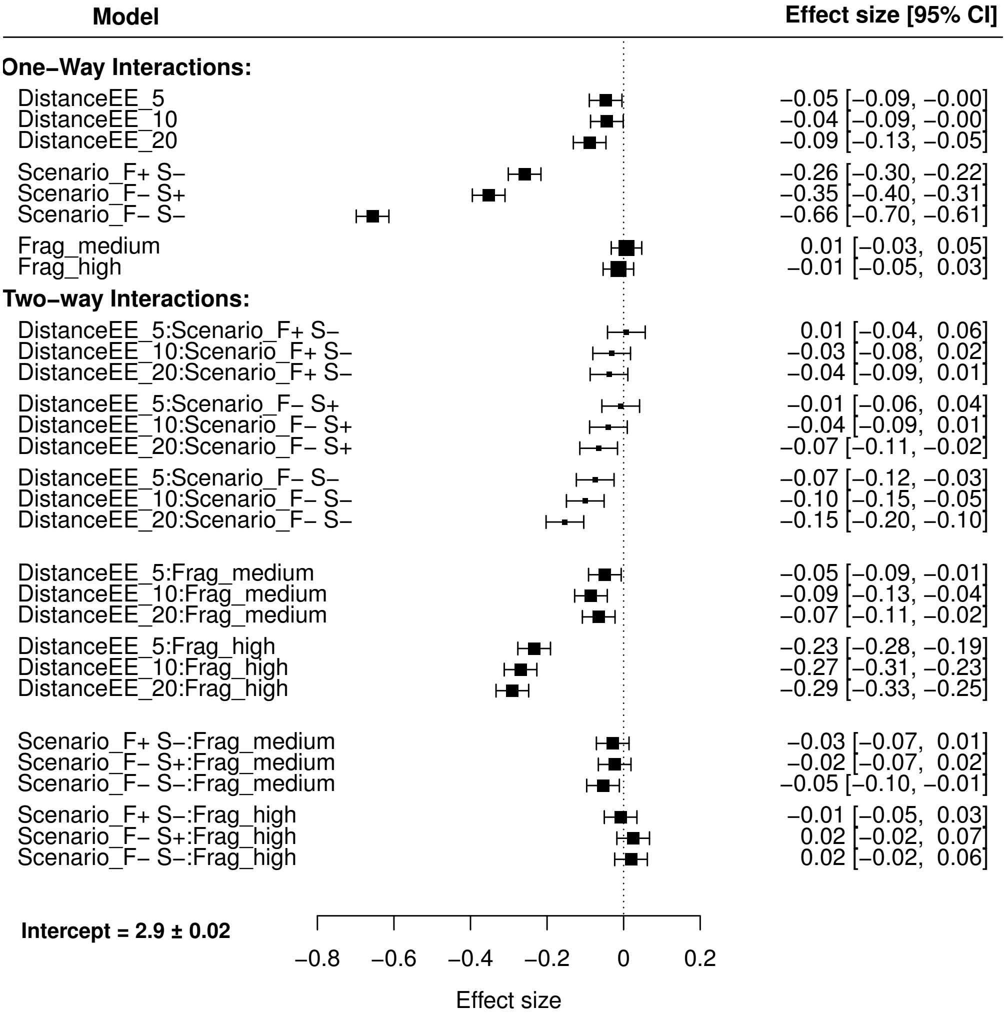

Fig. 3.4. Comparison of Shannon diversity in risk-aware prey communities. As a base model (intercept), the scenario F^+S^+ with no edge effects and low fragmentation was used. Values show the difference of the specific model from the base model. Habitat loss was set to 90%.

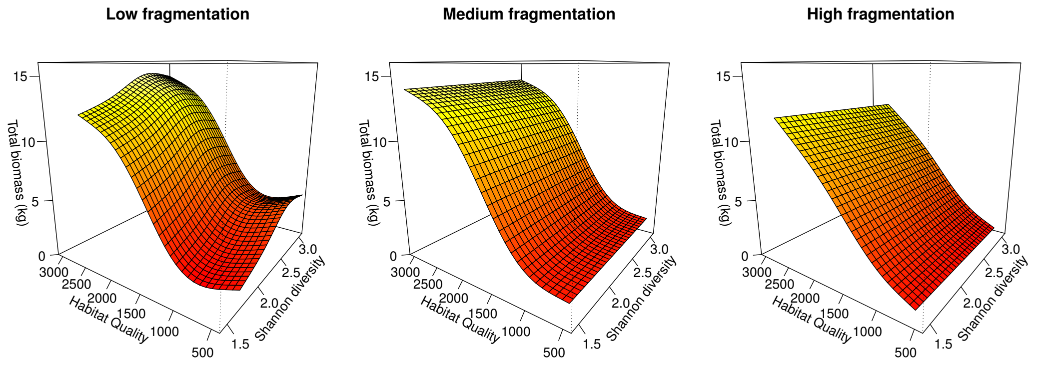

Fig. 3.5. Effect of habitat quality and Shannon diversity on total biomass for different degrees of fragmentation in risk-aware prey communities. Habitat loss was set to 90%.

3.5 Discussion

This study assessed the role of fear in terms of perceived predation risk in altering mammalian prey community responses to landscape changes such as fragmentation and habitat loss. We found that fear intensified the negative effects of fragmentation and habitat loss on prey communities. In risky environments, perceived predation risk was responsible for an additional reduction in prey diversity of up to 30%. Additionally, perceived predation risk reinforced changes in community composition, as large animals in the community were replaced by small animals. As for habitat properties, our results revealed that safe landscapes with a low degree of fragmentation promote the highest prey diversity. These results underline the importance of considering risk effects and assessing associated habitat properties when estimating community responses to landscape changes.

3.5.1 Impact of fear on prey diversity and community composition under habitat loss

General model predictions regarding habitat loss agree well with classical findings on the negative correlations between habitat loss and species diversity (e.g. Brooks et al., 2002; Hanski, 2011). With the inclusion of fear, the model results show that the magnitude of diversity losses is driven by perceived predation risk in the remaining habitat. In risky habitat remnants (S^{-}), the decrease in diversity under habitat loss was stronger than in control communities that did not respond to perceived predation risk. In contrast, the diversity of animal communities living in safe habitat remnants (S^{+}) decreased less sharply than in control communities. These results support findings on the importance of shelter availability for prey animals (Lima, 1998). Positive effects of safe areas on prey communities have been shown, especially in fish communities, such as in coral reefs where fish abundance and richness increase with refuge availability (Caley and St John, 1996; Hixon and Beets, 1993).

Diversity losses in risky habitat remnants were the result of decreasing numbers of individuals and decreases in large animal species. Higher vulnerability of large animals under habitat loss is consistent with theoretical assumptions (Buchmann et al., 2013; Ewers and

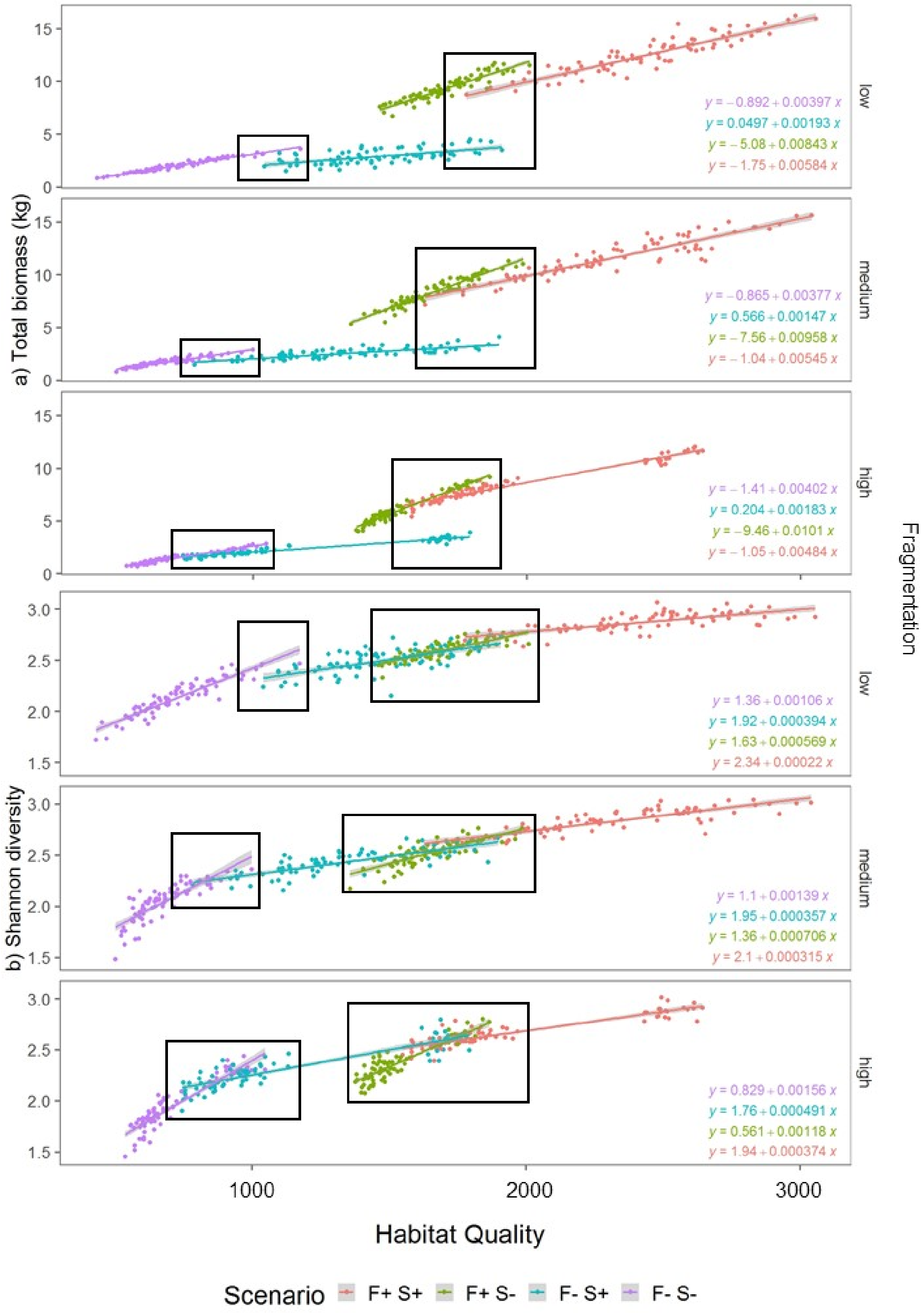

Fig. 3.6. Effect of habitat quality on Shannon diversity (a) and total biomass (b) in risk-aware prey communities for varying degrees of fragmentation. Each point represents a single prey community. Regression lines were fit using a linear model and equations are given in the corresponding color. Grey areas represent the 95% confidence interval of the regression line. Black rectangles mark areas in which different scenarios have the same habitat quality. Habitat loss was set to 90%.

Didham, 2006; Haskell et al., 2002), although the relationship between body size and extinction risk remains unclear in empirical studies (reviewed in Henle et al., 2004). Small species could establish their home range in small safe patches, since these provided sufficient food for them. Large animals had to include several small patches of safe areas in their home range or many risky patches, both resulting in long movement distances within the home range. As a consequence, movement costs exceeded food intake and the animals failed to find a home range in the landscape.

If mostly safe habitat patches remained (S^+), the diversity and species richness of risk-aware communities was similar or even slightly higher than in control communities. Especially in the scenarios with low food availability (F^-), communities consisted of larger animals compared to control communities. These findings suggest that positive effects of safe habitats can reduce the negative consequences of at least moderate habitat loss and fragmentation. Safe habitat patches have two advantages for foraging animals: First, animals have lower energy costs in these patches, for example due to a lower level of vigilance (Lima, 1998). Second, animals can have a higher food intake, since they are not disturbed by predators. Both mechanisms increase prey animals' food gain from safe patches and thus allow for smaller home ranges. Reduced movement costs and increased food intake favor large animals in particular, since they are now able to establish a home range within a small area. In mammals, for example, a reduction in cover can decrease the abundance of the dominant species and shift the size distribution towards smaller animals (Spencer et al., 2005). Another study on herbivores in southern Africa showed that large and medium-sized herbivores are most affected by disturbances (Wallgren and Skarpe, 2009).

3.5.2 Impact of fear on prey space use under landscape changes

Perceived predation risk affected foraging behavior and home range establishment under conditions of landscape change. Adapted foraging behavior of risk-aware animals had consequences for the level of food resources. Risky patches received lower foraging pressure, while foraging in safe patches was increased. This heterogeneous resource exploitation was even stronger under high habitat loss and could induce trophic cascades. Indirect effects of fear (trait-mediated indirect interactions) on food plant communities, such as the trophic cascade between aspen, elk and wolves (Ripple et al., 2001), have been extensively investigated, although their magnitude and importance can vary greatly between ecosystems (e.g. Abrams, 1991; Ripple and Beschta, 2004; Schmitz et al., 2004; Werner and Peacor, 2003). Our model results imply that these effects will increase with habitat loss. Furthermore, food patches in risky environments with low food productivity received more foraging by small animals, while patches in safe environments were foraged by animals with a higher body mass diversity. Since foraging efficiency and behavior of animals is body-mass dependent (Bakker et al., 2006; Olff and Ritchie, 1998), it is likely that food plant communities will be affected by changes in body mass of foraging animals.

As a consequence of altered feeding in risky and safe habitats, home range sizes of risk-aware animals differed from those of control animals, in that larger home ranges could be maintained if mostly risky habitat remained and smaller home ranges if safe habitat remained. These results fit with assumptions that the giving-up density of animals varies between patches with different predation risks (Brown, 1988). In order to have the same food intake, animals need to forage in more patches in risky landscapes compared to safe landscapes. Such increases in foraging area can be reduced by temporal risk allocation (Lima and Bednekoff, 1999), where animals limit their foraging activities to periods of low predator activity. An implementation of temporal risk allocation was beyond the scope of this study, but should be assessed in future studies.

3.5.3 Habitat properties

Although research on landscape changes often focuses on the quantitative availability of habitat and its fragmentation, there is increasing evidence that also the quality of the remaining habitat is a key factor in determining animal community patterns under landscape changes (Fleishman et al., 2002; Mortelliti et al., 2010). In this study, we showed that the total biomass and diversity of the community increase with overall habitat quality, but that the strength and shape of this increase is driven by specific habitat properties. Overall, landscapes with a low degree of fragmentation and a high food and shelter availability supported the most diverse prey communities with the largest total biomass. Fragmentation affected prey communities in two different ways: Firstly, the decrease in the size of remaining habitat patches reduced the number of large animals in the prey community, as they could not establish a home range in the remaining small habitat patches. This led to a decrease in diversity with increasing fragmentation. From the theoretical assumptions, it is assumed that animals with a larger body size are more strongly affected by fragmentation effects (Ewers and Didham, 2006). However, empirical studies have yielded mixed results on the relationship between body size and extinction risk under fragmentation (Henle et al., 2004).

Secondly, edge effects became stronger under high fragmentation. Due to the increasing number of edges, perceived predation risk in the remaining habitat patches increased more strongly than in low fragmented landscapes where habitat cores were not affected by edge effects. This increase in the overall risk led to a decrease in the total biomass and the diversity of the prey community, since food in risky patches was less accessible to the animals. Especially in landscapes where the remaining habitat was already risky, edge effects further reduced the diversity of the community, leading to a steep increase of diversity along with habitat quality in highly fragmented landscapes.

Increased predation risk at habitat edges is often associated with anthropogenic fragmentation, for example through the introduction of new predators such as cats (Doherty et al., 2015). Furthermore, humans themselves increase the perceived risk through disturbances and hunting (Ciuti et al., 2012; Kuijper et al., 2016). With increasing urban sprawl and road construction, these effects are likely to increase. Another reason for increased predation risk at edges could be mesopredator release. Crooks and Soulé (1999) found that the reduction or disappearance of large carnivores that are more vulnerable to habitat fragmentation leads to increases in small predators. Consequently, since large carnivores are the first to disappear at habitat edges, overall predation pressure by mesopredators at edges will increase, affecting local prey communities. However, animals are not always able to perceive increased predation risk at edges. "Ecological traps" occur if the habitat quality that an animal perceives does not match the true quality of the habitat (Battin, 2004; Gates and Gysel, 1978; Robertson and Hutto, 2006). Such a mismatch between perceived and real habitat quality is often associated with anthropogenic landscape changes (Best, 1986; Hale and Swearer, 2016; Schlaepfer et al., 2002). Future studies should assess how the landscape of fear is altered at habitat edges in order to better predict the consequences for the prey community. In this context, animals living at urban edges could provide a well-suited study system.

3.5.4 Model linkage to ecological systems

The model presented here allows us to assess the magnitude and consequences of perceived predation risk for prey communities facing landscape changes. Thus, it presents a useful extension to classical ecological experiments and field studies, since it explores communities and landscape scenarios which would be difficult to handle empirically.

In the model, we assumed the same landscape of fear for all prey animals in a community. However, predation risk is often negatively correlated with body size, because top predators affecting the largest prey in a community are rare (Preisser and Orrock, 2012; Urban, 2007a). Therefore, large animals should perceive a lower predation risk compared to small animals. However, if predator diversity is high, it can be assumed that larger prey animals perceive predation risk from larger predators. Future studies should investigate how the landscape of fear is affected by different predators and whether there are changes with the body mass of the prey. Our study focuses on non-lethal predator effects, which allows us to estimate their effect size on prey communities facing landscape changes. This improves our understanding of prey community structures, but further research is required to link the effects of lethal and non-lethal predator effects on prey communities experiencing landscape changes. In this context, demographic processes that are ignored in this study should be included. Extending our framework to dynamic community models is possible, but beyond the scope of the present study. Nevertheless, even the static approach led to community patterns that matched empirical observations (Buchmann et al., 2011; Prevedello et al., 2016).

3.5.5 Conclusions

In conclusion, our study provides the first comprehensive assessment of the role of perceived predation risk in altering prey community responses to landscape changes. Our findings show that perceived predation risk can increase losses in prey diversity by up to 30% and reinforces extinction of large prey animals. Regarding the management and conservation of prey species facing landscape changes, our results suggest that the highest prey diversity will be supported by large safe patches. To decrease negative impacts of habitat edges, landscape fragmentation should be reduced. Our results thereby provide decision support for modern conservation efforts that go beyond single species approaches, taking impending changes in species interactions into account.

3.6 Declaration of interest

None.

3.7 Acknowledgements

This work was supported by Deutsche Forschungsgemeinschaft in the framework of the BioMove Research Training Group (DFG-GRK 2118/1).

3.8 Supplementary Material

Appendix B.1: ODD-Protocol
Appendix B.2: Additional Figures

CHAPTER 4

Intra- and interspecific differences in the landscape of fear

Title	Individual landscapes of fear: Intra- and interspecific differences in risk perception modify space use, survival probability and prey community structure
Authors	Lisa Teckentrup, Ulrike E. Schlägel and Florian Jeltsch
Status	Ready for submission
Keywords	Predator-prey interactions, individual trait variation, personality, landscape of fear, perceived predation risk, home range, biodiversity, community

4.1 Abstract

Landscapes of fear allow us to gain a mechanistic understanding about animal movement decisions. Although the landscape of fear is acknowledged as a unique trait of an individual, it is commonly assessed on the population level. Thereby, individual differences in risk perception are ignored. However, an evaluation of individual differences and their consequences on community structure is crucial to enhance our understanding of predator-prey interactions. Since the experimental estimation of individual variation at the community level requires an enormous effort, we used an established individual-based and spatially-explicit model that simulates home range formation in prey communities and allows to derive community patterns. We modified the model to include individual differences in risk perception of prey animals and assessed how these differences affected space use, survival probability and community structure in comparison to prey communities in which individuals did not differ in their risk perception. Results showed a spatial segregation between animals differing in their risk perception in communities with individual variation. Animals with a high risk perception used safer areas of the landscape resulting in a higher survival probability while animals with a low risk perception preferred areas with a high energy gain. Prey community structure was correlated to the configuration of the landscape of fear. In safe and risky landscapes, communities with a high proportion of animals with a high risk perception (safe landscapes) respectively low risk perception (risky landscapes) had the highest diversity. In landscapes of fear with a heterogeneous risk distribution the highest diversity was reached by prey communities with variation in risk perception. Our study provides a first assessment of the consequences of intra- and interspecific differences in risk

perception on prey community structure. Thereby, it offers new insights in the consequences of predator-prey interactions and underlines the importance of including individual trait variation in community ecology.

4.2 Introduction

The concept of the "landscape of fear" has been developed in order to visualize the spatial distribution of predation risk that prey animals perceive (Laundré et al., 2001; Laundré et al., 2010). Landscapes of fear allow us to gain a mechanistic understanding about animal movement decisions especially when combined with further information such as energy landscapes (Gallagher et al., 2017). Since its development, landscapes of fear have been assessed for a number of animals such as rodents (van der Merwe and Brown, 2008), marine mammals (Wirsing et al., 2008), monkeys (Willems and Hill, 2009) and ungulates (Iribarren and Kotler, 2012). Although landscapes of fear are defined as "a behavioral trait of an individual animal" (Bleicher, 2017), they are "more commonly used on the population level" (Bleicher, 2017). Thus, by applying landscapes of fear to the population level, studies typically average out differences between individuals. Therefore, they fail to identify individual variation in space use due to differences in the predation risk that animals perceive.

Individual differences in space use and movement have recently been identified as a link between animal personality and spatial dynamics in animal populations (Spiegel et al., 2017). Personality-dependent differences in movement can result in personality-dependent habitat preferences (e.g. Pearish et al., 2013; van Overveld and Matthysen, 2010) and spatial structure of the population (e.g. Bonnot et al., 2015; Pruitt and Goodnight, 2014). These spatial differences can then have implications for many ecological processes such as intraspecific competition, niche partitioning or disease spread (Farine et al., 2015; Spiegel et al., 2017). Moreover, individual trait variation plays a fundamental role in many ecosystem processes (Albert, 2015; Bolnick et al., 2011). Recent experiments in plant communities revealed that individual variation increases species richness, productivity and stability (Agashe, 2009; Fridley and Grime, 2010). Similarly, including individual variation in a classical Rosenzweig-MacArthur model yielded increased stability of the predator-prey community (Okuyama, 2008). Thus, it can be expected that individual variation in landscapes of fear has strong consequences on community structure.

Causes for individual variation in risk perception are manifold. Clearly, one source of variation is the personality of the animal. The shy-bold continuum is found in many animal populations (Sih, 2004; Wolf and Weissing, 2012). For example, bold grey mouse lemurs tend to use riskier foraging options compared to shy individuals (Dammhahn and Almeling, 2012). Indeed, differences in predation risk could be the source how personalities in animal populations are created (Dingemanse et al., 2009). Further factors responsible for individual differences in predation risk are age (Réale and Festa-Bianchet, 2003; Wright et al., 2006), sex (Fitzgibbon, 1990), nutritional status (Godin and Crossman, 1994; Horat and Semlitsch, 1994; Murray, 2002) and body size (Preisser and Orrock, 2012; Urban, 2007a). Likewise, environmental conditions and habitat characteristics are of major importance in driving the animal's risk perception (Pettorelli et al., 2015; Sih, 2004).

Current studies of landscapes of fear not only ignore the role of intraspecific differences in the landscape of fear, they also do not account for interspecific differences. With the majority of studies focusing on the population level (Bleicher, 2017), a comparison between species and a prediction of consequences on community patterns is not possible. One reason why the community level has not yet been studied in more detail is the enormous effort of related experiments. In particular, addressing potential consequences of individual variation in the landscape of fear on the community level would require an enormous experimental effort that involves the monitoring of multiple individuals of interacting species with a high temporal resolution and over long timespans. Such difficulties could potentially be overcome by combining classical studies on giving-up density with video recordings (Bedoya-Perez et al., 2013) or by the usage of novel telemetry systems (e.g. ATLAS, Toledo et al., 2016; Weiser et al., 2016), but the amount of data produced and their handling remains highly challenging.

Given these empirical limitations, we here present a modelling study that evaluates the consequences of variation in individual risk perception on prey space use and prey community structure. Our study is based on an established individual-based and spatially-explicit model that simulates home range formation in a prey community and allows to derive community patterns (Buchmann et al., 2011; Teckentrup et al., 2018). We modified the existing model to assess how variation in risk perception affects prey space use, survival probability and community structure in comparison to a community without variation in risk perception. By using differently structured landscapes of fear we furthermore evaluate the effect of habitat characteristics on the prey community. Specifically, we ask the following questions: (1) How does inter-individual variation in risk perception affect prey space use, survival probability and community structure? (2) How does the configuration of the landscape of fear affect prey community structure in communities with and without individual variation in risk perception?

4.3 Methods

4.3.1 Model overview

We used an individual-based and spatially-explicit model to simulate home range formation of a mammalian prey community. The model is based on Teckentrup et al. (2018) using a modelling approach by Buchmann et al. (2011). A detailed documentation following the ODD protocol (Grimm et al., 2006; Grimm et al., 2010) is given in the Supplementary Material, Appendix C.1. Here, we only provide a brief description of the model and its most important processes.

Each model run starts with the generation of the landscape (see Landscape). In each step of the model a prey animal is drawn from a regional species pool (see Regional species pool) and gets assigned an individual risk perception (see Individual risk perception). Next, the animal searches for a home range in the landscape (see Home range search). Cells are added to the home range by using a trade-off between food resources and perceived predation risk. The home range needs to contain enough food resources to fulfill the daily energy requirements of the animal. If the animal has found a suitable home range it consumes the food resources within. Otherwise it is excluded from the community. Next, a new prey individual is chosen from the regional species pool. While more animals establish a home range in the landscape, food resources are depleted and the probability of animals to fail to find a suitable home range increases. If 100 animals were not able to find a home range, we assume that the community is saturated (see Community saturation). Afterwards, prey animals are killed based on a probability driven by the mean safety of their home range (see Predation mortality). Predators are not modeled explicitly but represented by the landscape of fear and by the killing of prey animals after home range establishment.

4.3.2 Landscape

Landscapes had a size of 129×129 cells with each cell representing $4\,\mathrm{m}^2$. The landscape consisted of two layers, the food landscape and the landscape of fear. We assumed that all prey animals are herbivorous and feed on the same food resource. Food resources (*p-food*) were distributed by using a well-established midpoint-displacement algorithm yielding realistic fractal landscapes (Körner and Jeltsch, 2008; Saupe, 1988). We used a moderate variance in the displacement of points (σ^2=30) and a medium degree of fragmentation (spatial autocorrelation, H=0.5). We scaled food resources to an average resource availability of 2.74 g dry biomass $\cdot$grid cell$^{-1} \cdot$ day^{-1}, a value which is typical for shrub- and grasslands (Whittaker, 1975). From these food resources 20% were available to the prey animal. The remainder was lost to other taxa or was not consumable (Buchmann et al., 2011).

The landscape of fear represented the spatial distribution of perceived predation risk. We used a relative scale for the safety in the landscape of fear (*p-safety*) with values ranging from 0 (risky cell) to 1 (safe cell, refuge). Depending on the individual degree of risk perception of the prey animal, the magnitude how much perceived predation risk affected the animal's decisions was varied (see Individual risk perception and Home range search). Perceived predation risk was in general negatively correlated to the food landscape, i.e. patches with a high food availability had a low safety and vice versa (see Teckentrup et al., under review for the consequences of different correlations between food and fear landscape). A negative correlation between food and safety represents a common situation that animals face in their environment (Lima, 1998). We tested four different landscapes of fear varying in the mean and variance of safety (Fig. 4.1). The overall safety decreases from safe via medium to risky landscapes of fear implying a decreasing abundance of predators. In bimodal landscapes of fear, mean safety is similar to the medium landscapes of fear but cells are either very risky or very safe. This represents a situation in which the predator is constrained to specific areas and not able to reach the prey in other areas, for example due to thick vegetation.

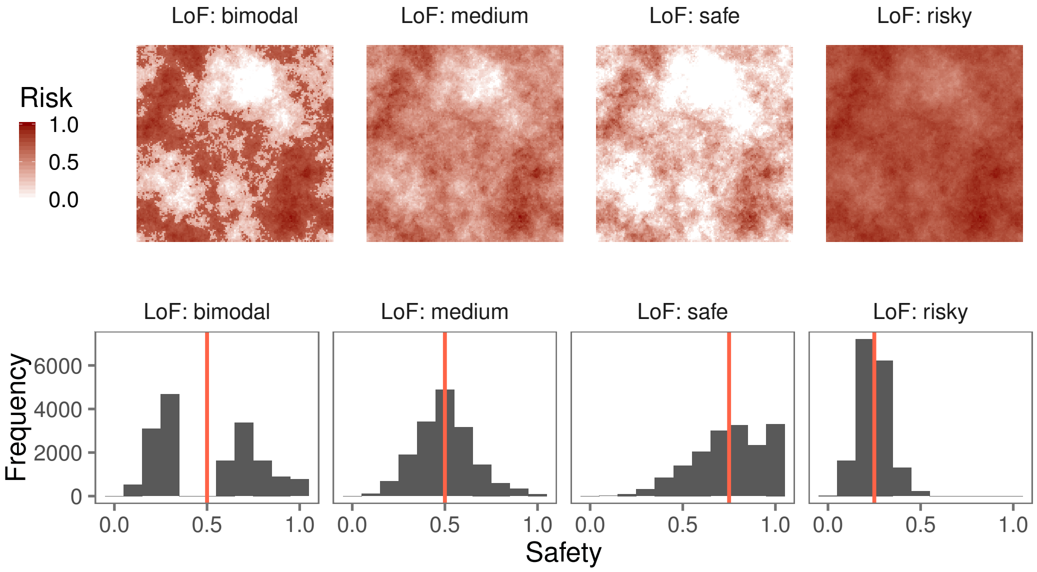

Fig. 4.1. Exemplary landscapes of fear (top) and the corresponding histogram of the safety distribution (bottom). The red line marks the mean safety of the landscape.

4.3.3 Regional species pool

Prey animals are characterized by their body mass and their individual risk perception. The body mass is drawn from a "body mass input distribution" representing the regional species pool. The body mass input distribution is a truncated power-law distribution with an exponent of -1.5 defining the probability density of a specific body mass (Buchmann et al., 2011; Buchmann et al., 2012). The distribution covers body masses ranging from 10g (e.g. mice and voles) to 1kg (e.g. rabbits). This is a typical range for an herbivorous, small mammal prey community that shares the same generalist predators (e.g. foxes, birds of prey). For an evaluation of the community structure, prey animals are assigned to specific species based on their body mass. Therefore, the body mass input distribution was divided into 50 body mass intervals. We defined the right border of the body mass interval (in g) by $10 + N^{1.77}$, with N as the species number from 1 to 50. The left border of the interval was the right border of the previous species and 10g for the first species. The exponent 1.77 was chosen to cover the whole range of body masses. We chose a number of 50 species to have a fine-scaled resolution of animals in the community.

Based on the body mass, additional traits of the animal, namely daily feeding rate, movement costs, maximum home range size and the resolution at which it can exploit food resources, were calculated using allometric relationships and assigned to the individual (see Supplementary Material, Appendix C.1, Table C.3 for details).

4.3.4 Individual risk perception

Besides allometric traits, animals get assigned an individual risk perception. This risk perception drives the decision of animals which cells they integrate in their home range and how much food they exploit in each cell of the home range. An individual risk perception of 0 indicates that the animal does not take perceived predation risk into account. With increasing risk perception the influence of perceived predation risk on the animal's decisions grows larger (see Home range search for exact equations).

We tested different distributions of risk perception in order to assess how variation in risk perception affected prey community structures (Fig. 4.2). Even though the occurrence of intra- and interspecific differences in risk behavior has been verified for many species (Preisser and Orrock, 2012; Sih, 2004), studies rarely assess which proportion of a population or community shows which behavior. Thus, we used different scenarios for the distribution of risk perception in the model in order to evaluate their potential consequences.

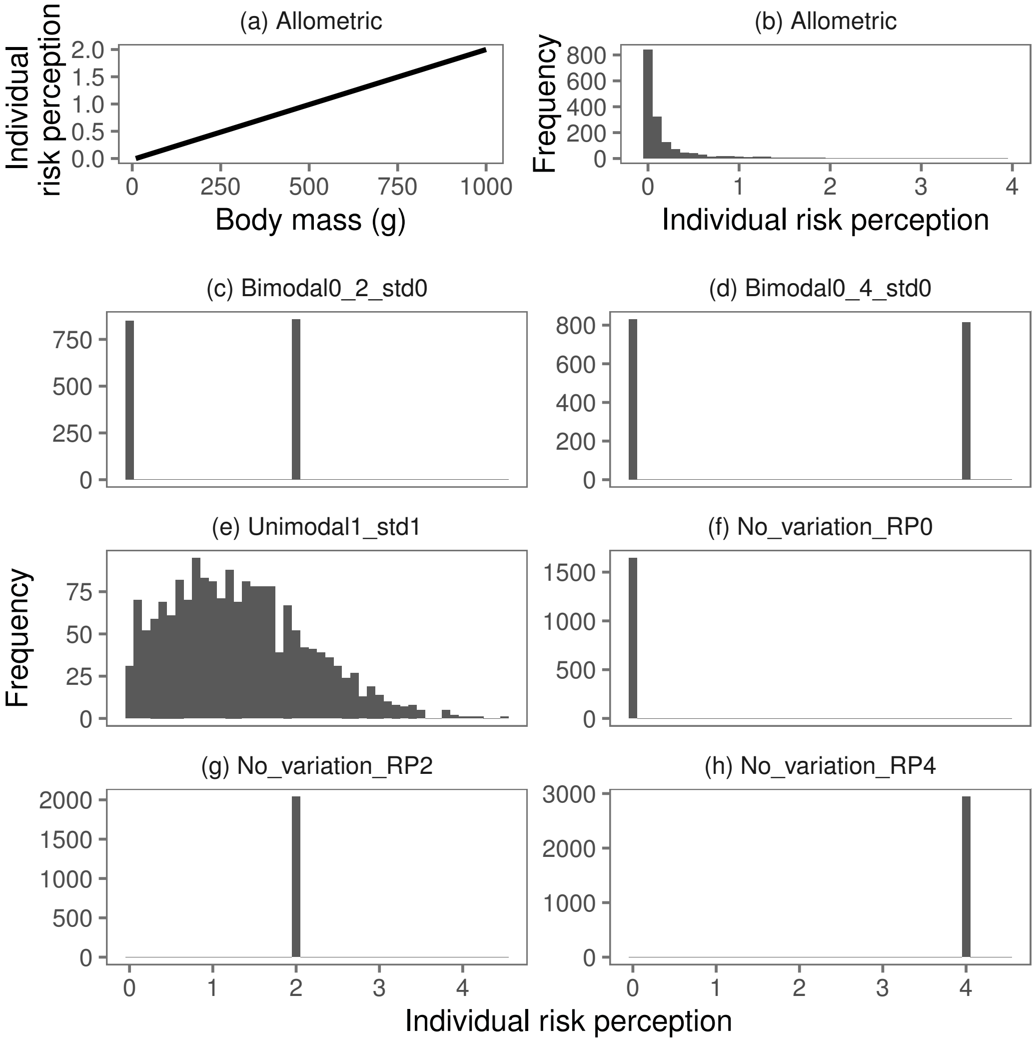

Fig. 4.2. Relationship between individual risk perception and body mass for prey communities with an allometric scaling of risk perception (a) and tested distributions of risk perception (b-h).

A common assumption is that antipredatory behavior including risk perception is related to the body mass of an animal (Preisser and Orrock, 2012). However, studies mostly focus on intraspecific differences in body size (e.g. Urban, 2007b) and not on interspecific differences. In order to estimate interspecific effects of body size on antipredatory behavior, Preisser and Orrock (2012) performed a meta-analysis examining species-level responses to predation risk. One of their findings was a decrease in open habitat use with increasing body size of the prey, suggesting a higher risk perception in large animals. Based on this result, we included a scenario in the model in which risk perception of the prey community increased with body mass (Allometric, Fig.4.2a).

Furthermore, differences in risk behavior are often reported in the context of animal personality. These differences can be in a continuum of behavior (Sih, 2004) or can be distinct strategies (e.g. in bluegill sunfish: Werner et al., 1981; Wilson, 1998). Overall, the environmental situation that animals encounter drives the evolution of individual differences in animals (Sih, 2004). In the model, we included two scenarios with distinct strategies of animals. Therefore, we used a bimodal distribution, one in which individuals randomly get assigned a risk perception of either 0 or 2 (Bimodal0_2_std0, Fig. 4.2b) and one in which they get assigned a risk perception of 0 or 4 (Bimodal0_4_std0, Fig. 4.2c). Additionally, we tested a scenario in which risk perception of animals was drawn from a normal distribution with a mean of 1 and a standard deviation of 1 (Unimodal1_std1, Fig. 4.2d).

We compared these scenarios with variation in risk perception to scenarios in which all animals of the prey community had the same risk perception. As a baseline scenario we used a community in which all animals were unaware of predation risk in the landscape (No_variation_RP0, Fig. 4.2e). Furthermore, we tested two other communities without variation in risk perception, one where all animals had a risk perception of 2 (No_variation_RP2, Fig. 4.2f) and one in which animals had a risk perception of 4 (No_variation_RP4, Fig. 4.2g).

4.3.5 Home range search

After the assignment of traits to the animal, this animal searches for a home range in the landscape. The home range must contain enough food resources to match the animal's daily energy requirements. All animals are central place foragers which means that they frequently return to their den within the home range. At the beginning of the home range search the animal randomly chooses a habitat cell and establishes its den therein. Outgoing from the den, neighboring cells are added to the home range until the animal's daily energy requirements are fulfilled. The animal has a perceptual range of 1 and can therefore sense food availability and predation risk (*p-safety*) in the neighboring cells. It chooses the cell to be added next to the home range from the neighboring cells of the cell that was previously added to the home range. The decision for one of these neighboring cells is based on food gain and perceived predation risk. For the decision, which of these cells is added to the home range the suitability of a cell is calculated by the "μ/f"-rule (death per unit energy Gilliam and Fraser, 1987):

$$\text{Suitability} = \text{Food gain}/(1 - \textit{p-safety})^{i-rp} \tag{4.1}$$

The exponent *i-rp* is the individual risk perception of the animal that was assigned before. Animals choose the cell with the highest suitability, i.e. they minimize the probability of death per unit energy. If several cells are equally suitable, the cell with the smallest distance to the den is chosen.

Food gain is the amount of energy that the individual can gain from a certain cell while accounting for the movement costs of foraging in this cell. It is calculated by:

$$\text{Food gain} = \text{Food intake} - \text{Movement costs} \tag{4.2}$$

The amount of food intake is the arithmetic product of food availability in the cell (*p-food*), the individual magnitude of food exploitation (*i-foodshare*) depending on body mass and the perceived predation risk:

$$\text{Food intake} = \textit{p-food} \cdot \textit{i-foodshare} \cdot (2 \cdot \textit{p-safety})^{\textit{i-rp}} \tag{4.3}$$

The parameter *i-foodshare* is used to distinguish the different consumption levels of local food resources by prey individuals of different body masses. The factor 2 was chosen in a way that the food intake of animals with risk perception (*i-rp* >0) in cells with a medium safety (*p-safety* =0.5) equals the food intake of animals that are unaware of predation risk (*i-rp* =0).

Movement costs are the allometric energy costs of an animal (*i-lococost*) for moving during foraging multiplied with the distance moved. Since the animal is a central place forager, we assume that it returns to its den each time when it has foraged in a cell. Movement costs are calculated by the product of the allometric costs and twice the distance to the den as the animal has to move back and forth to the cell in which it wants to forage:

$$\text{Movement costs} = \textit{i-lococost} \cdot 2 \cdot \text{distance}_{\text{den}} \tag{4.4}$$

When a cell was added to the home range, it is assessed whether the food gain from all cells in the home range is sufficient to fulfill the animal's daily energy requirements. If this is true, the animal stops the home range search, establishes its home range in these cells and consumes the food resources within. If energy requirements are not yet fulfilled, further cells are added to the home range until either the energy requirements are met or the home range size exceeds the maximum home range size. In the latter case, the individual is excluded from the community. We assume that this animal would migrate to another habitat patch outside of the modeled area or die.

4.3.6 Community saturation

During the simulation food resources are increasingly depleted by prey animals. This decrease in accessible food resources increases the number of animals that fail to find a home range. We assume that the community is saturated if 100 individuals have consecutively failed to find a home range. If such a high number of animals could sequentially not find a suitable home range, this indicates that the accessible food resources have been exploited and a further establishment of home ranges is not possible.

4.3.7 Predation mortality

After the saturation of the community, animals face predation mortality. The probability of being killed (P_{mort}) depends on the safety of the cells in the home range and the amount of food that the individual exploited in these cells. The amount of exploited food is a proxy for the time that an individual spends in a cell and thus defines how long the animal experienced a specific safety. We used a weighted geometric mean to calculate the overall safety of the home range (Safety$_{HR}$):

$$\text{Safety}_{HR} = \left(\prod_{i=1}^{n} p\textit{-safety}^{\text{food intake}} \right)^{\frac{1}{\sum_{i=1}^{n} \text{food intake}}} \tag{4.5}$$

with n as the number of cells in the home range.

The probability of being killed was then the inverse of the overall safety of the home range.

$$P_{\text{mort}} = (1 - \text{Safety}_{HR}) \tag{4.6}$$

This probability is compared to a random number between 0 and 1. If the random number is smaller than P_{mort} the animal is killed.

4.3.8 Simulation design and analyses

All simulations were conducted in NetLogo 6.0.2 (Wilensky, 1999). We tested each of the four prey communities with variation in risk perception (Allometric, Bimodal0_2_std0, Bimodal0_4_std0 and Unimodal1_std1) and each of the three different prey communities without variation in risk perception (No_Variation_RP0, No_Variation_RP2, No_Variation_RP4) in the four landscapes of fear (safe, medium, risky, bimodal). For each of these combinations 20 repetitions with varying food landscapes were performed. In order to further elucidate on the magnitude of risk perception we performed additional simulations for prey communities with a risk perception of 1, 3 and 5 and for prey communities with a bimodal distribution in risk perception where individuals had a risk perception of either 0 or 1, 3 respectively 5 in the four landscapes of fear. For these combinations we performed 10 repetitions. Statistical analyses were conducted in R, version 3.4.2 (R Core Team, 2017). Shannon diversity indices and species richness were calculated using the package "vegan", version 2.4-4 (Oksanen et al., 2017).

4.4 Results

4.4.1 Prey space use and survival probability

Risk perception affected animal's space use patterns (Fig. 4.3, Supplementary Material, Appendix C.2, Fig. C.4). Animals with a high risk perception established their home ranges mostly in safe areas of the landscape. In contrast, animals with a low risk perception used the whole landscape for home range establishment (Fig. 4.3). Patterns of giving-up density showed an increasing usage of safe areas in the landscape with increasing risk perception (Supplementary Material, Appendix C.2, Fig. C.4).

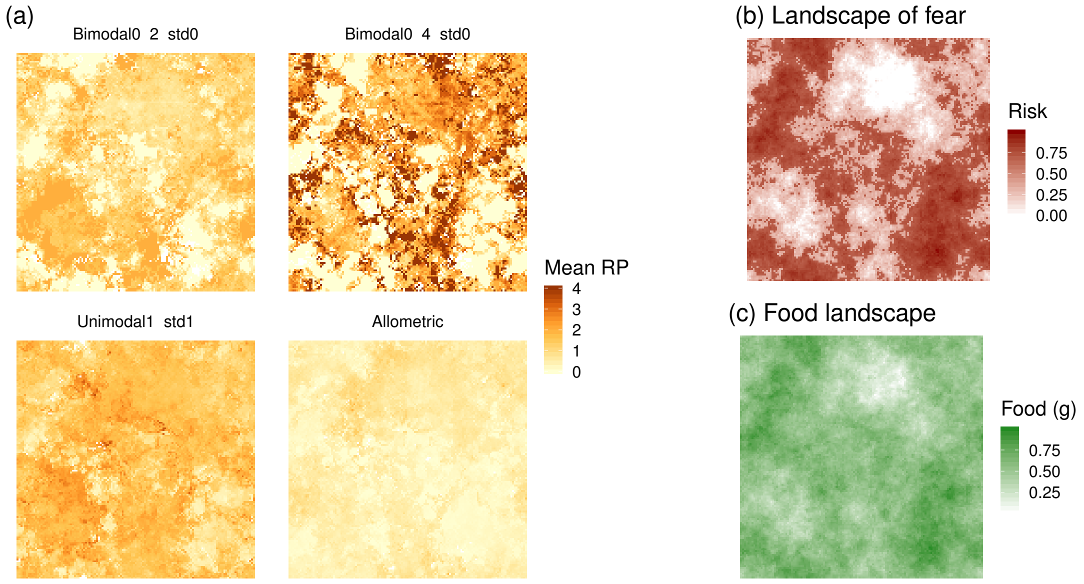

Fig. 4.3. Spatial patterns of prey animals based on individual risk perception for communities with varying risk perception (a). The color indicates the mean risk perception (mean RP) of all animals that integrated this cell in their home range. Patterns represent one exemplary simulation with a bimodal landscape of fear (b) and the food landscape shown in (c).

Modifications in space use due to individual risk perception consequently affected the overall safety of the home range (Fig. 4.4). For communities with variation in the individual risk perception (Bimodal0_2_std0, Bimodal0_4_std0, Unimodal1_std1 and Allometric, Fig. 4.4, second to fifth row) the safety of the home range increased with individual risk perception. This increase was strongest in bimodal landscapes. In prey communities without variation in risk perception (No_variation_RP0, No_variation_RP2, No_variation_RP4, Fig. 4.4, first row) safety of home ranges did not increase with increasing risk perception.

Differences in risk perception and the safety of the home range resulted in adapted survival probability of the prey animal (Fig. 4.5). In communities without variation in risk perception survival probability was similar to the mean safety of the landscape of fear. The degree of risk perception in the communities without variation had only weak effects on the survival probability. In bimodal, medium and risky landscapes of fear the highest survival probability was reached by prey communities in which all animals were unaware of predation risk (No_variation_RP0). In safe landscapes of fear, prey communities with a risk perception of 4 (No_variation_RP4) had the highest survival probability.

In communities in which animals differed in their individual risk perception survival probability increased with risk perception in all landscapes. If risk perception was larger than 1, the survival probability was higher than in communities without variation in risk perception. There is one exception to this case, namely in prey communities with allometric risk perception in risky landscape of fear. These communities had a lower survival probability

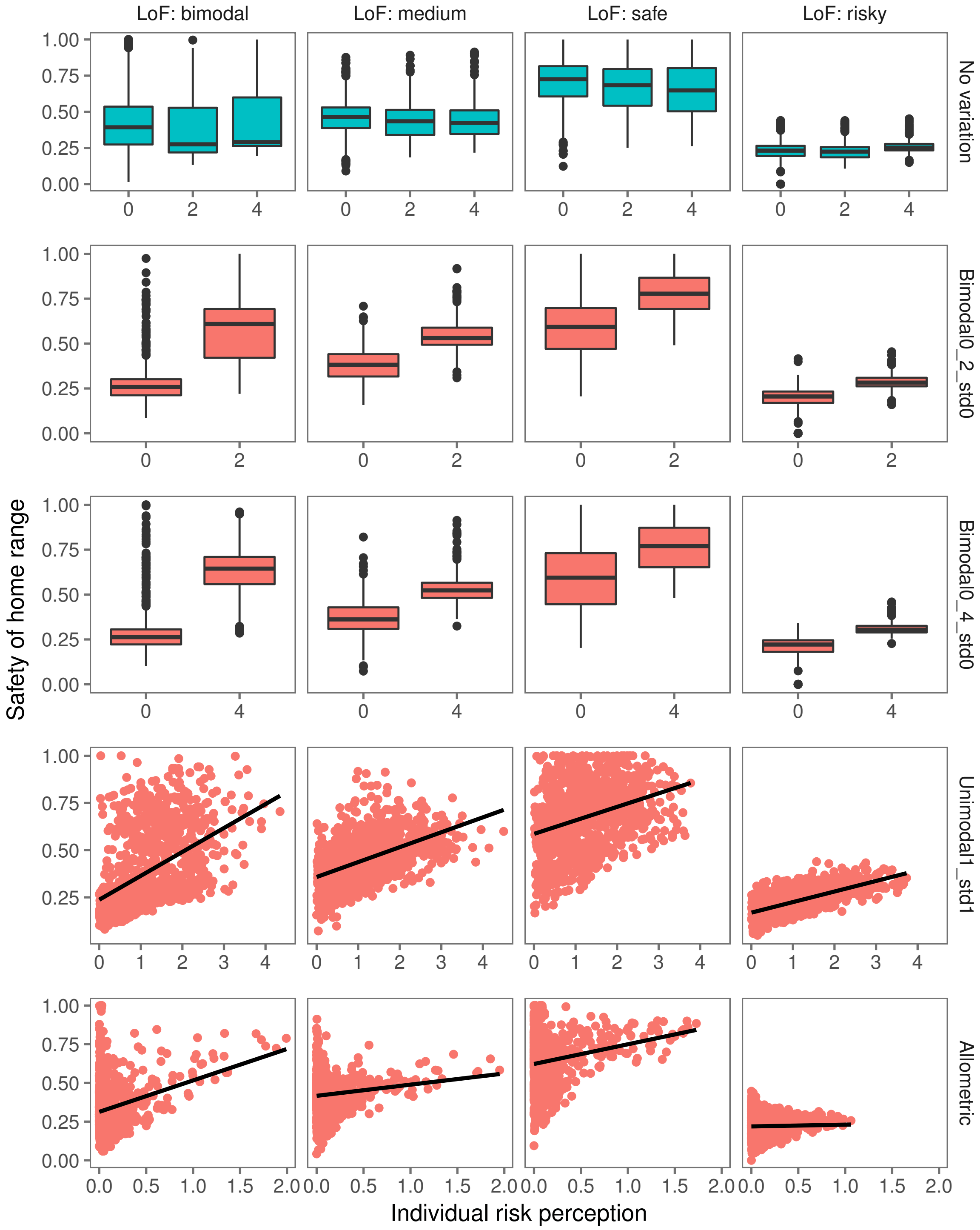

Fig. 4.4. Mean safety of home ranges for animals depending on their individual risk perception for prey communities with different distributions of risk perception (rows) and varying landscapes of fear (columns) in an exemplary simulation. Prey communities without variation in individual risk perception are marked in blue, prey communities with variation in red. For Unimodal1_std1 and Allometric a linear regression line (black) was fitted to the data.

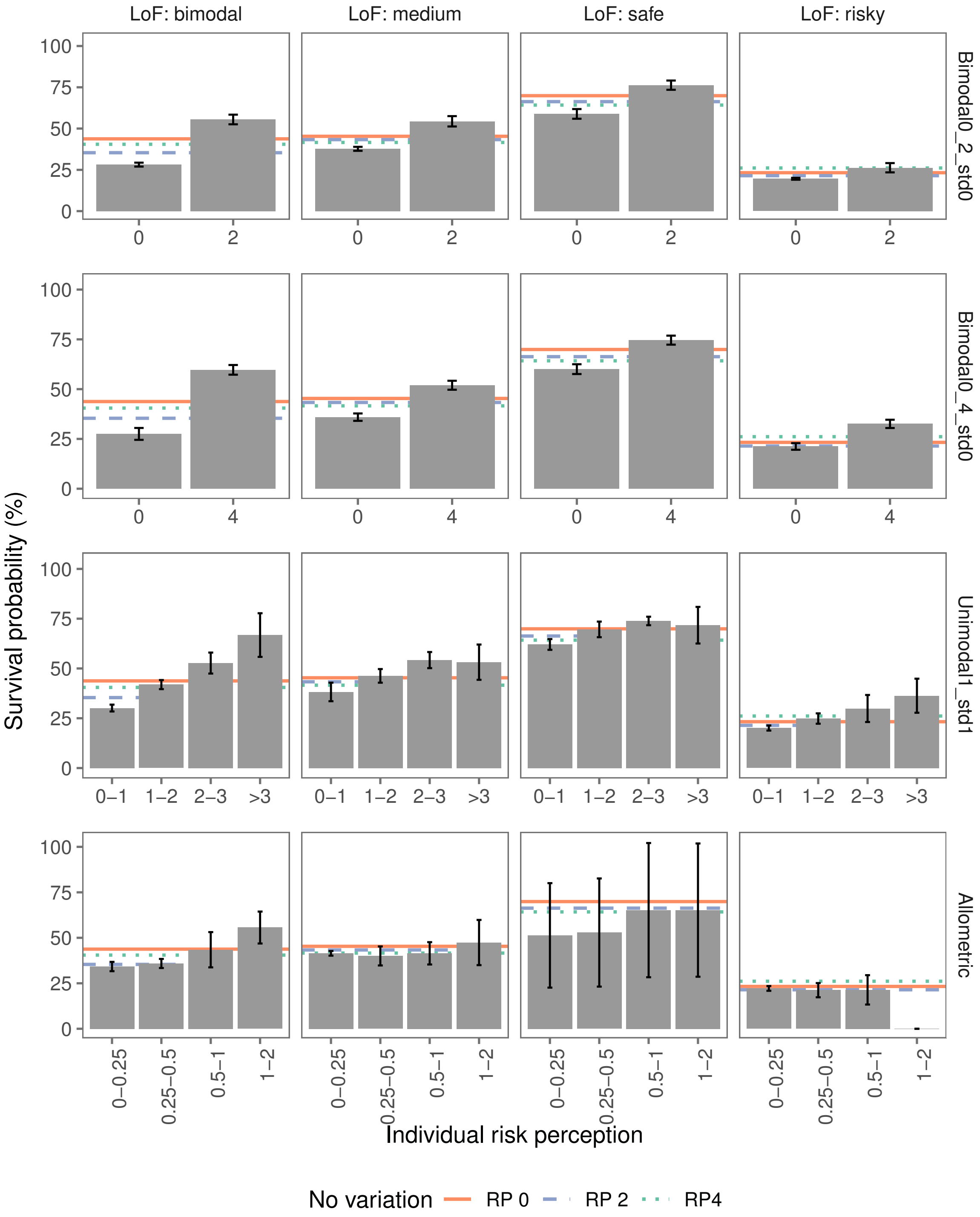

Fig. 4.5. Survival probability of animals depending on individual risk perception for varying landscapes of fear (columns) and distributions of risk perception in the community (rows). The lines represent the survival probability in prey communities without variation in risk perception. In the community with an allometric risk distribution, no animals with a risk perception above 1 were able to establish a home range in the risky landscape of fear.

for animals with a risk perception between 1 and 2 than animals in communities without variation.

4.4.2 Prey community structure

The distribution of risk perception in prey communities affected the community structure (Fig. 4.6). In bimodal landscapes of fear, prey communities in which animals differed in their individual risk perception (Bimodal0_2_std0, Bimodal0_4_std0, Unimodal1_std1 and Allometric) showed the highest diversity. Prey communities without a variation in risk perception showed a lower diversity. In medium landscapes of fear, prey communities had a similar diversity, only the prey community with a bimodal risk perception of 0 and 4 had a slightly higher diversity. In safe landscapes, communities that include animals with a high risk perception had the highest diversity. By contrast, in risky landscapes communities with a low risk perception showed the highest diversity. Regarding species richness and total biomass, patterns are similar to the patterns found for Shannon diversity. Only in bimodal landscapes prey communities with a risk perception of 2 and 4 and no variation had an equally high species richness as prey communities with a variation in risk perception whereas their Shannon diversity was lower.

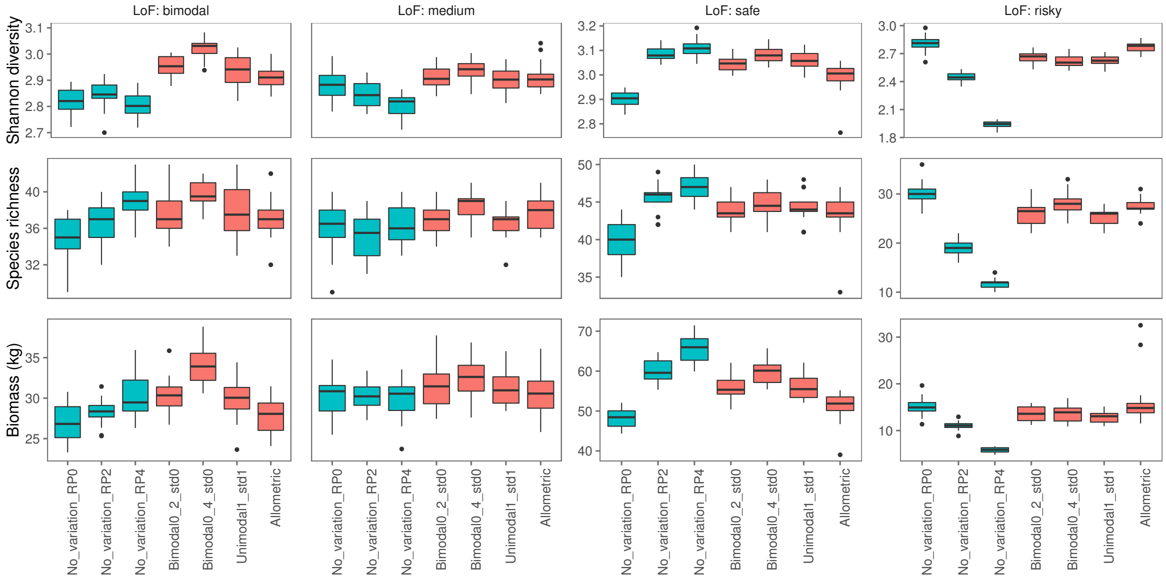

Fig. 4.6. Shannon diversity, species richness and total biomass in prey communities differing in their risk perception (colors) for varying landscapes of fear (columns). Note the different scales on the y-axis for safe and risky landscapes of fear.

In order to gain a better understanding of the influence of risk perception we gradually increased risk perception in prey communities without variation and in prey communities with a bimodal risk perception and evaluated the consequences on diversity, species richness and total biomass of the prey community (Supplementary Material, Appendix C.2, Fig. C.5). For increasing risk perception in the community, communities with a bimodal risk perception show an increase in diversity, species richness and biomass for bimodal, medium and safe landscapes and remain constant in risky landscapes (Supplementary Material, Appendix C.2, Fig. C.5). In contrast, prey communities without a variation in risk perception only show an increase in safe landscapes and in species richness of bimodal landscapes. In all the other cases, diversity, biomass and species richness decrease (risky landscapes) or stay constant (bimodal and medium landscapes) with increasing risk perception.

The median body mass and the number of individuals give further insights in community composition of prey communities (Fig. 4.7, first and second row). Communities with a high diversity also show a high median body mass, i.e. they consist of animals with a larger body mass. Regarding the number of individuals, most communities with a high median body mass have a low number of individuals and vice versa. In contrast, the prey community with allometric risk perception contains in general less individuals than all other communities, except for risky landscapes of fear where the variation in the number of individuals is very high. The median home range size increases with risk perception for communities without variation in risk perception in all landscapes of fear except for the safe landscape of fear where it decreases (Fig. 4.7, third row). In the scenario with the safe landscape of fear, the prey community without risk perception and the community with an allometric risk perception show the largest home ranges.

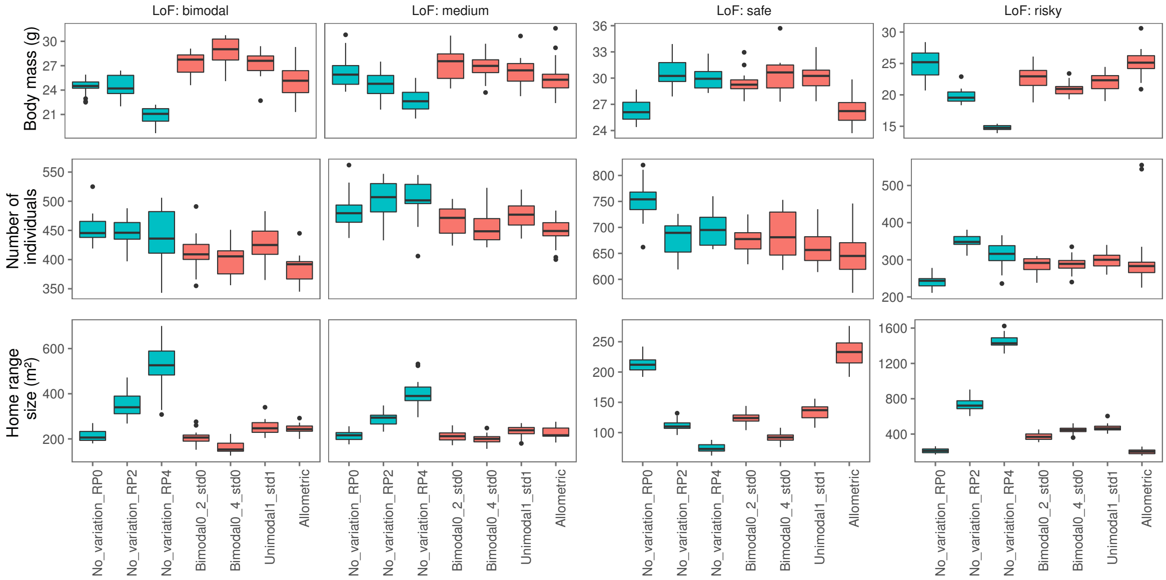

Fig. 4.7. Median body mass, number of individuals and median home range size in prey communities differing in their risk perception (colors) for varying landscapes of fear (columns). Note the different scales on the y-axis for safe and risky landscapes of fear.

4.5 Discussion

In this study we assessed how individual variation in risk perception of prey communities affects prey space use, survival probability and community structure. In communities with individual variation, animals showed a spatial segregation depending on their risk perception. Animals with a high risk perception preferred safe areas of the landscape resulting in safer home ranges and a higher survival probability. Animals with a low risk perception preferred areas with a high energy gain and consequently established their home ranges in the riskier parts of the landscape. In communities without variation no spatial segregation occurred. Home range safety and survival probability was lower compared to animals with a high risk perception in communities with individual variation. Prey community structure was highly dependent on the configuration of the landscape of fear. In risky landscapes, prey communities with a high proportion of animals with a low risk perception had the highest diversity. Vice versa, communities with a high proportion of animals with a high risk perception had the highest diversity in safe landscapes. In these landscapes, variation in risk perception had no strong influence on prey community structure. Contrastingly, in landscapes of fear with a bimodal or medium distribution of predation risk, individual variation in risk perception led to an increased diversity of the prey community.

4.5.1 Consequences of individual differences in risk perception on space use and survival

In communities without variation, all animals prefer the same area of the landscape for the establishment of the home range. Especially if risk perception of the animals is high, this results in strong competition for the establishment of home ranges in safe areas. If all accessible resources in these areas are occupied, animals eluded to a certain degree in areas with a lower safety. Therefore, safety of home ranges did not increase with risk perception in communities without variation. However, the elusion in riskier areas was limited because with increasing perceived predation risk the costs of foraging in risky areas exceeded the energy gain. Thus, animals in communities without variation could use less food resources of the landscape compared to animals in communities with variation in risk perception (Supplementary Material, Appendix C.2, Fig. C.4).

Prey communities with individual variation showed a spatial segregation between animals depending on their risk perception (Fig. 4.3). While foraging, animals tradeoff energy gain with potential predation risk (Lima, 1998; Lima and Dill, 1990). Consequently, individuals with a high risk perception predominantly used safe areas of the landscape while animals with a low risk perception established home ranges in areas with the highest energy gain. Individual differences in space use have been reported for many species (reviewed in Spiegel et al., 2017). Although most studies focus on personality-dependent dispersal syndromes, some studies have shown consequences on the home range level (Boon et al. 2008; Minderman et al. 2010; van Overveld and Matthysen 2010, Schirmer et al. under review; Spiegel et al. 2015). For example, aggressive sleepy lizards (*Tiliqua rugosa]*) use refuges less frequently than non-aggressive lizards (Spiegel et al., 2015). In North American red squirrels (*Tamiasciurus hudsonicus*) risk-taking behavior is associated with the activeness of the animal (Boon et al., 2008). Such differences in space use could be the result of variation in risk perception of the animal depending on their personality.

Furthermore, variation in space use and resulting differences in the safety of the home range in communities with variation in risk perception represent a form of individual niche specialization (Bolnick et al., 2003). Individual niche specialization is supposed to have large implications for ecological and evolutionary processes, especially as it affects the interactions of individuals with abiotic and biotic factors (Araújo et al., 2011; Bolnick et al., 2003; Hart et al., 2016). For example, individuals of bluegill sunfish (*Lepomis macrochirus*) show strong variation in their habitat usage, some individuals consistently use the open water zone, while others stay in the littoral zone (Werner et al., 1981). This variation results in different parasite loads of the two habitat specialists and differences in their susceptibility to human fishing methods (Wilson et al., 2011; Wilson, 1998).

Beside space use and safety of home ranges, individual risk perception affected survival probability of the prey. Animals from communities with variation and a risk perception above one mostly had a higher survival probability than animals in communities without variation. This would suggest that the proportion of animals with a high risk perception should increase in the population over time. However, survival probability of animals with a high risk perception in communities without variation is lower. Thus, if the proportion of individuals increases in the population, survival probability of these animals will decrease and slow down the selection for this individual type, maintaining a variation in risk perception in the population. A study by Wolf et al. (2007) suggests that differences in the trade-off between current and future reproduction are a source for individual variation in risk behavior. Animals that have much to lose should be more risk-averse compared to animals with low expectations (Wolf et al., 2007). If all animals are risk-averse, there will be high competition and expectations will lower. Therefore, more animals can assume a risk-taking behavior and both behavioral types are maintained in the community.

4.5.2 Consequences of individual differences in risk perception on community structure

Individual trait variation is often thought to be a promoter for the coexistence of large numbers of species in natural communities (Bolnick et al., 2011; Clark, 2010; Crawford et al., 2018; Violle et al., 2012). With the model, we compared the effects of individual variation in risk perception on several community parameters. Our results showed that in bimodal and medium landscapes of fear Shannon diversity of prey communities with variation was indeed higher compared to communities without variation. Increased diversity was the result of a higher body mass in communities with variation, i.e. these communities contain more animals with a high body mass. For species richness and total biomass no strong differences were visible between communities with and without variation. Experimental studies on the consequences of individual variation on community metrics are rare and focus on plant communities. For example, Fridley and Grime (2010) found an increase in species diversity with intraspecific genetic diversity, but no effect on community productivity. Theoretical studies showed that individual trait variation not necessarily increases species diversity, e.g. a study by Barabás and D'Andrea (2016) reported a decrease in species richness if individual trait variation was included, however, resilience to environmental disturbances increased if the variation was heritable. Another study demonstrated that individual trait variation only increases diversity if the diversity of the initial community is low (Crawford et al., 2018). Due to this partly contradicting and case-specific results, future studies investigating trait variation in vertebrate communities and their consequences on diversity are highly needed.

In our model, the configuration of the landscape of fear played a key role in shaping prey community structure. In bimodal and medium landscapes of fear, prey communities with individual variation in risk perception showed a higher diversity than prey communities without variation. These landscapes cover the whole range of possible safety values in the landscape. Therefore, animals differing in their risk perception are able to find a habitat that fits their needs. The risky and the safe landscape are characterized by containing either only very risky patches or only very safe patches. In these landscapes, communities with animals adapted to these conditions reached the highest diversity. In safe landscapes animals with a high risk perception are best adapted since they have low vigilance costs and can exploit food resources in safe areas more efficiently compared to animals with a low risk perception. In risky landscapes animals with a low risk perception are most successful. Since the whole landscape is risky, animals with a high risk perception are not able to shift their home ranges into safe areas and therefore face high vigilance costs.

These results indicate that individual variation in risk perception will only be maintained in landscapes of fear that contain both risky and safe habitats. According to Sih (2004) the environment that the individual encounters is the crucial factor determining the selection for a behavioral type. However, variation in perceived predation risk does not necessarily have to occur on a spatial scale to support the maintenance of different behavioral types, but could also be a temporal variation in safety. Beside space, temporal variation in the landscape of fear plays an important role in shaping antipredatory behavior (Lima and Bednekoff, 1999). Examples for temporal variation in the landscape of fear are seasonal changes (Dodson, 1990; Tolon et al., 2009) or differences in the light intensity due to the lunar cycle (Kotler et al., 1994; Palmer et al., 2017).

While effects of the distribution of risk perception on community metrics are often rather weak, differences in home range sizes between prey communities were more distinct. If conditions deteriorate, animals increase their home range size in order to fulfill their energy requirements (Harestad and Bunnel, 1979; Tufto et al., 1996; Ullmann et al., 2018). Only if a further increase of the home range is not possible anymore since movement costs exceeded energy intake, animals failed to establish a home range with consequences on the community structure. Home range size could be used as a first signal to identify stressed populations and take necessary conservation steps before consequences on diversity occur.

4.5.3 From theory to reality

Our model provides a first step into understanding the consequences of individual risk perception on prey space use, survival and community structure. Since individual landscapes of fear have not yet been assessed empirically (Bleicher, 2017), we had to use simplified assumptions on how risk perception varies between animals. With further development in tracking technology (Kays et al., 2015) in combination with camera traps (Haswell et al., 2018), an assessment of individual landscapes of fear should be possible for many species. With these landscapes, the model could be refined and better adapted to risk perception in natural communities.

Beside individual differences in prey behavior, variation also occurs on the level of the predator. The selection of prey animals by predators can vary due to many factors such as age (Ross et al., 1997), sex (Cooper et al., 2007) or reproductive status (Nilsen et al., 2009; Pierce et al., 2000). Another study found that neighboring kestrels sharing the same hunting grounds showed consistent individual differences in prey selection probably due to variation in their personality (Costantini et al., 2005). Such differences in the prey selection of the predator alter the predation risk for the animal. It is possible that prey animals will adapt their landscape of fear if they gain information about the preferences of the predator occurring in their habitat. Since predators are not explicitly modeled, such effects were beyond the scope of our study. Future research should take into account interactions between individual variation in predator and prey.

4.5.4 Conclusion

Our study lays the groundwork for future research on individual landscapes of fear. It provides a first assessment how individual differences in risk perception affect space use and survival in prey communities. By showing a spatial segregation between individuals differing in their risk perception the model provides insights how individual variation affects intra- and interspecific interactions. Furthermore, it improves our mechanistic understanding how complex ecological patterns emerge from simple individual rules (Spiegel et al., 2017). Additionally, the model links individual trait variation with consequences on the community level, satisfying recent calls for including individual trait variability in community ecology (Bolnick et al., 2011; Violle et al., 2012). The mechanistic basis of the model allows us to enhance our understanding of emerging community patterns.

Beside variation in risk perception, the configuration of the landscape of fear was identified as a driver of prey community structure. Landscapes of fear with a relatively homogeneous risk distribution were most suitable for prey animals with a risk perception that fitted the conditions of the landscape. In heterogeneous landscapes of fear, prey communities with a variation in risk perception showed the highest diversity. Trait variation is supposed to stabilize communities by increasing the ability of a population to adapt to new environmental conditions (Bolnick et al., 2011; Hooper et al., 2005). Many landscapes of fear underlie changes due to anthropogenic activity such as hunting and land use (Kuijper et al., 2016). An adaptation to such new conditions might only be possible if individual variation in the prey community is high enough.

4.6 Declaration of interest

None.

4.7 Acknowledgements

This work was supported by Deutsche Forschungsgemeinschaft in the framework of the BioMove Research Training Group (DFG-GRK 2118/1).

4.8 Supplementary Material

Appendix C.1: ODD-Protocol
Appendix C.2: Additional Figures

CHAPTER 5

General discussion

An understudied aspect of predator-prey interactions are the consequences of behavioral effects on prey community structure. The majority of studies either focuses on single prey species or concentrates on cascading effects of predator impacts such as consequences on vegetation structure. In this thesis, I filled this gap by assessing the role of behavioral effects in structuring prey communities. Thereby, the usage of an individual-based and spatially-explicit simulation model, enabled me to link emerging patterns of prey community structure and composition under fear of predators with individual-level processes such as foraging and home range formation.

In my first study, I showed how fear can shape prey community structure and identified two key mechanisms driving prey community responses towards fear: refuge availability and foraging strategy of the animal. Based on the importance of refuge availability for prey community structure under fear, I performed an in-depth examination of the consequences of habitat configuration on prey community responses towards fear in my second study. Focusing on landscape changes such as habitat loss and fragmentation I showed that fear increases negative effects of these changes, intensifying diversity losses and reinforcing shifts in community composition towards small animals. These negative effects can be mitigated by supporting landscapes with a high availability of refuges and low fragmentation degree. In my third study, I focused on the consequences of variation in risk perception of prey animals. I showed that prey communities in which animals differ in their perception of risk by predators, show a spatial segregation depending on their individual risk perception. Furthermore, in these communities, animals with a high risk perception had a higher survival probability. Regarding community structure, prey diversity was higher in communities with variation in risk perception if the landscape of fear had a heterogeneous structure.

In the following, I will synthesize these findings and integrate the achieved scientific progress in existing concepts and frameworks. First, I discuss findings regarding the structure of the landscape of fear. Second, I review the consequences of individual variation in risk perception. Third, I highlight the potential of modifications in prey space use and prey community structures to induce trophic cascades. Fourth, I discuss the linkage between community patterns and individual behavior in the model. Fifth, I assess the implication of my findings for conservation and nature management. Finally, I give an outlook on possible future developments in research on behavioral effects of predators and a conclusion.

5.1 Structure of the landscape of fear

The availability and quality of refuges play an important role in shaping prey behavior and population dynamics (Cooper et al., 2007; Stankowich and Blumstein, 2005). In my thesis, I went one step further and explored the consequences of refuge availability and quality on the level of the prey community. I showed that total biomass, species richness and diversity of the prey community increased with refuge availability (Fig. 2.5c, d). These findings agree well with a study on coral reef fish assemblages in which species abundance and richness increased with refuge availability (Caley and St John, 1996; Hixon and Beets, 1993). Furthermore, I could show that increasing refuge availability increased the abundance of large animals in the prey community (Fig. 2.5a, 2.6). Due to the linkage of community patterns with individual-based processes in the model, I was able to show that community patterns under increasing refuge availability emerged from reductions in the home range size of prey animals (Fig. 2.3). Refuges allowed animals to reduce antipredatory behavior which increased their foraging efficiency. As a consequence, home range size could be decreased and competition for safe areas was reduced.

Besides the availability of refuges, I had a closer look at the role of habitat quality and configuration of the landscape of fear (Chapter 3). In particular, I investigated how fear modifies community responses to landscape changes such as fragmentation and habitat loss. Landscape changes are a major cause for the current biodiversity loss (Newbold et al., 2015; Schipper et al., 2008). Furthermore, they are known to impact predator-prey interactions, even though the direction and strength of the impact remains unclear (Chalfoun et al., 2002; Ryall and Fahrig, 2006). In order to elucidate the impact of landscape changes on predator-prey interactions, I assessed the consequences of fear on prey community structure, since behavioral effects are often not considered in current studies on landscape changes. I found that fear intensifies negative effects of habitat loss on prey diversity in risky environments. In contrast, safe environments mediated negative consequences of habitat loss and fragmentation by promoting prey diversity (Fig. 3.3). These results suggest that the impact of landscape changes on predator-prey interactions depends on the predation risk in the remaining habitat.

Similar predictions were made by other theoretical models, focusing on the degree of specialization of predators (reviewed in Ryall and Fahrig, 2006). Specialized predators are assumed to depend on the same habitat type as the prey and it is predicted that predators are more strongly affected by habitat loss than their prey (Bascompte and Solé 1998; Kondoh 2003; Melián and Bascompte 2002; Nakagiri and Tainaka 2004; Nakagiri et al. 2001; Swihart et al. 2001, reviewed in Ryall and Fahrig 2006). Thereby, safety of the landscape will increase with habitat loss which has positive consequences on prey abundance for low to medium habitat loss (Bascompte and Solé 1998; Nakagiri and Tainaka 2004; Nakagiri et al. 2001; Prakash and De Roos 2002; Swihart et al. 2001, reviewed in Ryall and Fahrig 2006). In contrast, generalist predators that primarily live in the matrix are predicted to profit from habitat loss and will therefore increase the predation risk of prey animals in their habitat with potential negative consequences on prey survival (Swihart et al., 2001). In this context, empirical studies estimating the consequences of habitat loss and fragmentation on predator and prey communities including modifications in the landscape of fear are highly needed to validate theoretical findings.

Additionally to the consequences of the degree of safety in the remaining habitat, I disentangled the role of food and fear in shaping the prey community. In general, high food availability increased the total biomass and prey diversity of the prey community (Fig. 3.6). Positive effects of habitat quality have also been reported for snails (*Nucella lapillus*) which showed an increased growth and growth efficiency if the food availability in refuges was elevated (Donelan et al., 2017). Regarding fear, safe landscapes promoted a higher stability in prey diversity for changes in habitat quality, i.e. a reduction in food availability had smaller negative effects on prey diversity in safe environments compared to risky environments, especially in highly fragmented landscapes (Fig. 3.6b).

Concisely, my findings show that changes in prey behavior due to the structure of the landscape of fear have consequences on the level of the prey community, modifying prey diversity. Positive effects on prey diversity are predicted to occur if the availability of refuges is increased or the quality of existing refuges is raised. Furthermore, a high connectivity of refuge areas can promote an increased prey diversity. These results enhance our knowledge about the consequences of habitat heterogeneity on the prey community.

5.2 Individual differences in risk perception

The movement ecology paradigm by Nathan et al. (2008) proposes that animal's movement path is driven by four components: (1) *External factors* which include all abiotic and biotic conditions in the environment that influence movement. (2) The *internal state* of the animal which defines the proximate and ultimate goals of the animal's movement and addresses the question why the animal should move. (3) The *motion capacity* which accounts for the biomechanical properties that enable the animal to move, approaching the question how the animal moves. (4) The animal's *navigation capacity* which focuses on the question when and where to move and is specified by the ability of the animal to utilize information about the environment, orient itself in space and time and select specific targets for the movement.

The navigation capacity of animals is of key importance regarding responses of animals to fear. For example, red foxes respond to wolf urine by reducing their visits to food patches (Haswell et al., 2018), i.e. the utilization of the olfactory information allowed them to assess their risk of predation and adapt their movement accordingly. However, not all individuals perceive predation risk in the same way, some individuals consistently act in a more risk-taking or "bold" manner, while others act more risk-averse or "shy" (Lima and Steury, 2005; Sih, 2004; Wilson et al., 1994). As a consequence, bold and shy animals should have different landscapes of fear with potential consequences on their behavioral responses to predators.

Even though it is clear that landscapes of fear differ between individuals, they are commonly evaluated on the population level (Bleicher, 2017). Thereby, studies fail to assess the potential consequences of differences in prey behavior due to variation in their landscape of fear. In order to fill this gap, I evaluated the consequences of intra- and interspecific differences in risk perception on prey communities (Chapter 4). I showed that variation in the landscape of fear leads to a spatial segregation between animals with different degrees of risk perception (Fig. 4.3). Personality-dependent differences in space use have been reported in multiple species such as lizards (Spiegel et al., 2015), great tits (van Overveld and Matthysen, 2010) and voles (Schirmer et al. under review). Recently, Spiegel et al. (2017) have proposed a framework for personality-dependent spatial ecology. This framework links the consequences of personality on movement and space use with their ecological consequences such as disease spread, metapopulation dynamics and niche partitioning (Spiegel et al., 2017). My findings support this framework since individual variation in risk perception impacts prey home range formation with further consequences on prey community structure.

On the community level, variation in risk perception had consequences on prey diversity. Comparing prey communities with and without individual variation in risk perception showed that prey diversity was higher in heterogeneous landscapes of fear that offered both risky and safe habitat patches (Fig. 4.6). In these landscapes, animals were able to choose a location for their home range that was most efficient under their individual risk perception. Individuals with a high risk perception preferred safe patches to reduce the costs of antipredatory behavior. In contrast, individuals with a low risk perception chose patches with a high food availability allowing them to escape the high competition for safe patches. Such a specialization in different habitats is observed in bluegill sunfish (*Lepomis macrochirus*), in which some individuals consistently use the riskier open water while others stay in the safer littoral zone (Werner et al., 1981). This habitat specialization has consequences on the parasites and predators that the fish encounter (Wilson et al., 2011; Wilson, 1998). This example highlights the importance of considering personality-dependent space use for ecological processes. Individuals that perceive predation risk in a different way will use different parts of the landscape and interact with different species (Spiegel et al., 2017).

5.3 The induction of trophic cascades

Behavioral effects of predators can induce trophic cascades such as the structural changes observed in the Yellowstone ecosystem due to modified foraging patterns of elk under the absence of wolves (Ripple and Beschta, 2004). Although my work focused on consequences of fear on the prey community, conclusions regarding the effects of fear on food resources of the herbivorous prey could be drawn by analyzing the amount of remaining food in the landscape after community saturation. Comparing landscapes with and without predation risk, I found that fear increased food exploitation in safe areas while it decreased food exploitation in risky areas (Fig. 2.4, B.3, C.4). Thus, vegetation in safe areas will be foraged more extensively than in risky areas. Such heterogeneous feeding patterns can have cascading effects (Schmitz et al., 2004). For example, in pine savannas, white-tailed deer increase foraging in woody areas that offer cover in order to reduce predation risk (Cherry et al., 2016). Thereby, deer increased herbivory on oaks leading to a reduction in oak encroachment and fire suppression (Cherry et al., 2016).

Besides the intensity of foraging pressure, the composition of the herbivore community is a key driver of plant species diversity in many grasslands (Olff and Ritchie, 1998). With the model, I showed that fear leads to changes in prey community composition. In risky environments, the abundance of small animals increases, while the abundance of large animals decreases (Fig. 2.6, 3.3b). A field study on grassland sites in North America and Europe showed that large herbivores (>10kg) increase plant diversity under high productivity and decreased diversity under low productivity, while small herbivores (<10kg) had no consistent effect on plant communities (Bakker et al., 2006). Even though the scale of body size of prey animals in the model was different it can be expected that changes in the body mass of the herbivore community impact the vegetation. Future studies should investigate how changes in prey community composition due to fear of predators impact the effect of herbivorous prey species on the vegetation in order to predict potential cascading effects.

5.4 Linking community patterns with individual-level processes

Huston et al. (1988) stated that individual-based models will unify ecological theory since they link different hierarchical levels and allow to address patterns based on mechanisms. This is supported by two more recent papers (Grimm and Berger, 2016; Grimm et al., 2017) which argue that higher-level processes such as community patterns can only be understood when explanations are based on first principles. The model presented in this thesis links community patterns with the home range formation of individual animals. Home range formation is thereby based on first principles, animals try to maximize the energy intake while minimizing predation risk ($\mu/$f-rule, Gilliam and Fraser, 1987). Prey community structures emerge from these first principles which allows for a mechanistic understanding of the community patterns. A recent review by Cabral et al. (2017) emphasizes the importance of including mechanisms into simulation models and shows that current mechanistic simulation models can identify essential ecological processes.

A central problem in models that include the community level is their high complexity (Cabral et al., 2017; Grimm et al., 2017). This problem can be reduced if the same submodels can be used for different species and only the parameters are varied (Grimm et al., 2017). In the presented model, individual are characterized by their traits. Most of these traits are defined by an allometric relationship. Thus, the body mass can be used to calculate further traits of the animal regardless of the species identity. Due to the trait-based approach, the same submodels can be used for all animals and differences in behavior emerge from trait variation. Furthermore, due to the individual- and trait-based approach of the model, individual variation can be included easily into the model. The consideration of individual variation provides further insights into mechanisms shaping community structure and ecological processes.

In the model, prey community structure emerges from individual home range formation. Thereby, the model links movement behavior with species diversity. Jeltsch et al. (2013b) proposed an integrative framework that highlights the importance of movement ecology for biodiversity research (Fig. 5.1). The framework is based on the movement ecology paradigm (Nathan et al., 2008). This paradigm is extended with the concept of mobile links (Lundberg and Moberg, 2003) which describes the role of animal movement in connecting otherwise separated ecosystems. Furthermore, the concept of stabilizing and equalizing mechanisms for species coexistence (Chesson, 2000) is included into the framework.

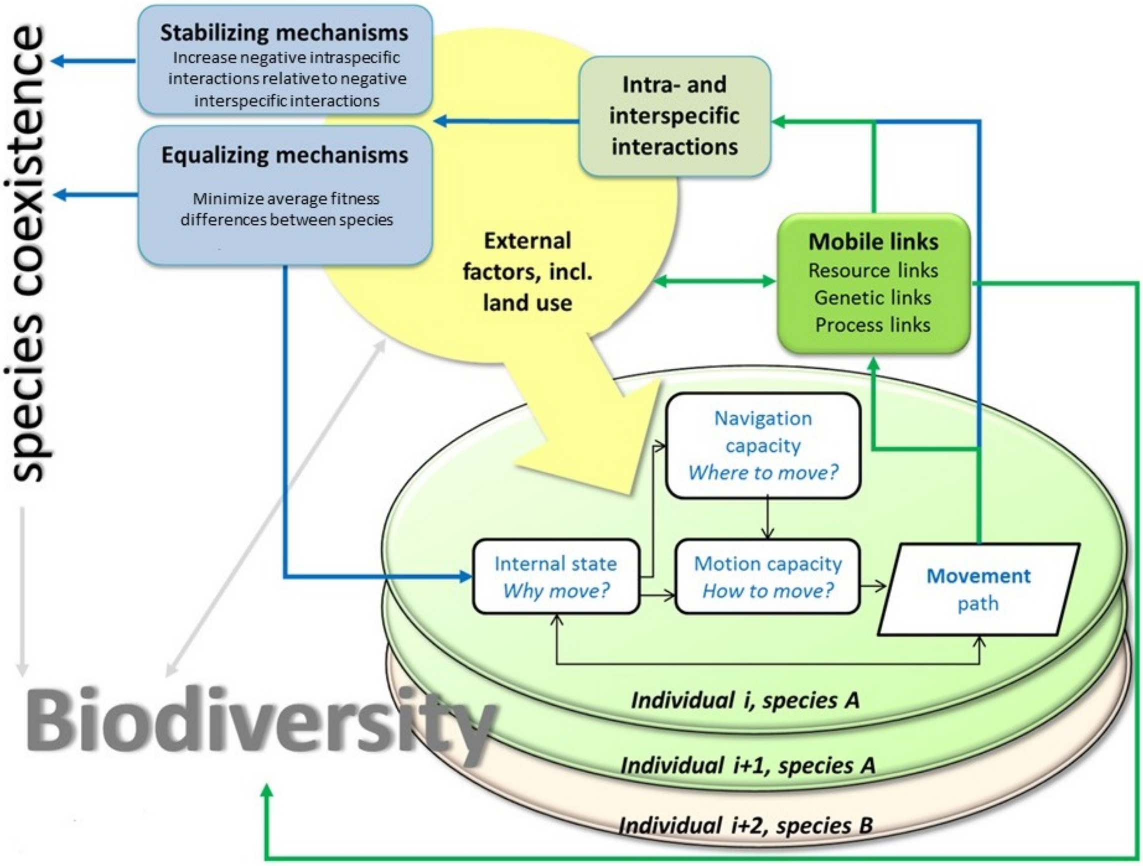

Fig. 5.1. Framework for the linkage between movement ecology and biodiversity research (Jeltsch et al., 2013b). The integrative framework combines the movement ecology paradigm (Nathan et al., 2008) with the mobile link concept (Lundberg and Moberg, 2003) and the concept of stabilizing and equalizing mechanisms for species coexistence (Chesson, 2000). This figure was modified from Jeltsch et al. (2013b).

The framework suggests that intra- and interspecific interactions can modify stabilizing and equalizing mechanisms and thereby affect species coexistence. Regarding my findings, the heterogeneous foraging patterns of prey animals under fear (Fig. 2.4, B.3, C.4) are likely to have consequences on the plant community. Selective grazing is a typical process link impacting species coexistence (Eccard et al., 2000; Eccard and Liesenjohann, 2008; Jeltsch et al., 2013b; McNaughton, 1984). Species diversity of the prey community itself is shaped by the home range formation of animals. If animals vary in their risk perception, they prefer different areas for the establishment of home ranges. Thereby, individual variation in risk perception leads to spatial resource partitioning which is a stabilizing mechanism (Chesson, 2000; Jeltsch et al., 2013b). Overall, I showed that fear is an important factor modifying prey space use with consequences on species coexistence.

5.5 Implications for conservation and nature management

My findings reveal that fear is an important driver of prey community structure and composition. Thereby, my findings extend current knowledge about the positive effects of shelter on prey growth and survival (Finstad et al., 2007; Lima, 1998) to the community level. Other community-level studies have been restricted to aquatic systems (Hixon and Beets, 1993). For example, a study on tropical reef fish assemblages reported positive effects of refuge availability on species richness (Caley and St John, 1996). Moreover, my results show that the highest prey diversity is achieved if refuges are large and well connected (Chapter 3). This is of special importance under habitat loss and fragmentation because refuges can reduce negative effects of landscape changes on prey communities.

Regarding individual variation in risk perception, my results show that the highest prey diversity is promoted in heterogeneous landscapes of fear (Fig. 4.6). These findings support the habitat heterogeneity hypothesis which states that the highest species diversity is achieved in complex habitats (Bazzaz, 1975). Thus, if landscapes are managed by including further refuges for prey animals, the effectiveness of these refuges should be varied. This variation supports the coexistence of prey animals with different demands for their habitat. My results support modern conservation approaches that call for the protection of species interactions in addition to protecting single species (Tylianakis et al., 2010). Only if species interactions are sustained, ecosystem functioning can be ensured (Tylianakis et al., 2008).

Apex predators have been extirpated in many ecosystems with cascading effects impacting disease and wildfire dynamics, invasive species and carbon sequestration (Estes et al., 2011). In many cases, humans have tried to compensate the function of apex predators, e.g. by controlling prey populations via hunting, but they are not able to fully replace the role of apex predators (Ripple et al., 2014). Therefore, the reintroduction of predators to restore ecosystems and sustain biodiversity is currently debated (Ritchie et al., 2012). In this context, my model can help to predict the consequences of behavioral effects of reintroduced predators on prey community structure. Ritchie et al. (2012) highlights the importance of understanding behavioral effects of predators in order to predict the outcome of their reintroduction. Furthermore, an understanding of the consequences on prey community composition is of crucial importance. For example, in Fennoscandia native red foxes (*Vulpes vulpes*) suppress the invasive American mink (*Neovison vison;* Carlsson et al., 2010). However, with the recolonization of lynx and wolves, red fox populations decrease (Elmhagen et al., 2010). This decrease is likely to lead to an increase in the mink population with negative effects on mink prey diversity (Banks et al., 2008; Fey et al., 2009). This example underlines the importance of understanding the consequences of predator effects on prey community structure to predict the impact of reintroductions and recolonization of predators.

Additionally, the human impact on landscapes of fear should be taken into account regarding potential conservation measures. Kuijper et al. (2016) argues that the impact of carnivores on the ecosystem will be very different in anthropogenic systems as human activities mediate predator effects. For example, high human activity on roads and trails can lead to the avoidance of these areas by predators but not by prey, allowing prey animals to use this areas as a refuge (Muhly et al., 2011). In contrast, if human activity is only low e.g. recreational hiking, the impact on animal space use is very small and predators often actively select trails for easier and faster movement (Kays et al., 2016). In this context, measuring the landscape of fear of prey and predators can provide a fast and accurate estimation of the consequences of human activities on wildlife without the need to wait for consequences on demographics (Bleicher, 2017).

In addition to disturbances by humans, many predators and prey species are affected by human hunting which can interfere with the density- and trait-mediated effects of predators on prey. For example, roe deer (*Capreolus capreolus*) in Norway face predation risk by lynxes (*Lynx lynx*) and humans (Lone et al., 2014). Humans predominantly use open areas for hunting, while lynxes as an ambush predator prefer areas with dense vegetation, leading to contrasting landscapes of fear for the roe deer (Lone et al., 2014). Thereby, human hunting reduces the availability of refuges for roe deer, increasing negative effects of fear on prey populations. To reduce these effects, hunting could be restricted to areas that are also used by lynxes. Another example reports that cougars (*Puma concolor*) increase their killing rate in areas of high human development due to more frequent disturbances during feeding (Smith et al., 2015). Such a behavioral change will increase the predation risk of prey animals close to human areas. Furthermore, the higher availability of carcasses can have cascading effects on other trophic levels (Smith et al., 2015). These examples highlight the importance of considering human activity when predicting consequences of predators on prey communities.

5.6 Model robustness and future directions

Clearly, the model presented in this thesis, includes simplified assumptions. Due to a lack of data, it is not possible to quantitatively validate the results of the model. However, as discussed in the paragraphs 5.1-5.5, qualitatively, patterns on different levels fit well with empirical findings. Nevertheless, a more thorough implementation of specific processes could impact the emerging patterns. Here, I will focus on one aspect, namely the temporal variation in risk and discuss the potential impact of including temporal changes in the model on the results.

The presented model focuses on the spatial component of fear effects on prey community. However, landscapes of fear are not only variable in space, but also in time (Laundré et al., 2010; Palmer et al., 2017). This temporal variation adds another dimension to the landscape of fear and allows prey animals minimize their predation risk by behavioral adaptations over time (Lima and Bednekoff, 1999; Lima and Dill, 1990). Temporal variation can occur on different scales, as predator activity varies daily (Kotler et al., 1994; Lone et al., 2016), with the lunar cycle (Kotler et al., 2002; Roeleke et al., 2018) or seasonal (Eccard et al., 2017; Tolon et al., 2009). Adaptation of prey animals to temporal variation in fear can modify cascading effects on other trophic levels. For example, Kohl et al. (2018) reported that elk use open, risky areas during times when wolves are not active. Such a behavior contradicts earlier hypothesis that elk avoid risky areas under the presence of wolves (Ripple and Beschta, 2004) and might explain why aspen are not recovering in risky areas of the Yellowstone National Park (Kauffman et al., 2010).

Therefore, findings and management recommendations that only include the spatial component should be considered with caution as temporal effects can impact the predicted patterns. To account for the variation of fear in time, temporal dynamics need to be included in the model. Thereby, the model should include temporal variation on different scales such as variation during the day, moon phases and seasons. As a first step, it should then be evaluated how temporal variation on these scales affects prey communities independent from spatial variation, i.e. in homogeneous landscapes of fear. In a second step, one could then assess the consequences of variation in fear in space and time and evaluate whether there are interactive effects. The separate assessment of fear effects in space and time allows for a better understanding of the processes and facilitates predictions how changes in the spatial or temporal component influence prey communities under fear.

Besides extensions of the model, theoretical results should be combined with empirical studies. Empirical studies assessing the consequences of fear on prey community structure of terrestrial mammals are currently lacking due to difficulties in manipulation of fear and observation of behavioral effects, large effort of evaluating consequences on the community level instead of single species and large generation times of mammals. Nevertheless, solutions or alternative approaches to these problems have been suggested and could be used in future studies. For example, Suraci et al. (2017) developed an "Automated Behavioral Response System" which includes a camera-trap and a motion-sensitive speaker system. If an animal passes such a system it is presented a sound cue from the predator and the direct behavioral response of the animal is recorded by the camera trap. This allows to asses behavioral responses without the need of having an observer present (Suraci et al., 2017). Furthermore, the playbacks manipulate the fear of the animals by simulating the presence of a predator. Thereby, behavioral responses of animals in areas without predators can be assessed. The evaluation of consequences on the community level is often associated with a high effort and costs. However, the development of new tracking technologies such as "ATLAS" (Toledo et al., 2016; Weiser et al., 2016) offer the possibility to track multiple species at the same time and with a high frequency. Thereby, interactions between individuals of the same and different species can be inferred from the movement tracks. In order to assess consequences on the community structure, experiments should ideally cover several generations. However, due to the long life span of many terrestrial mammals, such an approach is rarely possible. To overcome this challenge, a short-term experiment suggested by Ritchie et al. (2012) could be useful. The experiment measures alterations in home ranges, habitat use and daily activity patterns of prey animals under the presence and absence of predators using a two-site reversal design. Predators and prey (or mesopredators) are equipped with a tracking device that allows for continuous monitoring of their movement and behavior. Predators are then removed from site 1. After some weeks, predators are removed from site 2, but allowed to reinvade site 1. This design has the advantage that both sites act as a control and treatment (Ritchie et al., 2012). Such data of the behavior of prey animals could then be used in a model to predict the consequences on prey community structures.

5.7 Conclusion

The current biodiversity loss is accompanied by an even higher decrease in species interactions (Valiente-Banuet et al., 2015). This development is alarming because biotic interactions such as predator-prey interactions play a fundamental role in structuring ecosystems and sustaining biodiversity (Barbosa and Castellanos, 2005; Ritchie et al., 2012). An often overlooked part of predator-prey interactions are the consequences of behavioral effects on the prey community itself. Studies often only focus on the consequences on other trophic levels (Creel and Christianson, 2008), while the impact on prey community structure is neglected even though it has important implications for the strength of behavioral effects on other trophic levels.

In this thesis, I filled this gap by assessing the role of fear in shaping prey community structure and composition of terrestrial mammals. The used individual-based and spatially-explicit model links community patterns with individual movement behavior, bridging the gap between community, movement and behavioral ecology. My findings highlight the importance of the structure of the landscape of fear in shaping prey communities. Habitat heterogeneity is of crucial importance to sustain diverse communities and prevent the exclusion of large animals from the community. Especially under landscape changes such as habitat loss and fragmentation, landscapes of fear should be considered. If the availability of large and connected refuges is ensured in the landscape, negative effects of habitat loss and fragmentation on species diversity can be reduced. Moreover, I showed that individual variation in risk perception can be another driver of prey community structure. This variation reduces competition for refuges and allows for a higher species diversity in heterogeneous landscapes of fear.

Overall, my results give a comprehensive overview about the consequences of fear on prey space use and community structure. Furthermore, they allow for a mechanistic understanding of the emerging community patterns and bridge the gap between community, movement and behavioral ecology. Based on my results, empirical studies can be designed to test the model predictions. A combination of simulation models and empirical studies will be important to further increase our understanding of behavioral effects of predators and their consequences for ecosystem functioning. Furthermore, my findings support calls for modern conservation approaches that go beyond single species, focusing on the protection of species interactions.

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APPENDIX A

Supplementary Material to Chapter 2

A.1 ODD-Protocol

Purpose

The purpose of the model is to simulate the effects of perceived predation risk and food availability on home range formation in a prey community of herbivorous mammals. It aims to gain a mechanistic understanding about space use behavior under predation risk and about the consequences of adapted space use for community structures.

Entities, state variables and scales

The model consists of two entities, landscape cells and prey individuals (Table A.1). Landscape cells are described by the state variables location, food resources (*p-food*) and safety (*p-safety*); the latter feature defines the "landscape of fear". Cells containing food resources (*p-food* >0) are called productive cells. Landscape cells are square cells on a grid with a size of 100×100 cells. Each landscape cell represents $4\,\mathrm{m}^2$. In order to avoid edge effects, periodic boundary conditions were used. Individuals are characterized by their location, their body mass and their foraging strategy under predation risk. To simplify spatial calculations, the location of individuals can only be on the discrete landscape grid cells. The body mass of the individual is used to calculate further physiological traits by using allometric relationships. The foraging strategy of an individual represents a consistent behavioral strategy that defines the response to perceived predation risk (see Submodels: Trait assignment and Home range search for details on the different strategies). The model uses discrete time steps. Each step represents the home range search of one individual.

Process overview and scheduling

In each step of the model a new prey individual is created and performs the processes *trait assignment* and *home range search*. If the home range search is successful, the process *food consumption* is executed, otherwise the individual is excluded from the community. The simulation continues until the community is saturated, i.e. a specific number of individuals (*nfail*, see Table A.2) have consecutively not been able to establish a home range in the landscape (see Fig. A.1 for an overview of the processes). Food resources in the landscape are reduced according to the exploitation by prey animals within the process of food consumption, while

TABLE A.1: Entities and their state variables

Entity *State variable*	Unit	Description
Landscape cells		
p-food	Dry biomass, g/(cell · day)	Food resource availability in cell
p-safety	-	Safety of a cell, inverse to predation risk
Individuals		
i-bodymass	g	Body mass of individual
i-feartype	-	Foraging strategy of individual under predation risk
Allometric traits:		
i-feedrate	Dry biomass, g/day	Amount of food resources that need at least be contained in the home range
i-lococost	Dry biomass, g/cell	Locomotion costs for moving one cell forward
i-maxhr	cells	Maximum home range size
i-foodshare	-	Defines magnitude of food resource exploitation

the landscape of fear is static. The location and size of the home range are stored after the individual has executed the home range search.

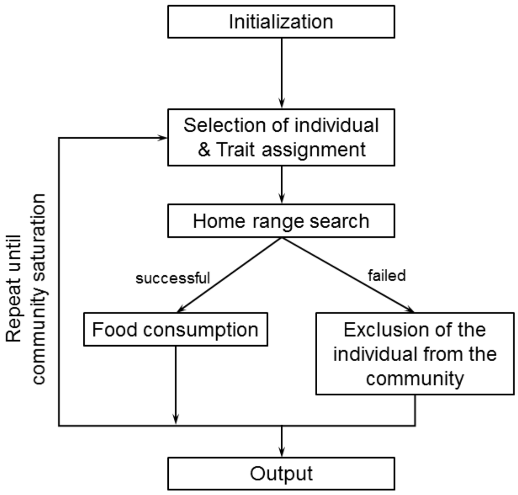

Fig. A.1. Schematic overview of processes in the model. After initialization, a new individual is created and gets assigned certain traits. This individual searches for a home range in the landscape that fulfills its daily energy requirements. The addition of cells to the home range is based on food availability and perceived predation risk in cells. If the home range search is successful, the individual consumes the food resources within, otherwise it is excluded from the community. These steps are repeated until the community is saturated.

Design Concepts

Basic principles

The model is based on a modelling approach developed by Buchmann et al. (2011). We extended this approach by including perceived predation risk. The model is individual-based (Grimm and Railsback, 2005) and uses the body mass as a main trait of individuals. By applying allometric relationships further traits such as energy requirements and locomotion costs can be calculated. Individuals choose a home range in the landscape depending on food availability, predation risk, physiological parameters and foraging strategies. The home range search is based on principles from optimal foraging theory, the area-minimizing principle (Mitchell and Powell, 2004) and the trade-off between foraging and predation risk (Brown, 1988). The model provides insights how adapted space use on the individual level due to different behavioral strategies, food and predation risk distributions affects community structures.

Emergence

Community structure and composition emerges from the group of individuals that successfully established a home range in the landscape. Home range establishment is driven by individual traits, food availability and predation risk in the landscape.

Adaptation

The decision of individuals which cell they add to their home range is driven by a trade-off between food availability and perceived predation risk in a cell. Individuals add cells with minimum predation risk and maximum food availability to their home range in order to achieve a high food gain with minimum costs. Depending on their foraging strategy, individuals adapt the food intake (risk-averse) or the movement activity (risk-taking) according to the predation risk in a cell.

Objectives

Animals aim to satisfy their energy requirements with the smallest possible home range (area-minimizing principle, Mitchell and Powell, 2004). Therefore, they add cells with the maximum food gain to their home range which is achieved in cells with a high food availability and a low predation risk.

Sensing

Individuals sense the food availability and the predation risk in the eight neighbouring cells to their current location.

Interaction

Individuals indirectly interact via resource competition during community assembly. By consuming resources after a successful home range search, individuals decrease the food availability in the landscape leaving less food resources for following individuals. We thus do not include territorial behavior, i.e. individuals do not defend territories.

Stochasticity

Landscape generation and the selection of body masses from the input distribution is stochastic. To account for this variability, 30 replicate simulations are executed for each scenario. During home range search animal decisions can be stochastic if several cells have the same suitability. In these cases, the incomplete knowledge of individuals about the landscape is the reason for stochasticity.

Observation

The values of all state variables of the landscape cells are collected at the beginning and the end of a simulation. Individual traits, home range sizes and cells within the home range are collected at the end of a simulation.

Initialization

Before each simulation a new landscape is generated and general model parameters are initialized (Table A.2). The landscape is characterized by the distribution of food resources and perceived predation risk. 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 contains food resources reflecting the average daily productivity in grass- and shrublands ($0.685\,\mathrm{g}/(\mathrm{m}^2 \cdot \mathrm{day})$ Whittaker, 1975). From these food resources, we assume that 80% of the food resources are lost to other taxonomic groups or not suitable for animal consumption so that only 20% of the average daily productivity can be used by prey animals (see Buchmann et al., 2011, for further discussion on this value). Food resources are exploited by animals during the simulation leading to a decrease in food availability and variation in the amount of food resources in the productive cells. Besides the productivity, cells either have a high predation risk (*p-safety = 0.1*) or a low predation risk (*p-safety = 0.9*). All non-productive cells have a high predation risk because we assume that a lack of vegetation corresponds with high predation risk. Productive cells can have a high or a low perceived risk of predation. In the following, we use the term "risky habitat" for productive cells with a high perceived predation risk and "refuge" for productive cells with a low perceived predation risk. The proportion of refuges is a systematically tested model parameter. We assume that the landscape of fear is static, i.e. the predation risk in the cells does not change during the simulation.

The main characteristic of the individuals in the model is their body mass. This is chosen from a "body mass input distribution", a truncated power-law distribution defining the probability density of a specific body mass (Buchmann et al., 2011; Buchmann et al., 2012). The body mass input distribution represents the regional species pool. It defines possible body masses for the individuals as well as their density. Additionally, the length of a simulation run is initialized. It is defined by the number of individuals that are consecutively not able to establish a home range (*nfail*).

Input data

The model does not include any external input.

TABLE A.2: Initialized parameter values of the model

Parameter	Value	Unit	Description
Food resources in productive cell (*p-food*)	0.548	Dry biomass, g/cell	20% of average productivity in grass- and shrublands (Buchmann et al., 2011; Whittaker, 1975)
Number of failed individuals (*nfail*)	100	-	Number of individuals that consecutively failed to find a home range in the landscape, used to stop the simulation
Body mass input distribution	M^{expo}	M in kg	Truncated distribution from which body masses of individuals are chosen
Exponent (*expo*)	-1.5	-	Exponent that yields realistic community structures (Buchmann et al., 2011)
Lower boundary (*lowB*)	0.01	kg	Lowest possible body mass of individuals
Upper boundary (*upB*)	1	kg	Highest possible body mass of individuals

Submodels

Trait assignment

In each step of the model a new individual is created. Individuals are characterized by different traits, mainly by their body mass and their foraging strategy. The body mass of the individual is drawn from a truncated body mass input distribution (see *Initialization*). Similar to the model by (Buchmann et al., 2011), allometric relationships are used to calculate further traits (Table A.3). We assume that individuals are central place foragers frequently returning to a central place, their den. The den is an absolute refuge where individuals do not face predation risk. A further characteristic of individuals is their foraging strategy under predation risk. Foraging animals need to balance energy intake against predation risk, especially if profitable patches have a higher predation risk than less profitable patches (Lima, 1998). Common responses of animals foraging under predation risk are adaptations in space use and/or activity levels (Lima, 1998). To explore the effects of different strategies we here implemented two exemplary foraging strategies under predation risk and compare them to a control foraging strategy in which animals do not respond to predation risk in the landscape i.e. their food intake only depends on food availability and physiological constraints. The rationale of these two strategies is described in the following; their implementation is described below, in the processes home range formation and food consumption.

The foraging strategy of risk-averse individuals focuses on adaptations in food intake between patches with different predation risk. Risk-averse animals show a reduced food intake in risky habitat patches to minimize the time they are exposed to this high risk. To compensate the lower food intake under high risk, they forage more intensively in refuges and show an increased food intake in these patches compared to control individuals. An example for such a foraging strategy are gerbils, which reduce foraging in open areas under the presence of owls and shift their foraging activities to bush areas that offer cover (Kotler et al., 1991). Similar patterns were shown for other small mammals (Jacob and Brown, 2000; Simonetti, 1989) and fish (Rozas and Odum, 1988; Werner et al., 1983).

Risk-taking individuals deal with predation risk by adapting their activity patterns. In risky habitat, risk-taking animals show short foraging bouts with frequent returns to the den and hiding in refuges in order to minimize encounters with a predator. These behaviors increase the energy costs of risk-taking animals under high predation risk. In refuges, risk-taking individuals have the same activity patterns as animals of the control. Exemplary for this strategy are birds that directly fly to cover when detecting a predator (Schneider, 1984) or animals that carry food item to their home to reduce the time they are exposed to the predator (Lima et al., 1985; Lima, 1985).

TABLE A.3: Allometric relationships used to calculate further traits of the individuals. M is the body mass of the individual in g.

Trait	**Allometric relationship**	**Unit**	**Description and references**
Feeding rate (*i-feedrate*)	$0.323 \cdot M^{0.744}$	Dry biomass, g/day	Least amount of food that individual needs to gain from home range cells for successful search Nagy (2001)
Locomotion costs (*i-lococost*)	$\frac{0.0976 \cdot M^{0.68}}{14 \cdot 10^{3}}$	Dry biomass, g/m	Costs of individual for moving from one place to another Calder (1996), Garland (1983), and Nagy (2001)
Magnitude of food exploitation (*i-foodshare*)	$\gamma \cdot M^{-0.25}$	-	Fractal characteristics affect the resolution at which individuals can exploit resources, γ was set to 1 Buchmann et al. (2011) and Haskell et al. (2002)
Maximum home range size (*i-maxhr*)	$0.0138 \cdot M^{1.18}$	ha	Used as a constraint for home range size, if *i-maxhr* is larger than the landscape size, it is set to the landscape size Kelt and Van Vuren (2001)

Home range search

The key process of the model is the home range search of the newly created individual. The home range needs to contain enough food resources to cover the individual's feeding rate and movement costs. We assume individuals to be central place foragers frequently returning to a central place, their den, within their home range. This is implicitly represented in the model by calculating the movement costs for the distance to a cell and the return. The home range search starts with the choice of a core cell, the central place of the home range where the den of the animal is located. This cell is chosen randomly from the pool of productive cells. The addition of a cell to the home range consists of two steps, the choice of which cell is added and the calculation of the food gain from the cell. The cell that is added next to the home range is chosen from the neighboring cells of the cell that was added last to the home range. We assume that the animal has a perceptual range of one cell, i.e. it can sense the food availability and the predation risk in the neighboring cells. For the decision, which of these cells is added to the home range the suitability of a cell is calculated by the product of food availability and predation risk:

$$\text{Suitability} = \textit{p-food} \cdot \textit{p-safety} \tag{A.1}$$

The cell with the highest suitability is added to the home range. For the control, only the food availability is taken into account (Suitability = *p-food*). If several cells have the same suitability, the cell with the minimum distance to the core is chosen. After the decision for a cell, the food gain from this cell is calculated. The food gain is the difference between the exploited food and the movement costs:

$$\text{Food gain} = \text{Exploited food} - \text{Movement costs} \tag{A.2}$$

The amount of exploited food is the arithmetic product of food availability in the cell (*p-food*) and the individual magnitude of food exploitation (*i-foodshare*). For risk-averse individuals predation risk additionally affects food intake. For the different foraging types exploited food is calculated by:

$$\text{Control:} \quad \text{Exploited food} = \textit{p-food} \cdot \textit{i-foodshare} \tag{A.3a}$$

$$\text{Risk-averse:} \quad \text{Exploited food} = \textit{p-food} \cdot \textit{i-foodshare} \cdot 2 \cdot \textit{p-safety} \tag{A.3b}$$

$$\text{Risk-taking:} \quad \text{Exploited food} = \textit{p-food} \cdot \textit{i-foodshare} \tag{A.3c}$$

The factor 2 in eq. A3b was chosen so that the food intake at a medium predation risk (*p-safety*=0.5) equals the food intake of the control. Movement costs are the product of the allometric costs and twice the distance to the core cell as the individual has to move to the foraging cell and back to the central place. In risk-taking individuals, high predation risk additionally affects movement costs. Movement costs for the the foraging types are calculated by:

$$\text{Control:} \quad \text{Movement costs} = 2 \cdot \textit{i-lococost} \cdot \textit{distance}_{\textit{core}} \tag{A.4a}$$

$$\text{Risk-averse:} \quad \text{Movement costs} = 2 \cdot \textit{i-lococost} \cdot \textit{distance}_{\textit{core}} \tag{A.4b}$$

$$\begin{aligned} \text{Risk-taking:} \quad & \text{Movement costs} = \\ & \textit{p-safety} \geq 0.5\text{: } 2 \cdot \textit{i-lococost} \cdot \textit{distance}_{\textit{core}} \\ & \textit{p-safety} < 0.5\text{: } 2 \cdot \textit{i-lococost} \cdot \textit{distance}_{\textit{core}} + \\ & \qquad \textit{p-food} \cdot \textit{i-foodshare} \cdot (1 - 2 \cdot \textit{p-safety}) \end{aligned} \tag{A.4c}$$

Movement costs in risk-taking individuals increase depending on the amount of food in the cell. We assume that the higher the food intake the more often the individual interrupts foraging to return to the den. In refuges (*p-safety* ≥ 0.5) risk-taking individuals have the same movement costs as risk-averse and control individuals. Exemplary calculations for the different foraging types during home range search are shown in Table A.4.

If the food gain from the added cells to the home range meets the daily energy requirements and the movement costs of the animal for foraging in the cells of the home range, the home range search is successful and the individual establishes its home range in these cells. If the amount of cells exceeds the maximum home range size before the energy requirements are achieved, the individual fails to find a home range and is excluded from the community, i.e. we assume that it disperses to another landscape part or dies.

TABLE A.4: Example calculations of suitability, exploited food movement costs and food gain for refuges and risky habitat and varying amount of food for the different foraging strategies. Calculations are based on an individual with a body mass of 50g. Exploited food, movement costs and food gain are given in g dry biomass.

	Control	**Risk-averse**	**Risk-taking**
Suitability			
p-food: 0.5 *p-safety*: 0.1	0.5	0.05	0.05
p-food: 0.5 *p-safety*: 0.9	0.5	0.45	0.45
p-food: 0.05 *p-safety*: 0.9	0.5	0.045	0.045
p-food: 0.45 *p-safety*: 0.1	0.5	0.045	0.045
Exploited food			
p-food: 0.5 *p-safety*: 0.1	0.188	0.0376	0.188
p-food: 0.5 *p-safety*: 0.9	0.188	0.338	0.188
Movement costs			
p-food: 0.5 *p-safety*: 0.1	$5.98 \cdot 10^{-4}$	$5.98 \cdot 10^{-4}$	0.151
p-food: 0.5 *p-safety*: 0.9	$5.98 \cdot 10^{-4}$	$5.98 \cdot 10^{-4}$	$5.98 \cdot 10^{-4}$
Food gain			
p-food: 0.5 *p-safety*: 0.1	0.187	0.037	0.037
p-food: 0.5 *p-safety*: 0.9	0.187	0.338	0.187

Food consumption

If the home range search was successful, food resources (*p-food*) of cells within the home range are reduced by the amount of exploited food calculated during the home range search. In the last cell it can occur that the calculated animal's resource gain is higher than the amount of resources needed to fulfill the feeding rate of the animal. In these cases only the amount needed to cover the feeding rate is subtracted from the total resource amount in the cell.

Community saturation

During the simulation more and more individuals establish a home range within the landscape and decrease the food resources. Due to the reduction of available food resources new individuals are less likely to establish a home range, i.e. the amount of cells added to the home range exceeds the maximum home range size before the energy requirements of the individual can be fulfilled. During the simulation the number of consecutively failing individuals is counted. The simulation stops if a specific number of individuals (*nfail*) have consecutively not been able to find a home range.

A.2 Comparison of community metrics

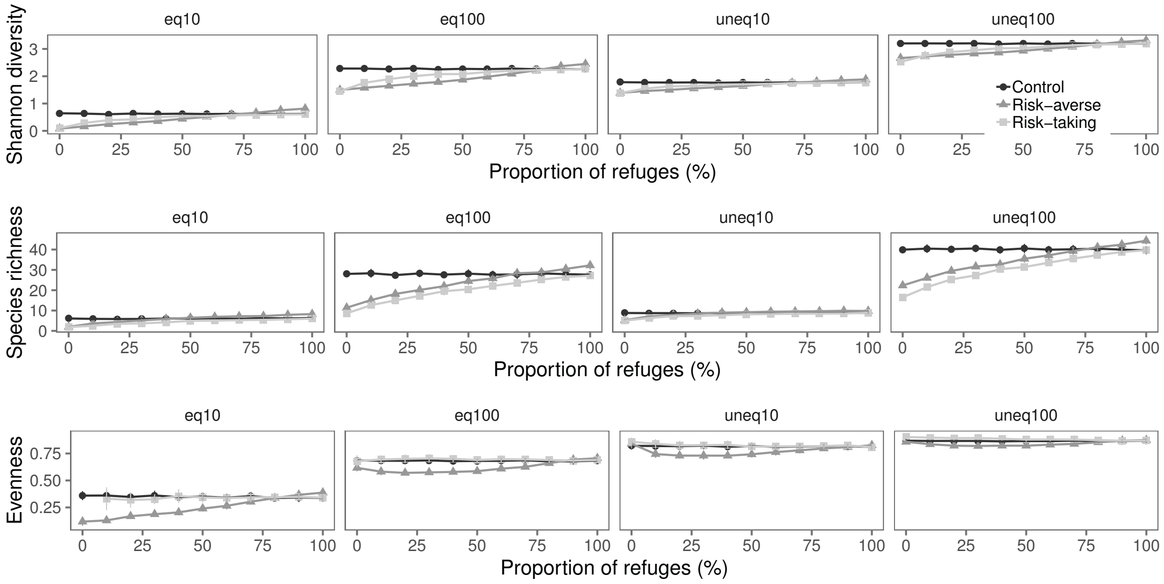

Fig. A.2. Comparison of community metrics for different body mass intervals and species numbers. The left panels ("eq10" and "eq100") show community metrics for evenly spaced body mass intervals and 10 respectively 100 species. Panels on the right side ("uneq10" and "uneq100") show results for unevenly spaced body mass intervals with 10 or 100 species.

APPENDIX B

Supplementary Material to Chapter 3

B.1 ODD-Protocol

Purpose

The purpose of the model is to evaluate the consequences of perceived predation risk on prey community assembly and home range formation under habitat loss and fragmentation.

Entities, state variables and scales

The model comprises two entities, landscape cells and prey individuals (Table B.1). Landscape cells are described by the state variables location, food resources (*p-food*) and safety (*p-safety*); the latter feature defines the "landscape of fear". Cells containing food resources (*p-food* >0) are called productive cells. Landscape cells are square cells on a grid with a size of 129 × 129 cells. Each landscape cell represents 4 m^2. We used periodic boundary conditions.

Prey individuals are characterized by their location and their body mass. To simplify spatial calculations, the location of individuals can only be on the discrete landscape grid cells. The body mass of the individual is used to calculate further physiological traits by using allometric relationships. The model uses discrete time steps. Each step represents the home range search of one individual.

Process overview and scheduling

In each step of the model a new prey individual is created and performs the processes *trait assignment* and *home range search*. If the home range search is successful, the process *food consumption* is executed, otherwise the individual is excluded from the community. The simulation continues until the community is saturated, i.e. a specific number of individuals (*nfail*, see Table B.2) have consecutively not been able to establish a home range in the landscape (see Fig. B.1 for an overview of the processes). Food resources in the landscape are reduced according to the exploitation by prey animals within the process of food consumption, while the landscape of fear is static. The location and size of the home range are stored after the individual has executed the home range search.

TABLE B.1: Entities and their state variables

Entity *State variable*	Unit	Description
Landscape cells		
p-food	Dry biomass, g/(cell · day)	Food resource availability in cell
p-safety	-	Safety of a cell, inverse to predation risk
Individuals		
i-bodymass	g	Body mass of individual
i-feartype	-	Foraging strategy of individual under predation risk
Allometric traits:		
i-feedrate	Dry biomass, g/day	Amount of food resources that need at least be contained in the home range
i-lococost	Dry biomass, g/cell	Locomotion costs for moving one cell forward
i-maxhr	cells	Maximum home range size
i-foodshare	-	Defines magnitude of food resource exploitation

Design Concepts

Basic principles

The model is based on a modelling approach developed by Buchmann et al. (2011). We extended this approach by including perceived predation risk. The model is individual-based (Grimm and Railsback, 2005) and uses the body mass as a main trait of individuals. By applying allometric relationships further traits such as energy requirements and locomotion costs can be calculated. Individuals choose a home range in the landscape depending on food availability, predation risk, physiological parameters and foraging strategies. The home range search is based on principles from optimal foraging theory, the area-minimizing

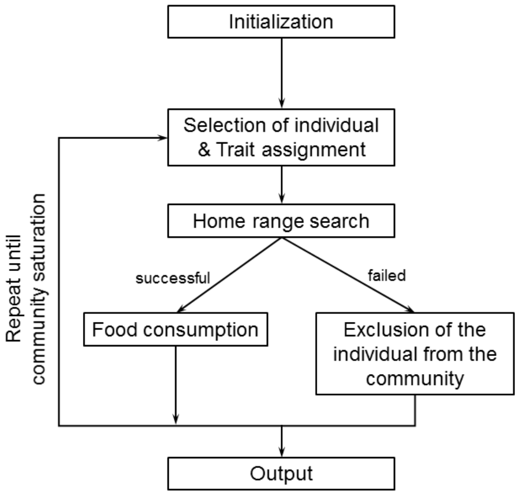

Fig. B.1. Schematic overview of processes in the model. After initialization, a new individual is created and gets assigned certain traits. This individual searches for a home range in the landscape that fulfills its daily energy requirements. The addition of cells to the home range is based on food availability and perceived predation risk in cells. If the home range search is successful, the individual consumes the food resources within, otherwise it is excluded from the community. These steps are repeated until the community is saturated.

principle (Mitchell and Powell, 2004) and the trade-off between foraging and predation risk (Brown, 1988).

The model does not include any direct predation effects but focuses on indirect, non-lethal effects of predators. Therefore, predators are not explicitly modelled but represented by the landscape of fear (Laundré et al., 2001; Laundré et al., 2010).

Decisions which of the neighboring cells should be added to the home range are based on the "minimize μ/f" (deaths per unit energy) rule by Gilliam and Fraser (1987) for risk-aware animals. In contrast, control animals apply the "maximize f" rule (energy per unit time Gilliam and Fraser, 1987). The model provides insights how adapted space use on the individual level due to different behavioral strategies, food and perceived predation risk distributions affects community structures.

Emergence

Community structure and composition emerges from the group of individuals that successfully established a home range in the landscape. Home range establishment is driven by individual traits, food availability and perceived predation risk in the landscape.

Adaptation

Animals adapt their home range size to resource availability and perceived predation risk in the landscape via the imposed "minimize μ/f"-rule. Home ranges have to be larger if resources are scarce or perceived predation risk is high in order to fulfill the animal's energy requirements.

Objectives

Animals aim to satisfy their energy requirements with the smallest possible home range (area-minimizing principle, Mitchell and Powell, 2004). Therefore, they add cells with the maximum food gain to their home range which is achieved in cells with a high food availability and a low predation risk.

Sensing

Individuals sense the food availability and the predation risk in the eight neighbouring cells to their current location.

Interaction

Individuals indirectly interact via resource competition during community assembly. By consuming resources after a successful home range search, individuals decrease the food availability in the landscape leaving less food resources for following individuals. We thus do not include territorial behavior, i.e. individuals do not defend territories.

Stochasticity

The selection of body masses from the input distribution is stochastic. To account for this variability, 20 replicate simulations are executed for each scenario. During home range search animal decisions can be stochastic if several cells have the same suitability. In these cases, the incomplete knowledge of individuals about the landscape is the reason for stochasticity.

Observation

Individual traits and home range size are collected at the end of a simulation. Home range sizes are the sum of cells that were added to the home range. Moreover, we collected the location of the home range of each individual in at least one repetition of each scenario. The values of all state variables of the landscape cells can be collected at the beginning and the end of a simulation.

Initialization

Before each simulation a new landscape is generated and general model parameters are initialized (Table B.2).

TABLE B.2: Initialized parameter values of the model

Parameter	Value	Unit	Description
Food resources in productive cell (*p-food*)	0.548	Dry biomass, g/cell	20% of average productivity in grass- and shrublands (Buchmann et al., 2011; Whittaker, 1975)
Number of failed individuals (*nfail*)	100	-	Number of individuals that consecutively failed to find a home range in the landscape, used to stop the simulation
Body mass input distribution	M^{expo}	M in kg	Truncated distribution from which body masses of individuals are chosen
Exponent (*expo*)	-1.5	-	Exponent that yields realistic community structures (Buchmann et al., 2011)
Lower boundary (*lowB*)	0.01	kg	Lowest possible body mass of individuals
Upper boundary (*upB*)	1	kg	Highest possible body mass of individuals

Landscape initialization

Realistic three-dimensional landscapes are read in at the beginning of each simulation (see Input data for landscape generation). The z-values of the landscape grid are interpreted as food resource availability (*p-food*). We differentiate between two different food scenarios, F^+ and F^-, representing contrasting effects of habitat loss on food resource availability. In F^+-scenarios, we directly use the read-in z-values as food resource availability, in F^--scenarios we use the inverse z-values as food resource availability. These scenarios represent different effects of habitat loss on habitat quality. In F^+-scenarios cells with a high food resource availability remain, representing systems where mostly habitat with a low quality is lost. In contrast, cells with a low food resource availability remain in F^--scenarios representing systems where mostly habitat with a high quality is lost. The role of habitat quality for animal community structures has been discussed to be as important as habitat quantity and configuration (Bragagnolo et al., 2007; Fleishman et al., 2002; Summerville and Crist, 2004).

In both scenarios, the z-values are scaled to an average resource availability of 2.74 g dry biomass $\cdot$grid cell$^{-1} \cdot$ day^{-1}, a typical value for shrub- and grasslands (Whittaker, 1975). Only 20% of these food resources are available to prey animals while the rest is lost to other taxa or not consumable (Buchmann et al., 2011), resulting in an average resource availability of 0.548 g dry biomass $\cdot$grid cell$^{-1} \cdot$ day^{-1}. We assume that all prey individuals are herbivorous and compete for the same, single resource. Food resources are exploited by animals during the simulation and not replenished, leading to a decrease in food resource availability.

For habitat loss, food resource availability in specific cells (depending on the landscape scenario, see explanation below) was set to 0 until only a certain proportion of cells containing food resources was left. We tested landscapes with a habitat loss ranging from 0% to 90% in intervals of 10%. Depending on the food scenario we set cells with the lowest z-values (F^+-scenarios) or the highest z-values (F^--scenarios) to 0. Cells with food resources are hereafter called "habitat cells" and cells that have been set to 0 due to habitat loss are called "matrix cells".

Besides food resources, all landscape cells have a specific perceived predation risk (*p-safety*). This perceived predation risk represents the landscape of fear of prey animals. Landscapes of fear are static, i.e. the perceived predation risk in the cells does not change during the simulation. Matrix cells represent a hostile environment for prey animals and therefore have a high perceived predation risk (*p-safety* = 0). Perceived predation risk in habitat cells is either positively or negatively correlated to food resource availability in the landscape. Similar to the food scenarios, we discriminate between two risk scenarios, S^+ and S^-. In S^+-scenarios mostly safe patches remain after habitat loss, i.e. habitat loss has negative effects on predators so that the relative perceived predation risk in habitat patches decreases. In S^--scenarios mostly risky patches remain, i.e. habitat loss has positive effects on predator abundance and thus the relative perceived predation risk in habitat patches increases. Food resource availability and safety of patches are positively correlated in the scenarios F^+S^+ and F^-S^-, i.e. cells with a high food availability are the safest and cells with a low food availability are the most risky. In the scenarios F^+S^- and F^-S^+ food and safety are negatively correlated, thus cells with a high food availability have the lowest safety and vice versa. The different scenarios of food and safety should represent a gradient of landscapes that animals might encounter in their habitat.

In specific scenarios, edge effects are included. We define edge effects as an alteration of perceived predation risk at the edges of the habitat in scenarios with a habitat loss of 10% or more. Food resource availability is not affected by edge effect. To implement edge effects, we defined all cells in a certain distance from the matrix as edge cells. We used scenarios with 5 m, 10 m and 20 m distance from the matrix. Distances were always calculated from the center of a cell. We assume that with edge effects perceived predation risk from the matrix affects perceived predation risk in habitat cells and vice versa. Thus, perceived predation risk in edge cells was modified to the average perceived predation risk of all cells in the radius where edge effects were effective.

Prey community

The main characteristic of the individuals in the model is their body mass. This is chosen from a "body mass input distribution", a truncated power-law distribution defining the probability density of a specific body mass (Buchmann et al., 2011; Buchmann et al., 2012). The body mass input distribution represents the regional species pool. It defines possible body masses for the individuals as well as their density.

Furthermore, we differentiate between risk-aware and risk-unaware (control) communities. Animals of control communities do not perceive predation risk in landscape cells and therefore do not change their foraging behavior, i.e. these animals do not suffer from non-lethal predator effects. In contrast, risk-aware communities perceive predation risk and adapt their foraging behavior accordingly (see Home range search for details on foraging behavior of control and risk-aware animals). By using risk-aware and control communities in separate model runs, consequences of perceived predation risk on prey community structure can be evaluated. Additionally, the length of a simulation run is initialized. It is defined by the number of individuals that are consecutively not able to establish a home range (*nfail*).

Input data

Landscapes are read in at the beginning of each simulation. Realistic three-dimensional fractal landscapes with a size of 129 × 129 cells are generated with the well-established midpoint-displacement algorithm (Hargrove et al., 2002; Körner and Jeltsch, 2008; Saupe, 1988). Each cell represents $4\,\mathrm{m}^2$. The configuration of these landscapes is controlled by σ^2, determining the variance in displacement of points and the Hurst-Factor H, determining the spatial autocorrelation of points. We use a moderate variance (σ^2=30) in all landscapes. For spatial autocorrelation we use three different values representing varying degrees of fragmentation of the landscape (H=0.1 for low fragmentation, H=0.5 for medium fragmentation and H=0.9 for high fragmentation).

Submodels

Trait assignment

In each step of the model a new individual is created. Individuals are characterized by different traits, mainly by their body mass and their foraging strategy. The body mass of the individual is drawn from a truncated body mass input distribution (see *Initialization*). Similar to the model by (Buchmann et al., 2011), allometric relationships are used to calculate further traits (Table B.3). We assume that individuals are central place foragers frequently returning to a central place, their den. The den is an absolute refuge where individuals do not face predation risk. Risk-aware animals need to balance energy intake against predation risk, especially if profitable patches have a higher predation risk than less profitable patches (Lima, 1998). Common responses of animals foraging under predation risk are adaptations in space use and/or activity levels (Lima, 1998). Here, we implemented a commonly used foraging strategy of animals that focuses on adaptations in food intake between patches with different predation risk. Risk-aware animals show a reduced food intake in risky habitat patches to minimize the time they are exposed to this high risk. To compensate the lower food intake under high risk, they forage more intensively in refuges and show an increased food intake in these patches compared to control individuals. An example for such a foraging strategy are gerbils, which reduce foraging in open areas under the presence of owls and shift their foraging activities to bush areas that offer cover (Kotler et al., 1991). Similar patterns were shown for other small mammals (Jacob and Brown, 2000; Simonetti, 1989) and fish (Rozas and Odum, 1988; Werner et al., 1983).

TABLE B.3: Allometric relationships used to calculate further traits of the individuals. M is the body mass of the individual in g.

Trait	**Allometric relationship**	**Unit**	**Description and references**
Feeding rate (*i-feedrate*)	$0.323 \cdot M^{0.744}$	Dry biomass, g/day	Least amount of food that individual needs to gain from home range cells for successful search Nagy (2001)
Locomotion costs (*i-lococost*)	$\frac{0.0976 \cdot M^{0.68}}{14 \cdot 10^3}$	Dry biomass, g/m	Costs of individual for moving from one place to another Calder (1996), Garland (1983), and Nagy (2001)
Magnitude of food exploitation (*i-foodshare*)	$\gamma \cdot M^{-0.25}$	-	Fractal characteristics affect the resolution at which individuals can exploit resources, γ was set to 1 Buchmann et al. (2011) and Haskell et al. (2002)
Maximum home range size (*i-maxhr*)	$0.0138 \cdot M^{1.18}$	ha	Used as a constraint for home range size, if *i-maxhr* is larger than the landscape size, it is set to the landscape size Kelt and Van Vuren (2001)

Home range search

The key process of the model is the home range search of the newly created individual. The home range needs to contain enough food resources to cover the individual's feeding rate and movement costs. We assume individuals to be central place foragers frequently returning to their den within the home range. This is implicitly represented in the model by calculating the movement costs for the distance to a cell and the return. The home range search starts with the choice of a core cell, the central place of the home range where the den of the animal is located. This cell is chosen randomly from the pool of cells containing food resources. Outgoing from this cell, further cells are added to the home range until the energy requirements of the animal are covered. . The cell to be added next is chosen from the neighboring cells of the cell that was previously added to the home range. We assume that the animal has a perceptual range of one cell, i.e. it can sense the food availability and predation risk in the neighboring cells. To decide which of these cells is added to the home range the suitability of a cell is calculated using the "μ/f"-rule (deaths per unit energy, Gilliam and Fraser, 1987)

$$\text{Suitability} = (1 - \textit{p-safety})/\text{Food gain} \tag{B.1}$$

The cell with the lowest suitability is added to the home range, i.e. the animal chooses the minimum predation risk per unit energy. For the control, the suitability of a cell is only defined by food gain (Suitability = Food gain) and the cell with the highest suitability is chosen. If several cells are equally suitable, one of the cells with the minimum distance to the core is chosen randomly. Food gain is the amount of energy that an animal can gain from a certain cell while accounting for the movement costs of foraging in this cell. It is calculated by:

$$\text{Food gain} = \text{Food intake} - \text{Movement costs} \tag{B.2}$$

The amount of food intake is the arithmetic product of food availability in the cell (*p-food*) and the individual magnitude of food exploitation (*i-foodshare*)depending on body mass:

$$\text{Control:} \qquad \text{Food intake} = \textit{p-food} \cdot \textit{i-foodshare} \tag{B.3a}$$

The parameter *i-foodshare* is used to distinguish the different consumption levels of local food resources by prey individuals of different body masses. For risk-aware individuals, perceived predation risk additionally affects food intake:

$$\text{Risk-aware:} \qquad \text{Food intake} = \textit{p-food} \cdot \textit{i-foodshare} \cdot 2 \cdot \textit{p-safety} \tag{B.3b}$$

The factor 2 in eq. B.3b was chosen so that the food intake at a medium predation risk (*p-safety*=0.5) equals the food intake of the control.

Movement costs are the product of the allometric costs (with increasing costs for large animals) and twice the distance to the core cell, as the individual has to move to the foraging cell and back to the central place.

$$\text{Movement costs} = \textit{i-lococost} \cdot 2 \cdot \text{distance}_{\text{core}} \tag{B.4}$$

Movement costs are the same for risk-aware and control animals.

After the addition of a cell to the home range, the food gain from all cells in the home range is compared with the daily energy requirements of the animal. If the food gain covers the daily energy requirements, the home range search is successful. The individual establishes its home range in these cells and consumes the resources within them. Otherwise, more cells are added to the home range. If the number of cells exceeds the maximum home range size before the energy requirements are met, the individual fails to find a home range and is excluded from the community, i.e. we assume that it relocates to another part of the landscape or dies.

Food consumption

If the home range search was successful, food resources (*p-food*) of cells within the home range are reduced by the amount of food intake calculated during the home range search. In the last cell it can occur that the calculated animal's resource gain is higher than the amount of resources needed to fulfill the feeding rate of the animal. In these cases only the amount needed to cover the feeding rate is subtracted from the total resource amount in the cell.

Community saturation

During the simulation more and more individuals establish a home range within the landscape and decrease the food resources. Due to the reduction of available food resources new individuals are less likely to establish a home range, i.e. the amount of cells added to the home range exceeds the maximum home range size before the energy requirements of the individual can be fulfilled. Thus, more and more animals fail to find a home range and the community becomes "saturated". The simulation stops if a specific number of individuals (*nfail*) have consecutively not been able to find a home range.

B.2 Additional figures

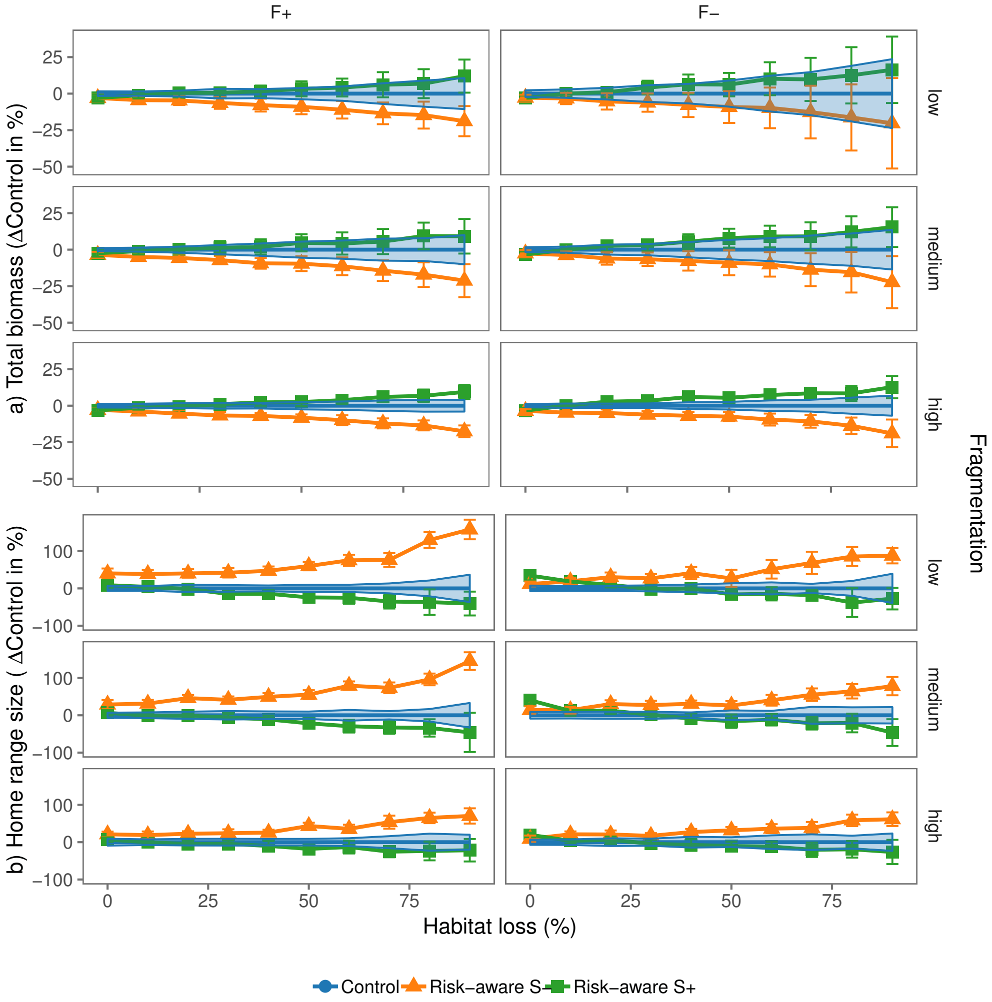

Fig. B.2. Deviation of total biomass (a) and median home range size (b) of risk-aware communities facing habitat loss and fragmentation for the two different food scenarios in comparison to the control community. Plots show the deviation in total biomass and home range size of the risk-aware community (orange triangles and green rectangles) from the control (blue circles). For risk-aware communities, two different landscapes of fear were assumed. In S^--scenarios (orange triangles) risky patches remain, in S^+-scenarios (green rectangles) safe patches remain.

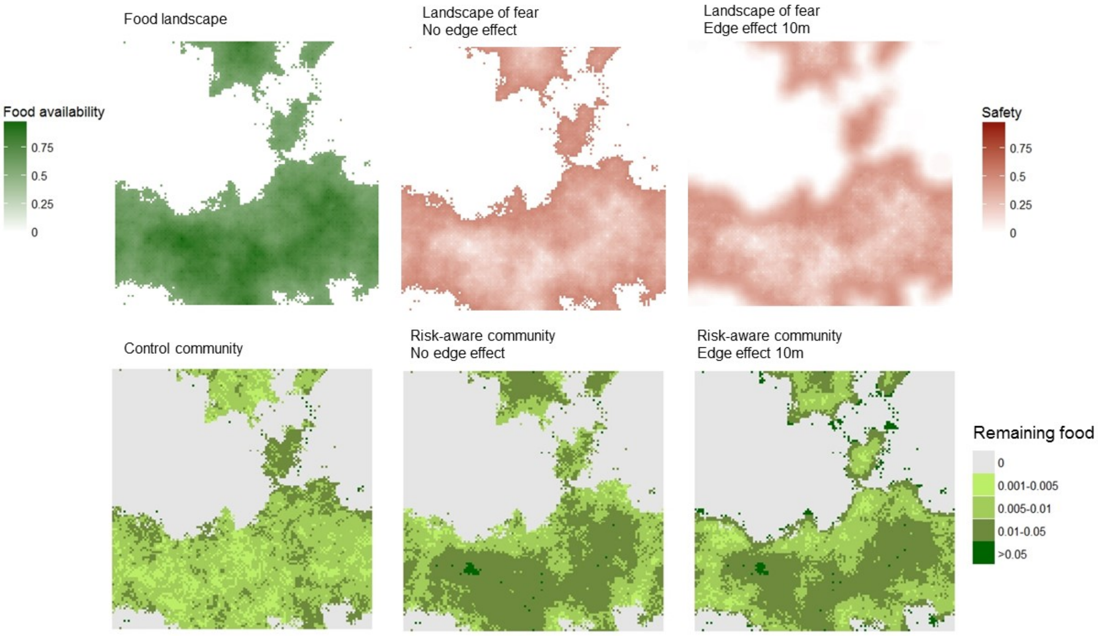

Fig. B.3. Remaining food in the landscape at the end of a simulation for control and risk-aware communities (F^+S^--scenario). Plots at the top from left to right show food availability (g) at the beginning of the simulation, landscape of fear without edge effects and with edge effects of 10 m. Plots at the bottom from left to right show the remaining food (in g) at the end of a simulation for control and risk-aware communities without edge effects and with edge effects of 10 m. Remaining food is similar to the giving-up density commonly measured in field experiments.

APPENDIX C

Supplementary Material to Chapter 4

C.1 ODD-protocol

Purpose

The purpose of the model is to evaluate the consequences of individual variation in risk perception on prey space use, survival probability and community structure.

Entities, state variables and scales

The model comprises two entities, landscape cells and prey individuals (Table C.1). Landscape cells are described by the state variables location, food resources (*p-food*) and safety (*p-safety*); the latter feature defines the "landscape of fear". Cells containing food resources (*p-food* >0) are called productive cells. Landscape cells are square cells on a grid with a size of 129 × 129 cells. Each landscape cell represents 4 m^2. We used periodic boundary conditions.

Prey individuals are characterized by their location, their body mass (*i-bodymass*) and their individual risk perception (*i-rp*). To simplify spatial calculations, the location of individuals can only be on the discrete landscape grid cells. The body mass of the individual is used to calculate further physiological traits by using allometric relationships. The model uses discrete time steps. Each step represents the home range search of one individual.

Process overview and scheduling

In each step of the model a new prey individual is created and performs the processes trait assignment and home range search. If the home range search is successful, the process *food consumption* is executed, otherwise the individual is excluded from the community. The simulation continues until the community is saturated (process *community saturation*), i.e. a specific number of individuals (*nfail*, see Table C.2) have consecutively not been able to establish a home range in the landscape. After the community is saturated, animals can be killed by a predator (process *Predation mortality*). An overview of the processes in the model is shown in Fig. C.1. Food resources in the landscape are reduced according to the exploitation by prey animals within the process of food consumption, while the landscape of fear is static. The location and size of the home range are stored after the individual has executed the home range search and consumed the food resources within.

TABLE C.1: Entities and their state variables

Entity *State variable*	Unit	Description
Landscape cells		
p-food	Dry biomass, g/(cell · day)	Food resource availability in cell
p-safety	-	Safety of a cell, inverse to predation risk
Individuals		
i-bodymass	g	Body mass of individual
i-rp	relative scale from 0 to 1	Individual risk perception
i-hrsize	cells	Home range size of prey animal, adds up during home range search
Allometric traits:		
i-feedrate	Dry biomass, g/day	Amount of food resources that need at least be contained in the home range
i-lococost	Dry biomass, g/cell	Locomotion costs for moving one cell forward
i-maxhr	cells	Maximum home range size
i-foodshare	-	Defines magnitude of food resource exploitation

Design Concepts

Basic principles

The model is based on a modelling approach developed by Buchmann et al. (2011). We extended this approach by including a landscape of fear, individual risk perception of animals and the process predation mortality. The model is individual-based (Grimm and Railsback, 2005) and uses the body mass as a main trait of individuals. By applying allometric relationships further traits such as energy requirements and locomotion costs can be calculated. Individuals choose a home range in the landscape depending on food availability, perceived predation risk, physiological parameters and foraging strategies. The home range search is based on principles from optimal foraging theory, the area-minimizing principle (Mitchell and Powell, 2004) and the trade-off between foraging and predation risk (Brown, 1988).

Decisions which of the neighboring cells should be added to the home range are based on the "minimize μ/f" (deaths per unit energy) rule by Gilliam and Fraser (1987).

Predators are not explicitly modeled, instead they are represented by the landscape of fear (Laundré et al., 2001; Laundré et al., 2010). Furthermore, prey animals face a real predation risk based on the overall safety of their home range. To calculate this overall safety a weighted geometric mean is used. It averages the safety of each cell in the home range and uses the amount of exploited food in this cell as weights. The amount of food represents the time that the animal spends in a cell, i.e. if it forages a high amount of food in a specific cell, it will stay longer in this cell and thus be exposed to the predation risk for a longer time.

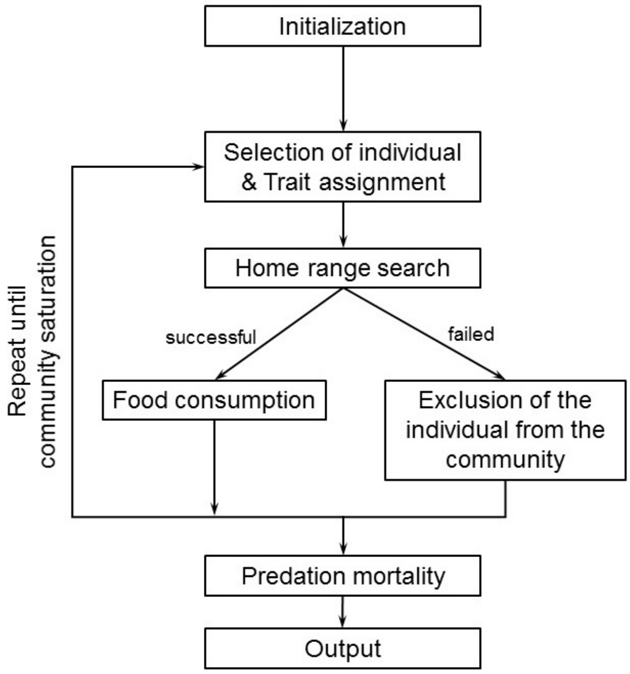

Fig. C.1. Schematic overview of processes in the model. After initialization, a new individual is created and gets assigned certain traits. This individual searches for a home range in the landscape that fulfills its daily energy requirements. The addition of cells to the home range is based on food availability and perceived predation risk in cells. If the home range search is successful, the individual consumes the food resources within, otherwise it is excluded from the community. These steps are repeated until the community is saturated. After community saturation, animals face predation mortality.

Emergence

Community structure and composition emerge from the group of individuals that successfully established a home range in the landscape and were not killed by predation. Home range establishment emerges from individual traits including risk perception, food availability and perceived predation risk in the landscape.

Adaptation

Animals use a trade-off between energy gain and perceived predation risk to decide which cell they add to their home range. This trade-off is based on the "μ/f-rule" (Gilliam and Fraser, 1987). Depending on the resource availability and perceived predation risk of the cells, animals adapt their decision which cell they add to their home range. Furthermore, animals adapt their home range size to resource availability and perceived predation risk in the landscape. Home ranges have to be larger if resources are scarce or perceived predation risk is high in order to fulfill the animal's energy requirements.

Objectives

Animals aim to satisfy their energy requirements with the smallest possible home range (area-minimizing principle, Mitchell and Powell, 2004). Therefore, they add cells with the maximum food gain to their home range which is achieved in cells with a high food availability and a low perceived predation risk.

Sensing

Individuals sense the food availability and the perceived predation risk in the eight neighboring cells to their current location.

Interaction

Individuals indirectly interact via resource competition during community assembly. By consuming resources after a successful home range search, individuals decrease the food availability in the landscape leaving less food resources for following individuals. We thus do not include territorial behavior, i.e. individuals do not defend territories. Even though predators are not explicitly modeled, prey animals respond to the landscape of fear imposed by predators and face a predation mortality.

Stochasticity

The selection of body masses from the input distribution is stochastic. To account for this variability, 20 replicate simulations are executed for each scenario. During home range search animal decisions can be stochastic if several cells have the same suitability. In these cases, the incomplete knowledge of individuals about the landscape is the reason for stochasticity. The decision whether an animal gets killed by a predator is stochastic with the overall safety of the home range driving the probability of an animal to be killed.

Observation

Individual traits and home range size are collected at the end of a simulation. Home range sizes are the sum of cells that were added to the home range. Additionally, we collect which individuals are killed by a predator. Moreover, we collected the location of the home range of each individual in one repetition of each scenario. The values of all state variables of the landscape cells can be collected at the beginning and the end of a simulation.

Initialization

Before each simulation a new landscape is generated and the regional species pool, the distribution of risk perception in the prey community as well as general model parameters are initialized (Table C.2).

Landscape initialization

Landscapes had a size of 129 × 129 cells with each cell representing 4 m^2. The landscape consisted of two layers, the food landscape and the landscape of fear. We assumed that all prey animals are herbivorous and feed on the same food resource. Food resources (*p-food*) were distributed by using a well-established midpoint-displacement algorithm yielding realistic fractal landscapes (Körner and Jeltsch, 2008; Saupe, 1988). We used a moderate variance in the displacement of points (σ^2=30) and a medium degree of fragmentation (spatial autocorrelation, H=0.5). We scaled food resources to an average resource availability of 2.74 g dry

TABLE C.2: Initialized parameter values of the model

Parameter	Value	Unit	Description
Food resources in productive cell (*p-food*)	0.548	Dry biomass, g/cell	20% of average productivity in grass- and shrublands (Buchmann et al., 2011; Whittaker, 1975)
Number of failed individuals (*nfail*)	100	-	Number of individuals that consecutively failed to find a home range in the landscape, used to stop the simulation
Body mass input distribution	M^{expo}	M in kg	Truncated distribution from which body masses of individuals are chosen
Exponent (*expo*)	-1.5	-	Exponent that yields realistic community structures (Buchmann et al., 2011)
Lower boundary (*lowB*)	0.01	kg	Lowest possible body mass of individuals
Upper boundary (*upB*)	1	kg	Highest possible body mass of individuals

biomass $\cdot$grid cell^{-1} $\cdot$ day^{-1}, a value which is typical for shrub- and grasslands (Whittaker, 1975). From these food resources 20% were available to the prey animal. The remainder was lost to other taxa or was not consumable (Buchmann et al., 2011).

The landscape of fear represented the spatial distribution of perceived predation risk. We used a relative scale for the safety in the landscape of fear (*p-safety*) with values ranging from 0 (risky cell) to 1 (safe cell, refuge). Depending on the individual degree of risk perception of the prey animal, the magnitude how much perceived predation risk affected the animal's decisions was varied (see Individual risk perception and Home range search). Perceived predation risk was in general negatively correlated to the food landscape, i.e. patches with a high food availability had a low safety and vice versa (see Teckentrup et al. (under review) for the consequences of different correlations between food and fear landscape). A negative correlation between food and safety represents a common situation that animals face in their environment (Lima, 1998). We tested four different landscapes of fear varying in the mean and variance of safety (Fig. C.2). The overall safety decreases from safe via medium to risky landscapes of fear implying a decreasing abundance of predators. In bimodal landscapes of fear, mean safety is similar to the medium landscapes of fear but cells are either very risky or very safe. This represents a situation in which the predator is constrained to specific areas and not able to reach the prey in other areas, for example due to thick vegetation.

Regional species pool, distribution of risk perception and general model parameters

The main characteristic of the individuals in the model is their body mass. This is chosen from a "body mass input distribution", a truncated power-law distribution defining the probability density of a specific body mass (Buchmann et al., 2011; Buchmann et al., 2012).

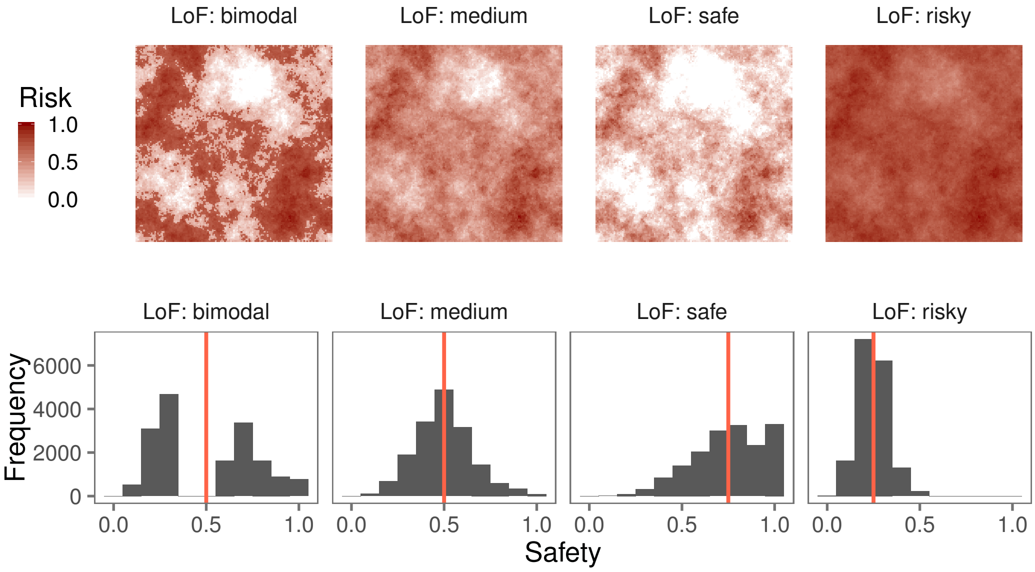

Fig. C.2. Exemplary landscapes of fear (top) and the corresponding histogram of the safety distribution (bottom). The red line marks the mean safety of the landscape.

The body mass input distribution represents the regional species pool. It defines possible body masses for the individuals as well as their density.

We tested different distributions of risk perception in order to assess how variation in risk perception affected prey community structures (Fig.C.3). Even though the occurrence of intra- and interspecific differences in risk behavior has been verified for many species (Preisser and Orrock, 2012; Sih, 2004), studies rarely assess which proportion of a population or community shows which behavior. Thus, we used different scenarios for the distribution of risk perception in the model in order to evaluate their potential consequences.

A common assumption is that antipredatory behavior including risk perception is related to the body mass of an animal (Preisser and Orrock, 2012). However, studies mostly focus on intraspecific differences in body size (e.g. Urban, 2007b) and not on interspecific differences. In order to estimate interspecific effects of body size on antipredatory behavior, Preisser and Orrock (2012) performed a meta-analysis examining species-level responses to predation risk. One of their findings was a decrease in open habitat use with increasing body size of the prey, suggesting a higher risk perception in large animals. Based on this result, we included a scenario in the model in which risk perception of the prey community increased with body mass (Allometric, Fig.C.3a).

Furthermore, differences in risk behavior are often reported in the context of animal personality. These differences can be in a continuum of behavior (Sih, 2004) or can be distinct strategies (e.g. in bluegill sunfish: Werner et al., 1981; Wilson, 1998). Overall, the environmental situation that animals encounter drives the evolution of individual differences in animals (Sih, 2004). In the model, we included two scenarios with distinct strategies of animals. Therefore, we used a bimodal distribution, one in which individuals randomly get assigned a risk perception of either 0 or 2 (Bimodal0_2_std0, Fig. C.3b) and one in which

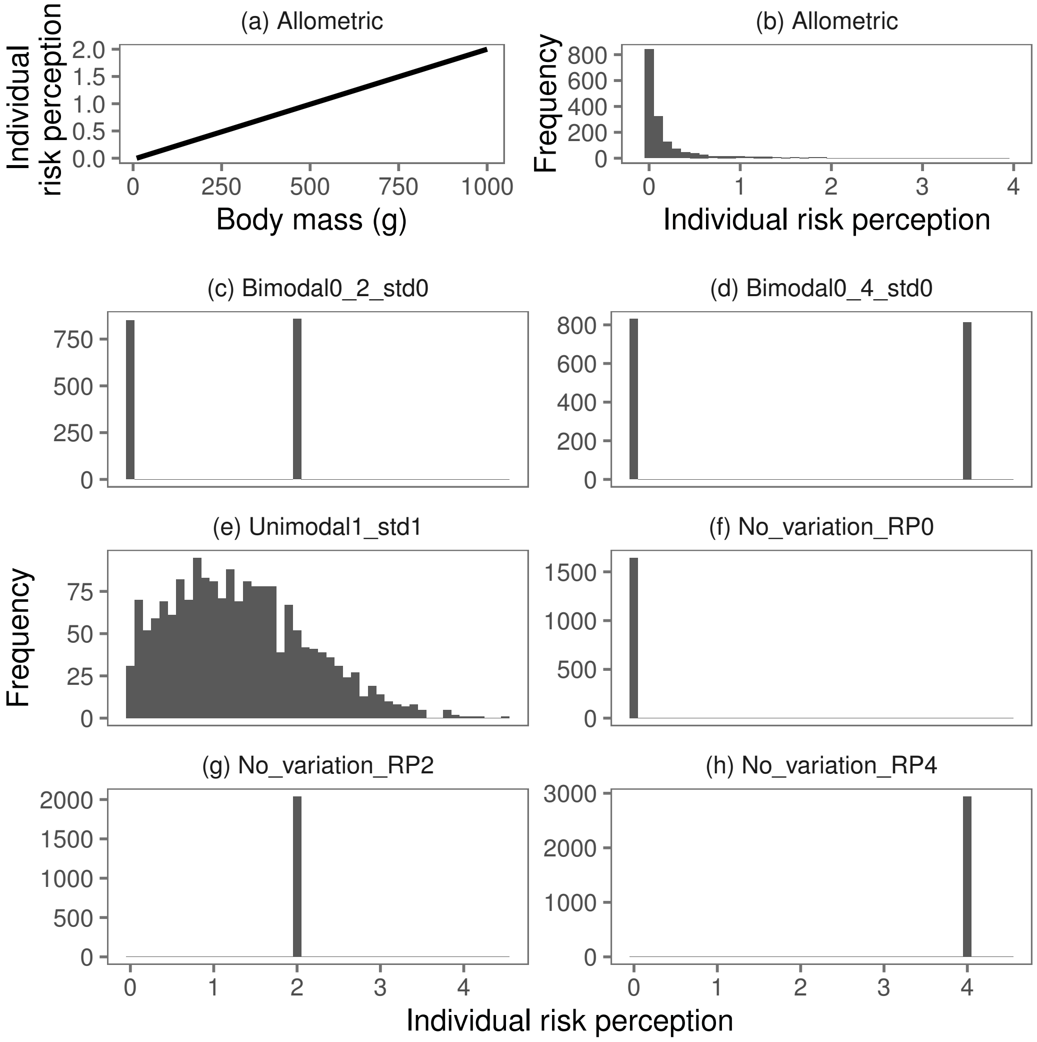

Fig. C.3. Relationship between individual risk perception and body mass for prey communities with an allometric scaling of risk perception (a) and tested distributions of risk perception (b-h).

they get assigned a risk perception of 0 or 4 (Bimodal0_4_std0, Fig. C.3c). Additionally, we tested a scenario in which risk perception of animals was drawn from a normal distribution with a mean of 1 and a standard deviation of 1 (Unimodal1_std1, Fig. C.3d).

We compared these scenarios with variation in risk perception to scenarios in which all animals of the prey community had the same risk perception. As a baseline scenario we used a community in which all animals were unaware of predation risk in the landscape (No_variation_RP0, Fig. C.3e). Furthermore, we tested two other communities without variation in risk perception, one where all animals had a risk perception of 2 (No_variation_RP2, Fig. C.3f) and one in which animals had a risk perception of 4 (No_variation_RP4, Fig. C.3g).

Additionally, the length of a simulation run is initialized. It is defined by the number of individuals that are consecutively not able to establish a home range (*nfail*, Table C.2).

Input data

Landscapes are read in at the beginning of each simulation. Realistic three-dimensional fractal landscapes are generated with the well-established midpoint-displacement algorithm (Hargrove et al., 2002; Körner and Jeltsch, 2008; Saupe, 1988). The configuration of these landscapes is controlled by σ^2, determining the variance in displacement of points and the Hurst-Factor H, determining the spatial autocorrelation of points. We use a moderate variance (σ^2=30) in all landscapes. For spatial autocorrelation we used a medium fragmentation degree (H=0.5 for medium fragmentation).

Submodels

Trait assignment

In each step of the model a new individual is created. Individuals are characterized by their body mass. The body mass of the individual is drawn from a truncated body mass input distribution (see Initialization). Similar to the model by Buchmann et al. (2011), allometric relationships are used to calculate further traits (Table C.3). Furthermore, animals get assigned an individual risk perception which is drawn from the initialized risk distribution (see Initialization for possible risk distributions). We assume that individuals are central place foragers frequently returning to a central place, their den. The den is an absolute refuge where individuals do not face predation risk.

Home range search

The key process of the model is the home range search of the newly created individual. The home range must contain enough food resources to match the animal's daily energy requirements. All animals are central place foragers which means that they frequently return to their den within the home range. At the beginning of the home range search the animal randomly chooses a habitat cell and establishes its den therein. Outgoing from the den,

TABLE C.3: Allometric relationships used to calculate further traits of the individuals. M is the body mass of the individual in g.

Trait	Allometric relationship	Unit	Description and references
Feeding rate (*i-feedrate*)	$0.323 \cdot M^{0.744}$	Dry biomass, g/day	Least amount of food that individual needs to gain from home range cells for successful search Nagy (2001)
Locomotion costs (*i-lococost*)	$\frac{0.0976 \cdot M^{0.68}}{14 \cdot 10^3}$	Dry biomass, g/m	Costs of individual for moving from one place to another Calder (1996), Garland (1983), and Nagy (2001)
Magnitude of food exploitation (*i-foodshare*)	$\gamma \cdot M^{-0.25}$	-	Fractal characteristics affect the resolution at which individuals can exploit resources, γ was set to 1 Buchmann et al. (2011) and Haskell et al. (2002)
Maximum home range size (*i-maxhr*)	$0.0138 \cdot M^{1.18}$	ha	Used as a constraint for home range size, if *i-maxhr* is larger than the landscape size, it is set to the landscape size Kelt and Van Vuren (2001)

neighboring cells are added to the home range until the animal's daily energy requirements are fulfilled. The animal has a perceptual range of 1 and can therefore sense food availability and predation risk (p-safety) in the neighboring cells. It chooses the cell to be added next to the home range from the neighboring cells of the cell that was previously added to the home range. The decision for one of these neighboring cells is based on food gain and perceived predation risk. For the decision, which of these cells is added to the home range the suitability of a cell is calculated by the "μ/f"-rule (death per unit energy Gilliam and Fraser, 1987):

$$\text{Suitability} = \text{Food gain}/(1 - \textit{p-safety})^{i-rp} \tag{C.1}$$

The exponent *i-rp* is the individual risk perception of the animal that was assigned before. Animals choose the cell with the highest suitability, i.e. they minimize the probability of death per unit energy. If several cells are equally suitable, the cell with the smallest distance to the den is chosen.

Food gain is the amount of energy that the individual can gain from a certain cell while accounting for the movement costs of foraging in this cell. It is calculated by:

$$\text{Food gain} = \text{Food intake} - \text{Movement costs} \tag{C.2}$$

The amount of food intake is the arithmetic product of food availability in the cell (*p-food*), the individual magnitude of food exploitation (*i-foodshare*) depending on body mass and the perceived predation risk:

$$\text{Food intake} = \textit{p-food} \cdot \textit{i-foodshare} \cdot (2 \cdot \textit{p-safety})^{\textit{i-rp}} \tag{C.3}$$

The parameter *i-foodshare* is used to distinguish the different consumption levels of local food resources by prey individuals of different body masses. The factor 2 was chosen in a way that the food intake of animals with risk perception (*i-rp* >0) in cells with a medium safety (*p-safety* =0.5) equals the food intake of animals that are unaware of predation risk (*i-rp* =0).

Movement costs are the allometric energy costs of an animal (*i-lococost*) for moving during foraging multiplied with the distance moved. Since the animal is a central place forager, we assume that it returns to its den each time when it has foraged in a cell. Movement costs are calculated by the product of the allometric costs and twice the distance to the den as the animal has to move back and forth to the cell in which it wants to forage:

$$\text{Movement costs} = \textit{i-lococost} \cdot 2 \cdot \text{distance}_{\text{den}} \tag{C.4}$$

When a cell was added to the home range, it is assessed whether the food gain from all cells in the home range is sufficient to fulfill the animal's daily energy requirements. If this is true, the animal stops the home range search, establishes its home range in these cells. If energy requirements are not yet fulfilled, further cells are added to the home range until either the energy requirements are met or the home range size exceeds the maximum home range size. In the latter case, the individual is excluded from the community. We assume that this animal would migrate to another habitat patch outside of the modeled area or die.

Food consumption

If the home range search was successful, food resources (*p-food*) of cells within the home range are reduced by the amount of food intake calculated during the home range search. In the last cell it can occur that the calculated animal's resource gain is higher than the amount of resources needed to fulfill the feeding rate of the animal. In these cases only the amount needed to cover the feeding rate is subtracted from the total resource amount in the cell.

Community saturation

During the simulation more and more individuals establish a home range within the landscape and decrease the food resources. Due to the reduction of available food resources new individuals are less likely to establish a home range, i.e. the amount of cells added to the home range exceeds the maximum home range size before the energy requirements of the individual can be fulfilled. Thus, more and more animals fail to find a home range and the community becomes "saturated". The simulation stops if a specific number of individuals (*nfail*, Tab.C.2) have consecutively not been able to find a home range.

Predation mortality

After the saturation of the community, animals face predation mortality. The probability of being killed (P_{mort}) depends on the safety of the cells in the home range and the amount of food that the individual exploited in these cells. The amount of exploited food is a proxy for the time that an individual spends in a cell and thus defines how long the animal experienced a specific safety. We used a weighted geometric mean to calculate the overall safety of the home range (SafetyHR):

$$\text{Safety}_{HR} = \left(\prod_{i=1}^{n} p\text{-}safety^{\text{food intake}} \right)^{\frac{1}{\sum_{i=1}^{n} \text{food intake}}} \tag{C.5}$$

with n as the number of cells in the home range.

The probability of being killed was then the inverse of the overall safety of the home range.

$$P_{\text{mort}} = (1 - \text{Safety}_{HR}) \tag{C.6}$$

This probability is compared to a random number between 0 and 1. If the random number is smaller than P_{mort} the animal is killed.

C.2 Additional figures

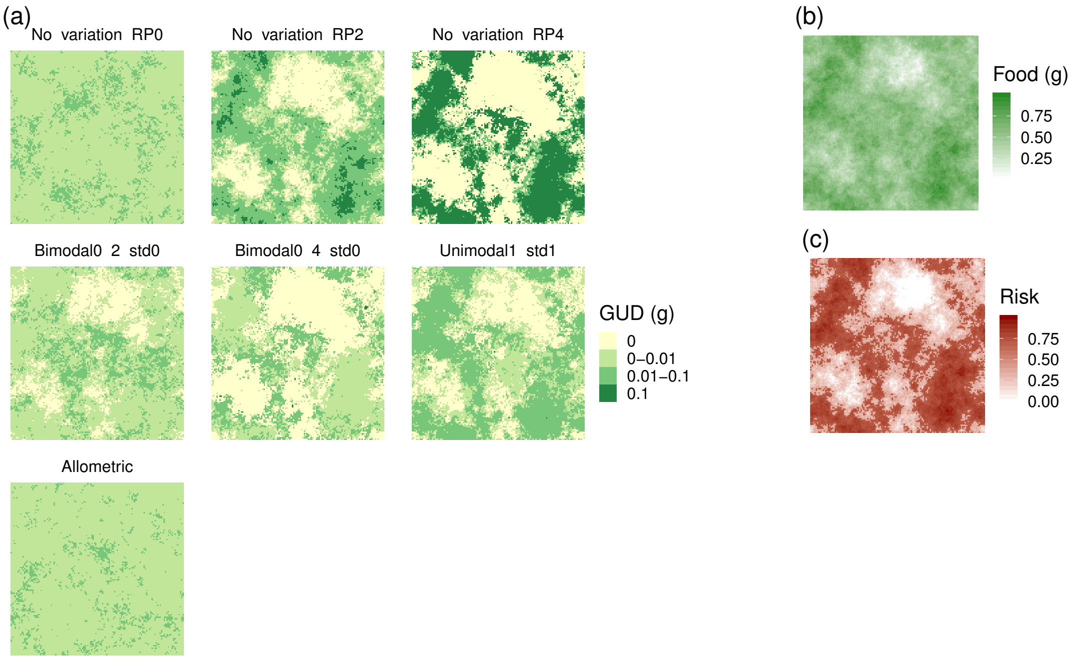

Fig. C.4. Giving-up density of prey communities with different distribution of risk perception (a). The giving-up density is the amount of food resources (in g dry biomass) that remains in each cell at the end of the simulation. Patterns represent one exemplary simulation with a bimodal landscape of fear (c) and the shown food landscape (b).

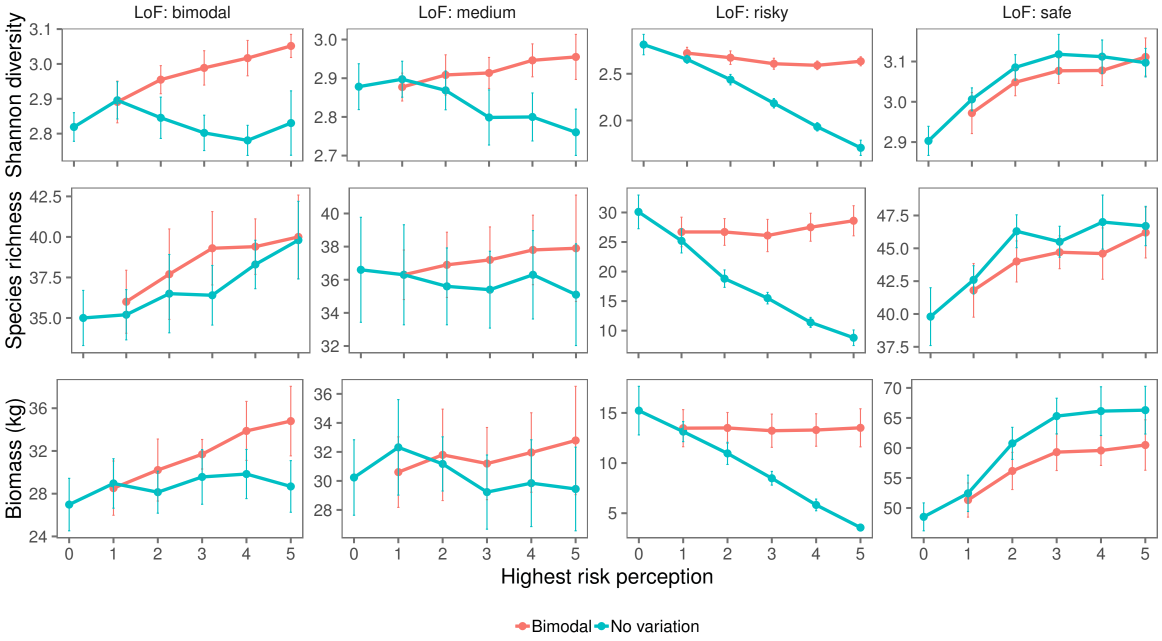

Fig. C.5. Diversity, species richness and total biomass for communities varying in the distribution of risk perception and different landscapes of fear. Unimodal communities are marked in blue, in these communities all animals have the same risk perception (x-axis). Bimodal communities are marked in red, in these communities animals have either a risk perception of 0 or the value indicated by the x-axis.

Acknowledgements

At first, I want to thank my supervisors Florian Jeltsch, Volker Grimm and Stephanie Kramer-Schadt for their amazing support. I am grateful to Florian for our frequent meetings, discussion of results and quick responses to questions. I am further grateful to Volker for his support in scientific writing, developing the storyline of the manuscripts and relaxed attitude. Another big thanks goes to Stephanie for her support, especially with statistics and R, quick responses and many useful comments on the manuscripts.

I further like to thank the BioMove Team for supporting me in the last years. I really enjoyed discussions with everyone during retreats, BioMove seminars and workshops. Thanks to all the other PhD students for sharing experiences and encouraging words. A big thanks to Annika and Antje for taking me to the Uckermark and teaching me everything about voles. Another thanks to Ulrike for quick help with math and other problems. Additionally, I would like to thank the DFG for funding (DFG-GRK 2118/1) which allowed me to fulfill this research and gave me the opportunity to participate in various conferences and summer schools.

Furthermore, I am thankful to the PENC working group for all the nice lunch breaks, support and advice. I am grateful to my office colleagues Merlin, Jette and Katrin for refreshing discussions, sharing experiences and quick help, especially when I couldn’t find the mistake in the code. Moreover, I would like to sincerely thank Jarro, Tobias and Jan for keeping the cluster alive and solving all the issues when things did not work.

I also thank all my friends apart from work for their support and distractions. A special thanks goes to Leonie, Chithra and Benedikt for our cooking events, listening to my problems and all the other activities we did together. I couldn’t have done it without you. I am further thankful to Gabriele for her friendship and taking care of my flat and plants whenever I was away.

Heartfelt thanks goes to my family for supporting me the whole time. Another thanks to Rocky, Sancho and Ronny for never failing to cheer me up. Eventually, I am infinitely grateful to Marc for all his love and support. Thank you for endless listening, encouragement and solving of weird math problems.

Declaration of Authorship

I hereby declare to have prepared this dissertation independently under the commonly accepted help of my supervisors. All direct or indirect sources used are given as references. All contributions of co-authors are acknowledged. This thesis has not been submitted to any other university or institution before.

Potsdam,

Lisa Teckentrup