Trends in Ecology & Evolution

CellPress REVIEWS

Review

Landscapes of Fear: Spatial Patterns of Risk Perception and Response

Kaitlyn M. Gaynor,[1,*,@] Joel S. Brown,[2,3,5] Arthur D. Middleton,[1,5] Mary E. Power,[4,5] and Justin S. Brashares[1]

Animals experience varying levels of predation risk as they navigate heterogeneous landscapes, and behavioral responses to perceived risk can structure ecosystems. The concept of the landscape of fear has recently become central to describing this spatial variation in risk, perception, and response. We present a framework linking the landscape of fear, defined as spatial variation in prey perception of risk, to the underlying physical landscape and predation risk, and to resulting patterns of prey distribution and antipredator behavior. By disambiguating the mechanisms through which prey perceive risk and incorporate fear into decision making, we can better quantify the nonlinear relationship between risk and response and evaluate the relative importance of the landscape of fear across taxa and ecosystems.

Highlights

Recent technological advances have provided unprecedented insights into the movement and behavior of animals on heterogeneous landscapes. Some studies have indicated that spatial variation in predation risk plays a major role in prey decision making, which can ultimately structure ecosystems.

The concept of the 'landscape of fear' was introduced in 2001 and has been widely adopted to describe spatial variation predation risk, risk perception, and response. However, increasingly divergent interpretations of its meaning and application now cloud understanding and synthesis, and at least 15 distinct processes and states have been described as landscapes of fear.

Here, we refocus the definition of the landscape of fear as an animal's perception of spatial variation in predation risk.

Predation risk, the landscape of fear, and prey antipredator responses map imperfectly onto each other, due to ecological constraints and trade-offs.

The relative importance of the landscape of fear in shaping population dynamics and species interactions varies across systems, and human activity is altering and creating new landscapes of fear for wild animals.

Introduction

The risk of predation plays a powerful role in shaping behavior of fearful prey, with consequences for individual physiology, population dynamics, and community interactions [1,2]. Theoretical and experimental research has revealed the importance of heterogeneity within and among habitats as a driver of spatial patterning of predation and prey response (Box 1). Moreover, recent technological advances in the collection of geospatial and animal movement data have allowed more detailed empirical studies of the spatial dynamics of predation and antipredator strategies [3]. Over the past two decades, ecologists have adopted the concept of the '**landscape of fear**' (see Glossary) to describe the spatial variation in **predation risk** as perceived by prey across their foraging or home range [4]. This concept draws on the disciplines of behavioral, population, community, and spatial ecology to consider the role of spatially heterogenous predation risk in driving prey behavior and trophic cascades (Box 2). Research on landscapes of fear has become central to the study of predator–prey interactions and has enhanced our understanding of animal ecology on heterogeneous, dynamic landscapes.

As noted in the past for transformative concepts in ecology such as keystone species [5] and trophic cascades [6], rapid and widespread adoption of the landscape of fear concept has led to inconsistent definitions and applications. Given the difficulties in measuring risk perception, researchers have adopted a broad range of operational definitions for the concept. Subsequently, 'landscape of fear' has become a catch-all for many spatial phenomena relating to predation and the term is increasingly applied to discussion of risk outside of a spatial context [7]. This drift toward ambiguity has, in turn, fueled significant inconsistencies in how landscapes of fear are measured. While some studies have considered the landscape of fear to be an intrinsic attribute of a physical landscape, others have suggested it is a spatial pattern resulting from predation, a cognitive map of risk perceived by prey, or a measurable response of prey manifested through their spatial distribution or foraging behavior (see supplementary Table S1

[1]Department of Environmental Science, Policy, and Management, University of California Berkeley, 130 Mulford Hall #3114, Berkeley, CA 94720, USA
[2]Department of Biological Sciences, University of Illinois at Chicago, 845 West Taylor Street (MC 066), Chicago,

Box 1. Precursors to the Landscape of Fear Concept

Behavioral and Population Ecology

Behavioral ecologists have long recognized the importance of spatially variable predation risk and prey responses in stabilizing predator–prey population dynamics [76–78]. Charnov introduced the concept of 'behavioral resource depression' to describe changes in prey microhabitat selection in response to predation risk, which made prey less accessible to predators [79]. Early studies of the 'ecology of fear' [80] combined mass action models (in which the lethal effects of predators drive numeric responses in prey populations), with optimal foraging theory [81]. These conceptual models provided the theoretical framework for empirical studies of free-ranging predators and prey on complex landscapes.

Subsequent studies linked antipredator strategies to physiological outcomes, including stress and reproduction [82,83]. Mesocosm experiments have demonstrated that in some contexts, these risk effects of predation have a greater influence on prey population dynamics than the consumptive effects [84]. While the study of risk effects has proven challenging in heterogeneous natural landscapes, patterns of spatial variation in predation risk and response likely have important consequences for spatial demographic patterns [85,86].

Community Ecology

Meanwhile, community ecologists observed that foraging behavior of fearful grazers structured the distribution of primary producers. Spatial variation in predation risk was hypothesized as a mechanism behind the formation of 'grazing halos', denuded areas at the edge of coral reefs where urchins sought refuge from predatory fish [87]. Similar patterns were observed in terrestrial systems; for example, the effects of pika (*Ochotona princeps*) on vegetation were strongest near rocks that provided refuge [88]. Through experiments, ecologists linked the structural complexity of the habitat back to predator efficiency, with refuges from predators reducing prey mortality rates and transforming prey communities [89]. Spatial variation in predation risk and accompanying patterns of prey foraging activity have been found to shape lower trophic levels via 'predator-induced resource avoidance' [90].

The indirect effects of predators on lower trophic levels, mediated by fear in prey, have come to be known as trait-mediated indirect interactions, or **behaviorally mediated trophic cascades** [91–93]. Many experiments have since found that trait-mediated interactions can be stronger drivers of food web dynamics than density-mediated effects [84]. These fear-driven interactions play out over landscapes where prey perception of risk is heterogeneous, and in turn, prey behaviors drive patterns of spatial heterogeneity in species distributions across trophic levels.

Box 2. Emergence and Limitations of the Landscape of Fear Concept

The 'landscape of fear' term was coined by Laundré and colleagues in 2001 in their paper on elk and bison vigilance and foraging behavior in response to wolf reintroduction in Yellowstone [4]. The core idea existed within earlier concepts (Box 1), like prey depression [79] or predator-induced resource avoidance [90]. However, the term 'landscape of fear' was widely adopted, as it evoked an individual animal navigating a spatially explicit environment of variable predation risk. The landscape of fear captures the human imagination, and is intuitive, evocative, and relatable; in fact, the term originated in the fields of anthropology and human geography, where it is still used to describe spaces that induce dread and terror in people [94]. While the accessibility of the term has made it appealing to researchers and the general public, it has also led to concerns about anthropomorphism and the attribution of conscious emotion to non-human animals [95]. Outside of the landscape of fear literature, there remains considerable debate among psychologists and animal behavior scientists about the definition and measurement of fear in both humans and non-human animals [95,96].

Despite the shortcomings of the term 'fear', it has caught on widely, and is generally considered by ecologists to be equivalent to conscious or unconscious risk perception. Fear as an adaptation allows the animal or organism to assign an activity cost to the risk of injury or death [97]. Initially, there was a taxonomic bias towards large terrestrial mammals in the landscape of fear literature. However, within the past several years, the term has been applied to a wide range of taxa, including birds [13,36], fish [98], and invertebrates [99,100]. Amidst this trend, it has become increasingly common to attribute observed ecological phenomena to landscapes of fear. However, given that at least 15 different processes and states have been called a landscape of fear (online supplementary Table S1), it is no surprise that some so-called landscapes of fear are implicated in so many studies. As the landscape of fear research continues to gain popularity, it is critical to examine its definition, application, and context in predator–prey theory, so that we can refine its use and better design studies to evaluate its role in ecosystems.

IL 60607, USA
[3]Department of Integrated Mathematical Oncology, Moffitt Cancer Center, 12902 Magnolia Dr., Tampa, FL 33612, USA
[4]Department of Integrative Biology, University of California Berkeley, 3060 Valley Life Sciences Building #3140, Berkeley, CA 94720, USA
[5]These authors contributed equally to this work
[@]Twitter: @kaitlyngaynor

*Correspondence: kgaynor@berkeley.edu (K.M. Gaynor).

online). Reflecting this confusion, recent studies have dedicated entire paragraphs to clarify their interpretation of the term among the conflicting definitions in the literature [8].

A common source of confusion among studies of the landscape of fear results from the conflation of spatial patterns of predation risk with prey perceptions of that risk, or with prey **antipredator behavior** in response to risk perception. The most immediate consequence of this ambiguity in definition is the inappropriate choice of proxies for measuring the phenomenon of interest, which can lead to circular inferences. For example, prey behavior, such as alarm calling or **vigilance**, is often used as a proxy for predation risk, which is then used to predict other aspects of prey response, such as distribution on a landscape [9]. Notably, the conflation of both predation patterns and prey behavior with the landscape of fear has impeded important discussions about mechanisms that link, or fail to link, risk and response. Amidst this confusion, there has been debate over the ecological importance of fear for prey species and community interactions, with different parties using different definitions for landscapes of fear (cf. [10–12]).

Here, in an effort to clarify and refocus the theory and science on landscapes of fear, we advocate for a definition of the landscape of fear as the spatial variation in prey perception of predation risk. The landscape of fear allows prey to integrate spatial variation in threats from predators with other spatially variable opportunities and hazards [13]. For animals with advanced cognition, the landscape of fear may exist as a 'mental map' that an animal proactively responds to, but the landscape of fear can also occur in real time as an animal navigates and responds to a landscape of heterogeneous risk. We introduce a framework around this definition that should allow researchers to better articulate what phenomena they are actually studying and measuring, rather than falling back on the term 'landscape of fear' (Figure 1, Key Figure). The framework aims to help researchers to generate hypotheses and understand underlying assumptions.

Below, we apply our framework to discuss how predation risk and behavioral responses map imperfectly onto one another. We contend that understanding these mismatches between risk, perception, and response will not only clarify definitions, but open doors to an array of important questions in predator–prey ecology and evolution and enable an understanding of the relative importance of the landscape of fear across systems.

Mismatches in Predation Risk and Prey Response

Our framework (Figure 1) envisions the landscape of fear at the center of distinct, measurable landscapes corresponding to the physical environment, predation risk, and prey response. By conflating these distinct spatial maps and referring to each of these elements as the landscape of fear (Figure 2, supplementary Table S1 online), scientists risk ignoring the important distinctions between them. Furthermore, many studies of the landscape of fear assume a linear relationship between these spatial patterns, but risk and response often fail to map closely onto one another due to nonlinear relationships between, for example, predator activity and predation risk, predator cues and prey perception, or fear and antipredator behavior. An understanding of the pathways linking habitat heterogeneity to antipredator behavior via a landscape of fear, as outlined in Figure 1, enables predictions about when mismatches will occur between the magnitude and spatial heterogeneity of actual predation risk and prey response to that risk (Figure 3).

First, the landscape of fear will map more or less precisely onto the landscape of predation risk based on the strength and reliability of cues and the sensory and cognitive ability of prey to associate those cues with predation [14]. Given that prey should experience strong selection to

Glossary

Antipredator behavior: any action taken by a prey animal to reduce its risk of predation. Antipredator behavior may be reactive (e.g., flight), in the presence of a predator, or proactive (e.g., vigilance), to increase detection of predators or probability of escape given an encounter. Some behaviors may serve proactive antipredator functions in addition to their primary function (e.g., movement, habitat selection).

Asset protection principle: an animal in a high energy state, with greater reproductive potential, has more to lose from being killed than an animal in a lower energy state, with a lower reproductive potential. Animals in poor body condition may therefore assess a lower foraging cost at a given level of predation risk.

Behaviorally mediated trophic cascade: a phenomenon in which predation risk drives changes in prey behavior (e.g., foraging) and thus alters the composition and structure of lower trophic levels.

Giving-up density (GUD): the density of a food resource in a natural or artificial food patch at which a prey animal will cease foraging and abandon the patch. GUDs can be used to evaluate the foraging cost of predation risk, or prey perception of risk.

Landscape of fear: the spatial variation in prey perception of predation risk.

Predation risk: the likelihood of a prey animal being killed by a predator. Predation risk varies at multiple scales in space and time and among individual prey.

Risk effects: the nonlethal or nonconsumptive effects of predators on a prey population, brought about by costly antipredator behavior that affects survival and reproduction.

Vigilance: monitoring of the environment to detect threats, including predators.

Trends in Ecology & Evolution

CellPress REVIEWS

Key Figure

A Framework for Understanding the Ecological Context of the Landscape of Fear

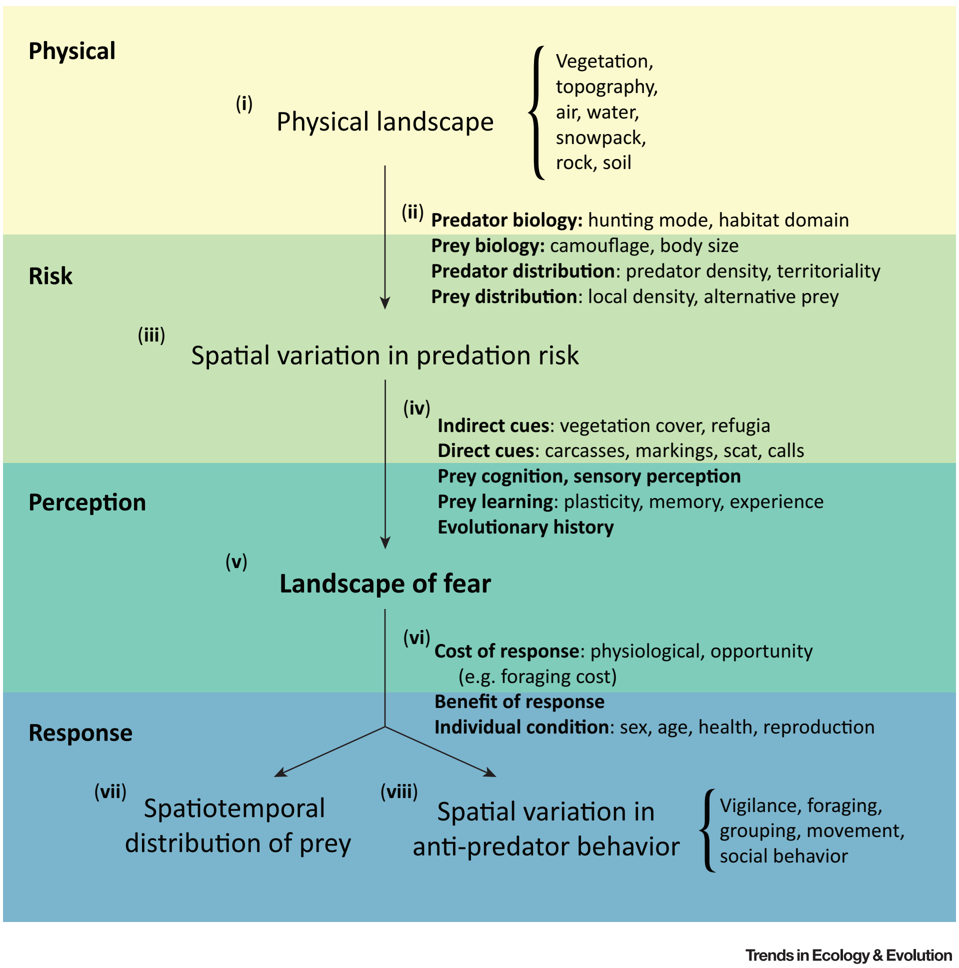
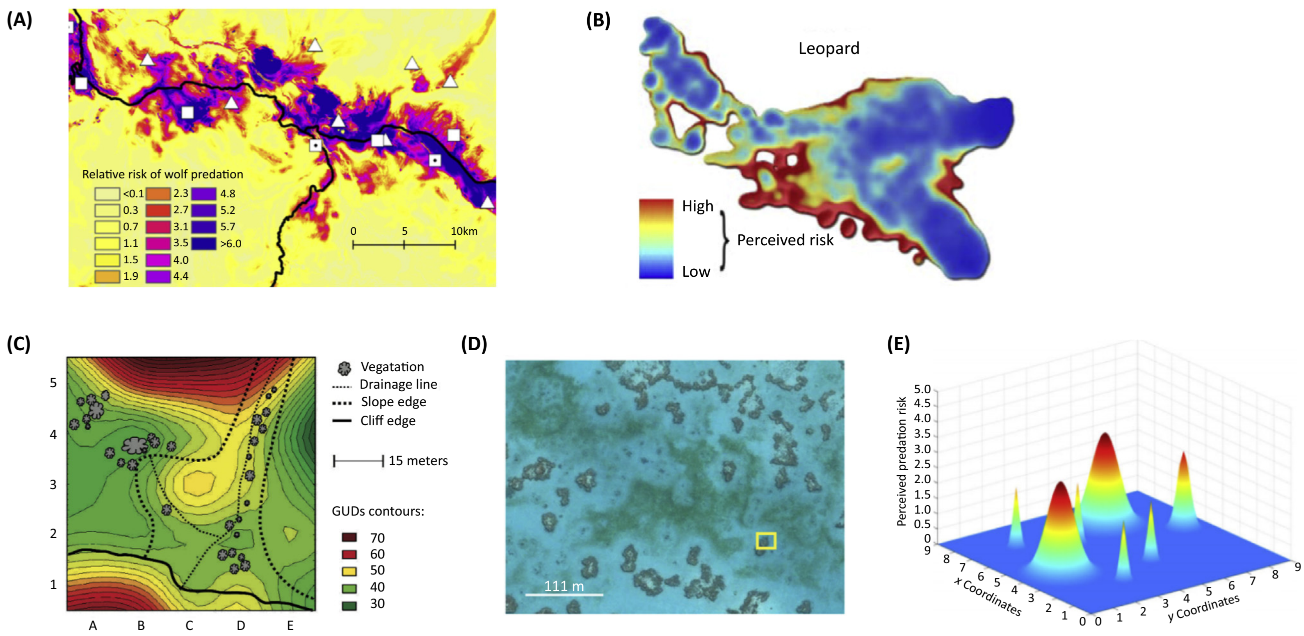


Figure 1. The (i) underlying physical landscape shapes visibility, detection, and movement before and during a predator–prey encounter. The structure of the landscape interacts with (ii) aspects of predator and prey biology to determine patterns of predator and prey distribution and risk. The physical landscape thus sets the stage for (iii) spatial variation in predation risk, or the likelihood of a predation event. This risk is then (iv) imperfectly perceived by prey, based on the reliability of cues, the sensory and cognitive capacities of the prey, and past experiences with predation in the individual's lifetime or in the species' evolutionary history. Cues of predation risk may be indirect (associated with the physical landscape) or direct (associated with predators themselves). The (v) landscape of fear is manifested in measurable behavioral outcomes, as prey (vi) incorporate information about predation risk into decisions about where to go and how to behave. The landscape of fear thus generates two behavioral strategies to proactively minimize risk: (vii) avoidance of high-risk areas, and (viii) modulation of behavior to reduce the probability of suffering predation while at a given location.

Cell Press REVIEWS

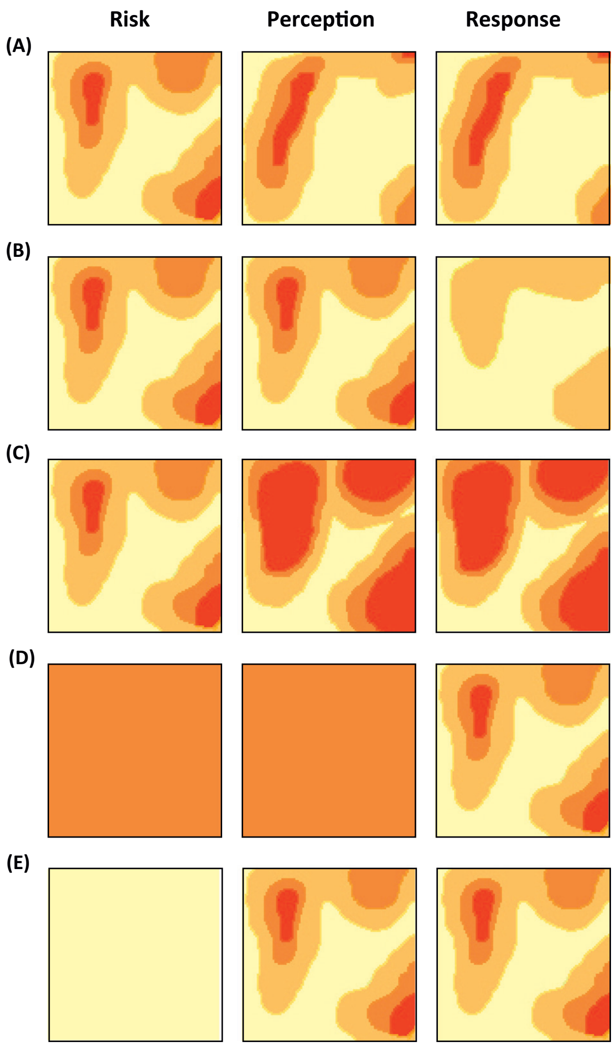


Trends in Ecology & Evolution

Figure 2. Visualized Landscapes of Fear from the Literature. Conflicting definitions of the landscape of fear have generated a contrasting range of methods to quantify and visualize these landscapes, most often by measuring either the physical landscape, predation, predator presence, or prey response (see also supplementary Table S3 online). Our framework provides a useful way to compare approaches across studies by articulating the differences between predation, risk, fear, and prey response. Representations of these phenomena in the literature include spatial variation in: (A) predation risk: modeled risk of wolf (*Canis lupus*) predation on elk (*Cervus elaphus*), based on known kill locations, habitat features, and elk density (squares and triangles represent study plots) [10]; (B) reactive antipredator responses: density of observed leopard (*Panthera pardus*) alarm call vocalizations by vervet monkeys (*Cercopithecus aethiops*) [9]; (C) proactive antipredator behavior: contour lines of experimentally determined giving-up densities (GUDs) for Nubian ibex (*Capra nubiana*) [74]; (D) effects of prey responses on vegetation: satellite imagery of grazing halos around reefs, resulting from foraging of fearful prey [75]; (E) perceived risk, (true landscape of fear): conceptual representation of fear in the mind of a theoretical prey animal [3].

be able to detect and respond to predators, mismatches between actual and perceived risk should be common in response to rare or novel habitats or predators [15]. Invasive predators or human-induced habitat changes may create ecological traps, in which prey fail to optimize behavior due to anachronistic landscapes of fear [16]. Such mismatches in actual versus perceived risks may be a hallmark of some captive animals, limiting inferences based on laboratory studies of the landscape of fear [17]. Detection of cues will still be imperfect among prey species that have coevolved with their predators, as predators have evolved crypsis and hunting strategies to avoid detection [18]. When studying landscapes of fear, it is therefore important to understand the cues that are most salient to prey, and the spatial and temporal scales of cue perception [3]. Studies of the chemosensory mechanisms underlying prey risk perception, for example, may provide insight into taxonomic differences in risk perception for many groups of species [19,20].

Given the large fitness cost of predation, some prey animals may have evolved a tendency to perceive a higher probability of predation than is actually present, and to 'play it safe' [21], particularly when the cost of responding is low [22]. By perceiving high risk as a default, prey may exhibit more homogenous antipredator behavioral responses when compared with the heterogeneous landscape of predation risk. The landscape of fear can also amplify underlying variation in predation risk, if cues associated with risk drive exaggerated risk



Trends in Ecology & Evolution

Figure 3. Mismatch between Predation Risk, the Landscape of Fear, and Prey Antipredator Behavior. The landscape of fear mediates the relationship between spatial variation in risk and prey response. Prey response includes both spatiotemporal distribution (as prey avoid areas of high risk) and spatial variation antipredator strategies at a given place (including vigilance and grouping). There is often a mismatch in risk and response, due to limitations in prey perception and the trade-offs associated with decision making. (A) Prey may have imperfect information about predation risk, resulting in slight mismatches in their risk perception and response. (B) Constraints on prey behavior, and steep costs associated with response, may lead to a reduced, more homogenous behavioral response to risk despite accurate perception of risk. (C) Risk-averse prey may err on the side of caution, exhibiting more amplified antipredator responses than the underlying risk surface (conversely, bold prey may exhibit muted antipredator responses). (D) Intrinsic risk and risk perception may be homogenous across a landscape, but spatial heterogeneity in forage quality, and therefore in behavioral trade-offs, may result in heterogeneity in prey distribution or antipredator behavior. (E) Predators may be extirpated in a system, resulting in no risk across the landscape, but evolved responses to cues can persist and influence prey behavior despite no actual risk.

perception. Furthermore, many prey species now live in predator-free environments but still associate landscape cues with predation risk [23]. Such inaccuracies in risk perception suggest that behavior may not always be an appropriate proxy for the actual risk of predation.

Even when prey perceive risk with high accuracy, spatial patterns of prey distribution and antipredator behavior rarely correlate perfectly with the landscape of fear due to cost–benefit trade-offs, including those associated with foraging (Figure 1F). Prey must balance predator avoidance with other critical life functions, such as acquiring food, and nearly all antipredator strategies entail energetic or opportunity costs. Simply put, predation risk is not the only concern of most prey animals. Physiological, phylogenetic, or ecological constraints may limit a prey animal's ability to respond to perceived predation risk [24]. If required resources like food and water are limited and concentrated, prey may have no choice but to use inherently risky areas [25,26]. Prey territoriality may also limit prey ability to adjust spatial distributions to avoid predation [27]. Given these constraints, an animal may fail to exhibit antipredator behavior, even when its landscape of fear accurately maps onto landscapes of risk.

If the relative costs or benefits of antipredator responses vary spatially, prey may exhibit spatial variation in antipredator behavior that does not reflect the landscape of fear. In high-quality forage patches, for example, the costs of antipredator behavior may outweigh benefits of increased foraging, and in very risky areas, antipredator behavior may not substantively reduce probability of detection or escape. For example, arboreal grey squirrels (*Sciurus carolinensis*) in open areas are less vigilant than squirrels near trees, fitting the prediction that the benefits of vigilance will be greater when there is an easy escape route [28]. To more fully understand how risk translates (or fails to translate) into behavior, we must examine how other fitness-enhancing opportunities and behavioral trade-offs vary in space and time.

Trade-offs associated with foraging and the landscape of fear will also vary greatly with an individual prey animal's state and marginal valuation of food. According to the **asset protection principle**, an animal in better physical condition has more to lose from being killed than one in poorer condition [29]. Thus, a hungry animal will assess a lower foraging cost at the same level of risk than one that is well-fed, and animals with different resource needs will manifest more or less rugose spatial landscapes of behavioral response [30]. In the extreme, an animal on the verge of starvation should cease to show any spatial variation in fear responses if food is present throughout the landscape, even when predation risk varies strongly in space [31].

Predicting Landscape of Fear Effects

As the concept of the landscape of fear has gained prominence, researchers increasingly attribute a range of ecological outcomes to predation **risk effects** [32], and the role of fear in driving trophic cascades has even become a common media narrative [33]. While fear can play a critical role in determining individual fitness, population dynamics, and community interactions, its relative importance will vary across systems with different predator and prey species and landscape features [24,34,35]. By understanding the ecological processes that give rise to, and arise from, the landscape of fear, we can predict where the landscape of fear will have meaningful consequences for prey population dynamics and community structure (see supplementary Table S2 online).

Landscape of fear effects on populations and communities should be most pronounced in landscapes that are highly heterogeneous, since the physical landscape sets the stage for spatial variation in predation risk and associated behavioral trade-offs [36]. For example, in African and North American savannas, structural diversity in the form of open grassland and shrub or wooded patches provides diverse opportunities for escape, hiding, detection, ambush, and capture for prey and predators alike [37]. Prey may not experience or respond to predictably variable predation risk in more homogenous systems like mature European forests [25] and the open ocean [38]. Even in systems with heterogeneous risk, clumped resources may limit foraging opportunities and therefore constrain the ability of prey to incorporate fear into their behavioral decisions [25].

For landscapes of fear to exist, predation risk must not only vary in space but must vary predictably, and must be associated with cues that create generally reliable signals for prey [39]. Prey may perceive greater risk from cues associated with ambush predators, which require certain forms of habitat structure for cover, than from cues associated with active or coursing predators [40], a pattern supported by mesocosm studies [41]. Prey must also have the ability to associate cues with risk. In the absence of strong selective pressure on predation risk perception and response over evolutionary history, prey species may fail to perceive a landscape of fear from rare or novel predators [42]. If prey do not perceive and respond to predation risk, landscapes of fear will not play a major role in determining fitness and population dynamics.

Differences in predator and prey densities can lead to widespread variation in predation rates across systems, with implications for landscape of fear dynamics [43]. Landscapes of fear are more likely to influence prey behavior where encountering a predator brings a high risk of attack, but encounters are infrequent. Conversely, as summarized by the risk allocation hypothesis, prey experiencing frequent encounters with predators may live in a state of constant fear and exhibit less spatial structure in their antipredator responses [44]. Furthermore, for a given prey species, the population effects of landscapes of fear should be strongest when there are similar spatial patterns of predation risk for all of their predators. In contrast, when prey must trade off contrasting landscapes of risk among multiple predators, the landscape of fear may be relatively homogenous, particularly under predator facilitation where each predator is more dangerous in a different habitat [45–47].

Finally, even when predictable landscapes of fear exist and generate prey responses, these responses may not meaningfully impact prey population dynamics. While classical models of the landscape of fear assume there to be a strong cost to antipredator behavior due to trade-offs between risk avoidance and foraging or other activities, such trade-offs may not always occur, particularly when prey rely more strongly on physical defenses than behavioral defenses [24]. Also, prey with dietary breadth or plasticity, or abundant food resources, may be able to choose among equivalent foraging areas to reduce predation risk [26], particularly when predators have a narrow habitat domain [34]. Sometimes, the riskiest habitat is also the habitat with the lowest-quality forage [48], and prey may be able to avoid risk while tracking food [49]. In these cases, landscapes of fear will play a negligible role in prey population level outcomes, although they may still alter community structure at lower trophic levels. Furthermore, risk mitigation strategies, like vigilance, may not be mutually exclusive with other fitness-enhancing behaviors, like foraging, depending on an animal's physiology. Even where trade-offs do exist, and predation risk generates costly responses in prey, such costs may be insufficient to determine reproductive (fitness) outcomes or drive population dynamics and trophic cascades [43].

Studying Landscapes of Risk and Response

As scientists utilize remote sensing, geographic information systems (GIS), and global positioning system (GPS) technology, there is growing interest in moving beyond simple designations of safe and risky habitats to quantify spatially explicit landscapes of risk and prey response. Much of our understanding of nonlethal predator effects comes from laboratory or mesocosm experiments, and there is a need to examine the determinants and consequences of landscapes of fear in natural systems [7]. Opportunities exist to evaluate the hypotheses that emerge from our framework regarding the causes and consequences of mismatch between predation risk and prey response, and the relative strength of landscape of fear effects on population dynamics and species interactions.

Thus far, ecologists have used a wide range of observational and experimental methods to measure and map what they have defined as a landscape of fear (Figure 2), and these different approaches have hindered comparisons across systems [50]. For example, distribution of kill sites by a predator is often used to infer landscapes of fear [50], but predation patterns can be skewed by variation in density and activity of prey across the landscape. Vigilance by prey is another commonly used proxy for measuring risk, but, as discussed above, vigilance may actually be lower in the riskiest habitats, and 'safe' places may be made so by heightened vigilance [28]. Mapping activity patterns of prey across space is also commonly related to predation risk [46], but these patterns are often linked to other features of the landscape, such as patterns of resource productivity or distribution of potential competitors (intra- or interspecific) or mates. Spatial variation in **giving-up densities (GUDs)** in natural or experimental food patches across a landscape may indicate differences in the perceived foraging cost of predation, proportional to predation risk [1], although GUDs pose methodological challenges (see [51,52]).

This diversity of imperfect approaches for measuring landscapes of fear is understandable, given the complexities of ecological systems (Box 3) and the challenges associated with quantifying perception. While there have been recent advances in our understanding of the cognitive basis of risk perception [53,54], studying cognition in wild animals presents significant challenges. Perceived risk may be associated with quantifiable physiological parameters, such as glucocorticoid stress hormones and heart rate [55,56], but these physiological responses do

Box 3. A Community Level Perspective

The simplest models of the landscape of fear assume a single predator and prey, but the consequences of landscapes of fear often involve multiple trophic levels. Acknowledging the complexity of landscapes of fear within a community ecology framework is essential for realistically quantifying their role in shaping ecosystem dynamics [32]. While we present the landscape of fear as an experience of an individual prey animal navigating risk trade-offs, it corresponds to related patterns at other trophic levels. The landscape of fear for a prey species is simultaneously a landscape of opportunity for predators, and a landscape of refuge for the species consumed by prey [101].

There are dynamic feedbacks across trophic levels, as predators perceive and respond to the prey species' response [102]. Ultimately, underlying habitat heterogeneity can be shaped by fear responses of foraging prey through behaviorally mediated trophic cascades, feeding back (e.g., through vegetation height or density) to alter spatial patterns of predation risk. Often the standing crop of resources will be the inverse of the landscape of fear as animals deplete food availability where they feel safe and leave more food behind where risky [98]. Prey can also intentionally engineer the physical landscape to reduce predation risk in a given area [103].

Efforts to quantify cascading consequences of fear provide compelling new insights on the ecosystem impacts of individual responses to fear. For example, an apex predator can alter the landscape of fear of a herbivore through fear-induced behavioral changes in an intervening mesopredator [104]. Lower-trophic level prey may even deliberately select for areas with apex predators, using them as cover from mesopredators that present more risk to the prey in question [105].

Multi-predator systems require that prey respond to multiple sources of risk, which can be additive or orthogonal depending on predator distributions and hunting modes [46]. To explore this complexity, some studies have overlain multiple maps of predation risk arising from different types of predators in an attempt to quantify their relative effects on prey behavior [9]. Furthermore, the availability of alternative prey species can affect predation risk, dependent on prey switching and predator preferences. In multi-prey systems, competition and apparent competition can influence landscapes of predation risk and response [106]. For example, caribou perceive heightened predation risk in areas of high moose density, presumably because moose are a primary prey species for wolves [107].

not always align well with cognitive processes given their energetic costs and associated trade-offs [55]. Furthermore, lag times in physiological responses can complicate studies of spatio-temporal variability.

Given the difficulties associated with measuring the cognitive or emotional state of an animal, research on the landscape of fear may be better served by explicitly measuring predation risk and behavioral responses and exploring congruence or mismatch between them, rather than further attempts to map the landscape of fear itself. Progress in the study of landscapes of fear will depend on researchers becoming more deliberate in selecting relevant variables to quantify (i.e., predation events, predation risk, prey distribution, prey behavior), choosing suitable methods, and clearly defining concepts and the relationships among variables of interest. In the online supplementary Table S3, we compile a list of measurable proxies for both spatial variation in predation risk and behavioral responses of prey and describe how each of these proxies relates mechanistically to the landscape of fear.

Ideally, by clarifying the elements that comprise a landscape of fear (Figure 1) we aim to reduce some of the difficulties outlined above by guiding study designs that account for the factors influencing the spatial and temporal scales of landscape of fear dynamics. In addition to reflecting the home range sizes and body sizes of both predator and prey, ecologically relevant scales will depend on the hunting behavior of predators, flight and escape behavior of prey, and detection abilities of predators and prey [57]. Individual animals experience and respond to landscapes of fear at multiple scales, incorporating risk into selection of both broad habitat and

Box 4. Landscapes of Fear in the Anthropocene

Our framework highlights pathways through which disturbance alters and creates landscapes of fear. Changes in land use through agriculture [108] and deforestation [109], as well as pollution [110], shape habitat structure, quality, and heterogeneity. Human activity thus alters the playing field for predator–prey dynamics, changing the effectiveness of predator and prey strategies and prey trade-offs, constraining the spatial scale of prey responses, and sometimes even altering sensory cues [99]. Climate change has also been implicated in reshaping landscapes of fear by changing habitat structure and habitat domain of predators and prey [111,112].

Human activity has also fundamentally changed the nature of predation risk. The decline of large terrestrial carnivores through persecution and habitat loss has had clear consequences through the creation of landscapes of fearlessness, and many studies have documented fearless prey transforming ecosystems in the absence of predators [23,113]. Consequently, some conservation biologists have advocated for the restoration of landscapes of fear through carnivore reintroductions [114], although some studies suggest prey exhibit atypical fear responses to reintroduced predators [115]. In other cases, the provision of anthropogenic subsidies to predators or the introduction of invasive predators has increased populations or changed hunting patterns, with consequences for landscapes of fear in native prey [116].

In addition to disrupting predation risk, humans also represent a new apex 'super-predator' [117,118]. In places with hunting, lethal human activity creates potentially novel landscapes of fear for targeted species [119], with possible consequences for physiology, prey demographics, and the structure of human-natural communities. However, animals perceive risk from humans even in the absence of lethal reinforcement [120], and anthropogenic landscapes of fear have been linked to demographic consequences [121]. Human activity can also initiate behaviorally mediated trophic cascades: 'human shields' can arise when a predator avoids humans, leading prey to preferentially seek refuge in those areas [58,122]. Ultimately, the landscape of fear associated with humans selects for species with plastic responses to threatening stimuli, resulting in habituation to nonlethal human activity over time [123].

The landscape of fear framework can inform the design of strategies to reduce human–wildlife conflict, including threats to people, livestock, agriculture, and property. Many conflict mitigation techniques, like novel sensory stimuli or targeted lethal control, for example, are aimed at imposing landscapes of fear on target species so that animals avoid areas of potential conflict [124,125]. By understanding the sensory cues that generate fear in animals, and the behavioral responses and trade-offs associated with them, managers can better design mitigation strategies to effectively change wildlife behavior [126].

microhabitat [58,59]. Furthermore, while terrestrial landscapes of fear are often conceptualized and mapped as two-dimensional, many volant, arboreal, subterranean, or aquatic animals experience 3D landscapes of fear [60,61].

Regular changes at any given site in habitat structure, resource distribution, and productivity over time further complicate efforts to depict a single landscape of fear. Studies often present the landscape of fear as temporally static, but prey experience temporal variation in the magnitude of predation risk and in resource trade-offs, often on multiple time scales. Understanding the temporal dynamics of predator and prey ecology and behavior is as important as defining appropriate geographic scales in studies of the landscape of fear. Landscapes of fear vary predictably with daily [8,62], monthly (lunar) [63,64], or seasonal cycles [65,66]. Studies should account for this temporal variation by framing the question of interest. The measurement of a landscape of fear may be a single snapshot in time if the question concerns how the temporary presence of a predator influences the animal's fear responses. But this scale may not be useful when integrating across time scales where prey modulate their activity to take advantage of safe times and places to obtain food, and consequently influence the distribution and abundance of their food.

Finally, our framework emphasizes that the landscape of fear also varies among individual animals living on the same physical landscape and at the same time. Factors like sex, age, reproductive status, and body condition can affect an individual's vulnerability to predators, its perception of risk at a given time and place, and the trade-offs involved in its response [67,68]. Recent studies have linked antipredator behavior to personality or behavioral syndromes, with some individuals inherently more fearful than conspecifics [69–71]. Thus, population level results should be interpreted with the understanding that they may describe an averaging of individual prey responses.

Concluding Remarks

The landscape of fear is an important concept in ecology, integrating behavioral, population, and community responses to predation and providing a central organizing principle for the study of predator–prey dynamics on heterogeneous landscapes. Despite broad acceptance and growth in the application of the landscape of fear concept, inconsistencies in its definition and application have clouded synthesis and advancement of theory. The landscape of fear has been repeatedly conflated with the physical landscape, spatial patterns of predation and predation risk, and heterogeneity in prey distribution and behavior. We suggest the use of a narrower definition of the landscape of fear as spatial variation in risk perception, and advocate for the use of more precise and appropriate terminology to describe the patterns of risk and prey behavior that are actually being studied (Figure 1).

By clarifying nonlinear relationships between the physical landscape, predation risk, risk perception, and prey response, we highlight the complexity of animal fear while clarifying concepts to guide future research. While our landscape of fear framework is grounded in predator–prey interactions, it provides a useful lens to conceptualize the way that animals perceive and respond to various risks as they navigate complex environments, including, for example, competition [72] and parasite or disease risk [73]. A synthetic understanding of the landscape of fear will enable comparisons of its role across taxa and ecosystems and improve predictions and studies of the effects of the landscape of fear on individual fitness, population dynamics, and community interactions (see Outstanding Questions). Such research is especially critical as humans reshape landscapes of fear through predator removal and reintroduction, habitat modification, and intensification of activities such as hunting and recreation (Box 4).

Outstanding Questions

What predation risk cues are most salient for prey species in generating a landscape of fear?

At what spatial and temporal scales do prey perceive and respond to heterogeneity in predation risk?

How does a species' evolutionary history influence its landscape of fear dynamics, including mismatch/alignment between risk, perception, and response?

How do predator responses to prey antipredator strategies reshape landscapes of fear?

What are the dynamics of landscapes of fear in multi-predator, multi-prey systems?

Under what ecological conditions do landscapes of fear scale up to drive population demographics and trophic interactions?

Acknowledgments

This work was supported by an NSF GRFP grant to K.M.G. We thank E. Lacey, A. McInturff, B. Abrahms, J. Miller, L. Rich, D. Bolnick, members of the Brashares Group, and anonymous reviewers for sharing thoughts and comments on the manuscript.

Supplemental Information

Supplemental information associated with this article can be found, in the online version, at https://doi.org/10.1016/j.tree.2019.01.004.

References

1. Brown, J.S. and Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7, 999–1014
2. LaManna, J.A. and Martin, T.E. (2016) Costs of fear: behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecol. Lett.* 19, 403–413
3. Jordan, L.A. and Ryan, M.J. (2015) The sensory ecology of adaptive landscapes. *Biol. Lett.* 11, 20141054–20141064
4. Laundré, J.W. *et al.* (2001) Wolves, elk, and bison: reestablishing the landscape of fear in Yellowstone National Park, U.S.A. *Can. J. Zool.* 79, 1401–1409
5. Power, M.E. *et al.* (1996) Challenges in the quest for keystones. *Bioscience* 46, 609–620
6. Polis, G.A. *et al.* (2000) When is a trophic cascade a trophic cascade? *Trends Ecol. Evol.* 15, 473–475
7. Peers, M.J.L. *et al.* (2018) Quantifying fear effects on prey demography in nature. *Ecology* 99, 1716–1723
8. Kohl, M.T. *et al.* (2018) Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* 88, 638–652
9. Willems, E.P. and Hill, R.A. (2009) Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology* 90, 546–555
10. Kauffman, M.J. *et al.* (2010) Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91, 2742–2755
11. Beschta, R.L. and Ripple, W.J. (2013) Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: comment. *Ecology* 94, 1420–1425
12. Fortin, D. *et al.* (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330
13. Masello, J.F. *et al.* (2017) How animals distribute themselves in space: variable energy landscapes. *Front. Zool.* 14, 33
14. Luttbeg, B. and Trussell, G.C. (2013) How the informational environment shapes how prey estimate predation risk and the resulting indirect effects of predators. *Am. Nat.* 181, 182–194
15. Abom, R. and Schwarzkopf, L. (2016) Differential behavioural flexibility in response to predation risk in native and introduced tropical savannah rodents. *Anim. Behav.* 122, 117–124
16. Schlaepfer, M.A. *et al.* (2005) Introduced species as evolutionary traps. *Ecology* 8, 241–246
17. Troxell-Smith, S.M. *et al.* (2016) Foraging decisions in wild versus domestic *Mus musculus*: what does life in the lab select for? *Behav. Proc.* 122, 43–50
18. Abrams, P.A. (2000) The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.* 31, 79–105
19. Katz, L.B. and Dill, L.M. (1998) The scent of death: chemosensory assessment of predation risk by animals. *Ecoscience* 5, 361–394
20. Jurcak, A.M. and Moore, P.A. (2018) Sensory signals and the reaction space in predator?prey interactions. *Hydrobiologia* 816, 137–152
21. Bouskila, A. and Blumstein, D.T. (1992) Rules of thumb for predation hazard assessment: predictions from a dynamic model. *Am. Nat.* 139, 161–176
22. Abrams, P.A. (1994) Should prey overestimate the risk of predation? *Am. Nat.* 144, 317–328
23. Bonnot, N.C. *et al.* (2016) Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) adjust habitat selection and activity rhythm to the absence of predators. *Can. J. Zool.* 94, 385–394
24. Creel, S. (2011) Toward a predictive theory of risk effects: hypotheses for prey attributes and compensatory mortality. *Ecology* 92, 2190–2195
25. Schmidt, K. and Kuijper, D.P.J. (2015) A "death trap" in the landscape of fear. *Mamm. Res.* 60, 275–284
26. Valeix, M. *et al.* (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90, 23–30
27. Ford, A.T. and Goheen, J.R. (2015) An experimental study on risk effects in a dwarf antelope, *Madoqua guentheri*. *J. Mammal.* 96, 918–926
28. Brown, J.S. (1999) Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.* 1, 49–71
29. Clark, C.W. (1994) Antipredator behavior and the asset-protection principle. *Behav. Ecol.* 5, 159–170
30. Catano, L.B. *et al.* (2015) Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. *J. Anim. Ecol.* 85, 146–156
31. Brown, J.S. *et al.* (1997) Competition between birds and mammals: a comparison of giving-up densities between crested larks and gerbils. *Evol. Ecol.* 11, 757–771
32. Teckentrup, L. *et al.* (2018) Community consequences of foraging under fear. *Ecol. Model.* 383, 80–90
33. Mech, L.D. (2012) Biological conservation. *Biol. Conserv.* 150, 143–149
34. Schmitz, O.J. (2005) Behavior of predators and prey and links with population-level processes. In *Ecology of Predator-Prey Interactions* (Barbosa, P. and Castellanos, I., eds), Oxford University Press
35. Heithaus, M.R. *et al.* (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *J. Anim. Ecol.* 78, 556–562
36. Atuo, F.A. and O'Connell, T.J. (2017) The landscape of fear as an emergent property of heterogeneity: contrasting patterns of predation risk in grassland ecosystems. *Ecol. Evol.* 7, 4782–4793
37. Eccard, J.A. and Liesenjohann, T. (2014) The importance of predation risk and missed opportunity costs for context-dependent foraging patterns. *PLoS One* 9, e94107
38. Hammerschlag, N. *et al.* (2015) Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. *Ecology* 96, 2117–2126
39. Weissburg, M. *et al.* (2014) The sensory ecology of nonconsumptive predator effects. *Am. Nat.* 184, 141–157
40. Schmitz, O.J. *et al.* (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* 7, 153–163
41. Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science* 319, 952–954
42. Soluk, D.A. and Collins, N.C. (1988) Balancing risks? Responses and non-responses of mayfly larvae to fish and stonefly predators. *Oecologia* 77, 370–374
43. Middleton, A.D. *et al.* (2013) Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology* 16, 1023–1030

44. Lima, S.L. and Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649–659
45. Murray, D.L. *et al.* (1995) Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. *Anim. Behav.* 50, 1203–1210
46. Cresswell, W. and Quinn, J.L. (2013) Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behav. Ecol.* 24, 871–876
47. Kotler, B.P. *et al.* (1992) Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann. Zool. Fenn.* 29, 199–206
48. Pierce, B.M. *et al.* (2004) Habitat selection by mule deer: forage benefits or risk of predation? *J. Wildl. Manag.* 68, 533–541
49. Bakker, E.S. *et al.* (2005) Experimental manipulation of predation risk and food quality: effect on grazing behaviour in a central-place foraging herbivore. *Oecologia* 146, 157–167
50. Moll, R.J. *et al.* (2017) The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *J. Anim. Ecol.* 86, 749–765
51. Bedoya-Perez, M.A. *et al.* (2013) A practical guide to avoid giving up on giving-up densities. *Behav. Ecol. Sociobiol.* 67, 1541–1553
52. McMahon, J.D. *et al.* (2018) Covariance between predation risk and nutritional preferences confounds interpretations of giving-up density experiments. *Ecology* 99, 1517–1522
53. Marzluff, J.M. *et al.* (2012) Brain imaging reveals neuronal circuitry underlying the crow's perception of human faces. *Natl. Acad. Sci.* 109, 15912–15917
54. Staples, L.G. *et al.* (2009) Long-lasting FosB/ΔFosB immunoreactivity in the rat brain after repeated cat odor exposure. *Neurosci. Lett.* 462, 157–161
55. Clinchy, M. *et al.* (2013) Predator-induced stress and the ecology of fear. *Funct. Ecol.* 27, 56–65
56. Støen, O.-G. *et al.* (2015) Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiol. Behav.* 152, 244–248
57. Padié, S. *et al.* (2015) Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. *Oikos* 124, 1536–1546
58. Kuijper, D.P.J. *et al.* (2015) Context dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest. *Behav. Ecol.* 26, 1558–1568
59. Stears, K. and Shrader, A.M. (2015) Increases in food availability can tempt oribi antelope into taking greater risks at both large and small spatial scales. *Anim. Behav.* 108, 155–164
60. Makin, D.F. *et al.* (2012) Foraging in a 3-D world: how does predation risk affect space use of vervet monkeys? *J. Mammal.* 93, 422–428
61. Emerson, S.E. *et al.* (2011) Identifying Sykes' monkeys, *Cercopithecus albogularis erythrarchus*, axes of fear through patch use. *Anim. Behav.* 81, 455–462
62. Tolon, V. *et al.* (2009) Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Can. J. Zool.* 87, 1129–1137
63. Palmer, M.S. *et al.* (2017) A "dynamic" landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecol. Lett.* 20, 1364–1373
64. Bouskila, A. (1995) Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76, 165–178
65. Hopcraft, J.G.C. *et al.* (2014) Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecol. Monogr.* 84, 355–372
66. Druce, D.J. *et al.* (2009) Spatial and temporal scaling in habitat utilization by klipspringers (*Oreotragus oreotragus*) determined using giving-up densities. *Aust. Ecol.* 34, 577–587
67. McArthur, C. *et al.* (2014) The dilemma of foraging herbivores: dealing with food and fear. *Oecologia* 176, 677–689
68. Lagos, P.A. and Herberstein, M.E. (2017) Are males more scared of predators? Differential change in metabolic rate between males and females under predation risk. *Physiol. Behav.* 173, 110–115
69. Spiegel, O. *et al.* (2016) What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol. Lett.* 20, 3–18
70. Bonnot, N. *et al.* (2015) Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behav. Ecol.* 26, 105–114
71. Quinn, J.L. *et al.* (2012) Personality predicts individual responsiveness to the risks of starvation and predation. *Proc. R. Soc. B* 279, 1919–1926
72. Swanson, A. *et al.* (2016) In the absence of a "landscape of fear": how lions, hyenas, and cheetahs coexist. *Ecol. Evol.* 6, 8534–8545
73. Buck, J.C. *et al.* (2018) Ecological and evolutionary consequences of parasite avoidance. *Trends Ecol. Evol.* 33, 619–632
74. Iribarren, C. and Kotler, B.P. (2012) Foraging patterns of habitat use reveal landscape of fear of Nubian ibex *Capra nubiana*. *Wildl. Biol.* 18, 194–201
75. Madin, E.M.P. *et al.* (2011) Landscape of fear visible from space. *Sci. Rep.* 1, 14
76. Huffaker, C.B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27, 795–835
77. Gilliam, J.F. and Fraser, D.F. (1987) Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68, 1856–1862
78. Sih, A. (1987) Prey refuges and predator-prey stability. *Theor. Popul. Biol.* 31, 1–12
79. Charnov, E. *et al.* (1976) Ecological implications of resource depression. *Am. Nat.* 110, 247–259
80. Brown, J.S. *et al.* (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80, 385–399
81. Sih, A. (1980) Optimal behavior: can foragers balance two conflicting demands? *Science* 210, 1041–1043
82. Creel, S. *et al.* (2007) Predation risk affects reproductive physiology and demography of elk. *Science* 315, 960
83. Zanette, L.Y. *et al.* (2011) Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334, 1398–1401
84. Preisser, E.L. *et al.* (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86, 501–509
85. Hopcraft, J.G.C. *et al.* (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. *J. Anim. Ecol.* 74, 559–566
86. Matassa, C.M. and Trussell, G.C. (2011) Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. *Ecology* 92, 2258–2266
87. Ogden, J.C. *et al.* (1973) Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182, 715–717
88. Huntly, N.J. (1987) Influence of refuging consumers (pikas: *Ochotona princeps*) on subalpine meadow vegetation. *Ecology* 68, 274–283
89. Crowder, L.B. and Cooper, W.E. (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63, 1802–1813
90. Power, M.E. (1984) Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology* 65, 523–528
91. Schmitz, O.J. *et al.* (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78, 1388–1399
92. Bolker, B. *et al.* (2003) Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* 84, 1101–1114

93. Werner, E.E. and Peacor, S.D. (2006) Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity. *Ecology* 87, 347–361
94. Tuan, Y.-F. (1979) *Landscapes of Fear,* University of Minnesota Press
95. Adolphs, R. (2013) The biology of fear. *Curr. Biol.* 23, R79–R93
96. LeDoux, J.E. (2014) Coming to terms with fear. *Proc. Natl. Acad. Sci. U. S. A.* 111, 2871–2878
97. Kotler, B.P. and Brown, J.S. (2017) Fear and loathing on the landscape: what can foraging theory tell us about vigilance and fear? *Anim. Sentience* 83, 1–5
98. Gil, M. *et al.* (2017) Context-dependent landscape of fear: algal density elicits risky herbivory in a coral reef. *Ecology* 98, 534–544
99. Hintz, W.D. and Relyea, R.A. (2017) A salty landscape of fear: responses of fish and zooplankton to freshwater salinization and predatory stress. *Oecologia* 185, 147–156
100. Hermann, S.L. and Landis, D.A. (2017) Scaling up our understanding of non-consumptive effects in insect systems. *Curr. Opin. Insect Sci.* 20, 54–60
101. Laundré, J.W. *et al.* (2010) The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* 3, 1–7
102. Lima, S.L. (2002) Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.* 17, 70–75
103. Caro, T. (2005) *Antipredator Defenses in Birds and Mammals,* University of Chicago Press
104. Frid, A. *et al.* (2008) Do shark declines create fear-released systems? *Oikos* 117, 191–201
105. Gordon, C.E. *et al.* (2015) Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proc. R. Soc. B* 282, 20142870–20142878
106. Laundré, J.W. *et al.* (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95, 1141–1152
107. Avgar, T. *et al.* (2015) Space-use behaviour of woodland caribou based on a cognitive movement model. *J. Anim. Ecol.* 84, 1059–1070
108. Hof, A.R. *et al.* (2012) Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Anim. Behav.* 83, 1099–1106
109. Sahlén, E. *et al.* (2016) Phantoms of the forest: legacy risk effects of a regionally extinct large carnivore. *Ecol. Evol.* 6, 791–799
110. Kerby, J.L. *et al.* (2012) Impacts of the insecticide diazinon on the behavior of predatory fish and amphibian prey. *J. Herpetol.* 46, 171–176
111. Schmitz, O.J. and Barton, B.T. (2013) Climate change effects on behavioral and physiological ecology of predator-prey interactions: implications for conservation biological control. *Biol. Control* 75, 87–96
112. Riginos, C. (2014) Climate and the landscape of fear in an African savanna. *J. Anim. Ecol.* 84, 124–133
113. Creel, S. *et al.* (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397
114. Manning, A.D. *et al.* (2009) Restoring landscapes of fear with wolves in the Scottish Highlands. *Biol. Conserv.* 142, 2314–2321
115. Nicholson, K.L. *et al.* (2014) Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. *Oecologia* 176, 69–80
116. Gompper, M.E. and Vanak, A.T. (2008) Subsidized predators, landscapes of fear and disarticulated carnivore communities. *Anim. Conserv.* 11, 13–14
117. Darimont, C.T. *et al.* (2015) The unique ecology of human predators. *Science* 349, 858–860
118. Clinchy, M. *et al.* (2016) Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. *Behav. Ecol.* 27, 1826–1832
119. Norum, J.K. *et al.* (2015) Landscape of risk to roe deer imposed by lynx and different human hunting tactics. *Eur. J. Wildl. Res.* 61, 831–840
120. Frid, A. and Dill, L.M. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11
121. Sawyer, H. *et al.* (2017) Mule deer and energy development—long-term trends of habituation and abundance. *Glob. Change Biol.* 121, 3–9
122. Leighton, P.A. *et al.* (2010) Conservation and the scarecrow effect: can human activity benefit threatened species by displacing predators? *Biol. Conserv.* 143, 2156–2163
123. Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* 85, 1077–1088
124. van Eeden, L.M. *et al.* (2018) Carnivore conservation needs evidence-based livestock protection. *PLoS Biol.* 16, e2005577
125. Cromsigt, J.P.G.M. *et al.* (2013) Hunting for fear: innovating management of human-wildlife conflicts. *J. Appl. Ecol.* 50, 544–549
126. Atkins, A. *et al.* (2017) Experimentally manipulating the landscape of fear to manage problem animals. *J. Wildl. Manag.* 74, 1863–1867