Review

Dynamic landscapes of fear: understanding spatiotemporal risk

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The landscape of fear (LOF) concept posits that prey navigate spatial heterogeneity in perceived predation risk, balancing risk mitigation against other activities necessary for survival and reproduction. These proactive behavioral responses to risk can affect individual fitness, population dynamics, species interactions, and coexistence. Yet, antipredator responses in free-ranging prey often contradict expectations, raising questions about the generality and scalability of the LOF framework and suggesting that a purely spatial, static LOF conceptualization may be inadequate. Here, we outline a 'dynamic' LOF framework that explicitly incorporates time to account for predictable spatiotemporal variation in risk–resource trade-offs. This integrated approach suggests novel predictions about predator effects on prey behaviors to refine understanding of the role predators play in ecological communities.

Role of predation risk in ecological systems

With growing recognition of the pivotal yet complex role of **predation risk** (see Glossary) in ecological systems [1], the **landscape of fear (LOF)** is increasingly invoked to describe spatial variation in prey perception of predation risk [1–3]. This metaphor encapsulates the idea that prey perception of encounter, attack, and/or kill probabilities varies across space, generated by predictable interactions among the physical environment, predator density and hunting mode, and prey vulnerability [4–6]. Prey are predicted to proactively mitigate these threats by avoiding dangerous areas and/or by modulating other behaviors (e.g., vigilance, foraging, activity levels) across the landscape according to levels of perceived risk. Such behavioral responses often bear costs, such as reduced foraging time or increased stress [1,7], which can scale-up to exert **non-consumptive effects** on prey survival, reproduction, and population structure [8,9].

The understanding that animals proactively alter antipredator behaviors across gradients of perceived risk was advanced by models and controlled experiments involving small consumers (e.g., fish, insects, rodents), typically at small spatial (e.g., mesocosms) and temporal (e.g., days, weeks) scales (see [3]). However, many question the extent to which spatial patterns of risk predict the behavioral and ecological dynamics of large, long-lived, and wide-ranging animals, which interact over expansive and complex natural landscapes and often exhibit cultural evolution and learning [10–12]. Strong behavioral responses to risky places and resultant non-consumptive effects have been documented in some such systems but not others; even within a given system, studies have yielded divergent results that seem difficult to reconcile with the notion of pervasive and predictable spatial structure in predation risk and prey response (e.g., North American wolves *Canis lupus* and cervids [11,13,14]; African wild dogs *Lycaon pictus* and antelopes [15,16]). These discrepancies suggest that there are complex relationships between spatial patterns of predation risk and prey responses.

Highlights

Ecologists use the 'landscape of fear' framework to describe spatial variation in perceived predation risk and prey response, despite mixed empirical evidence.

However, risk and response are dynamic in time as well as space; we explore what drives cycles of risk and how these cycles structure antipredator decision-making in time.

Temporal and spatial heterogeneities in risk interact to create spatiotemporal 'dynamic landscapes of fear', where spatial hotspots of risk vary across temporal cycles.

Predictions from a dynamic fear landscape differ from those of a static, spatial landscape of fear, with consequences for forecasting prey behavior, non-consumptive effects, and behaviorally mediated trophic cascades.

This framework helps resolve discrepancies between conventional fear theory and empirical data, enabling a more precise understanding of how fear structures ecological communities.

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Time as a crucial dimension in landscapes of fear

We argue that time is a critical dimension that remains poorly integrated in research on the LOF. It has long been recognized that risk (real and perceived) varies in time (e.g., [17–20]) as well as in space. Nonetheless, spatial patterns of perceived predation risk are typically represented as a temporally static or time-averaged phenomenon [2,3,7] in which prey responses to perceived risk are governed by the interaction of landscape features that vary slowly over time (such as habitat architecture [16,21,22]) and species' intrinsic traits (such as predator hunting mode [23,24] and prey antipredator strategies [25]). Purely spatial models of risk are appealing insofar as the relative constancy of landscape features may allow prey to anticipate localized threats and proactively avoid being attacked [2,3]. However, these static spatial models of risk implicitly assume that risk is constant [26] or that averaged long-term patterns of risk at a given site [12] adequately predict short-term antipredator behaviors.

Yet both risk and response can also be predictably structured in time [17,18,27]. The ways in which temporal pulses [19] and spatial patterns [18,27] of risk influence antipredator decision-making have independently received much theoretical and empirical investigation. However, fewer studies have explicitly integrated these threads by situating predictable cycles of risk within a spatial context and exploring how periodic temporal shifts in risk may influence spatial decision-making. Cyclical temporal dynamics are ubiquitous across ecosystems (Table 1), creating **schedules of fear** (sensu [28]) that prey can anticipate and respond to. These schedules arise from variation in organismal and environmental factors that predictably constrain predator activity and prey vulnerability (Figure 1). Prey may perceive patterns of risk that vary across time and space simultaneously and the ability of mobile animals to move selectively in and modulate their activities across heterogeneous space-time may allow them to proactively minimize risk and reduce foraging costs and stress (Figure 2 but see Box 1 and Outstanding questions).

A growing number of empirical studies have documented fine-scale spatiotemporal variation in prey behavior when spatial patterns of risk contrast between day and night [28–30] or across seasons [31,32] (Table 1 and Figure 2). For example, in South America, puma (*Puma concolor*) are consistently active in vegetated and rugged areas from dusk until dawn; their main prey, vicuña (*Vicugna vicugna*), avoid or reduce their overall activity in these areas at night but select for vegetated locations during the day [33]. In Shark Bay, Australia, seasonally migrating tiger sharks (*Galeocerdo cuvier*) frequent shallow banks where fish biomass is high but are largely absent from deeper channels. During months when sharks are present, bottlenose dolphins (*Tursiops aduncus*) avoid resource-rich shallows for the impoverished deeps; when sharks are absent, dolphins distribute themselves in proportion to food availability [34]. These and other studies (Table 1) demonstrate the need to integrate space and time in theoretical and empirical studies of prey behavioral responses to predation risk in complex natural environments.

Dynamic LOF framework

We present a framework for understanding **dynamic landscapes of fear (dynamic LOFs)** [11,35] to guide future research on how prey perceive and respond to predation risk across both space and time simultaneously (Figures 1 and 3). The dynamic LOF integrates temporal variation and spatial heterogeneity to derive predictions about prey behavioral decision-making (e.g., distribution, activity levels, vigilance, association patterns [11,33,36]) and its potential consequences for individual fitness [32], species interactions and coexistence [37], and broader ecological processes [38].

Explicitly considering the spatiotemporal structure and scale of predation risk, as well as spatiotemporal constraints on prey behavior, can inform debates about the ecological role of risk across systems. We might expect spatial variation in predation risk perception to impose strong costs on

prey if antipredator behaviors interfere with foraging opportunities, with possible cascading effects of predator avoidance on other trophic levels [2,3]. However, temporal cycles of predator activity may enable prey to modulate their spatial activity in time, for instance, by utilizing temporal refuges to access otherwise dangerous areas [33,35,36]. If so, then strong antipredator responses might not trigger non-consumptive effects [32,37] or behaviorally mediated trophic cascades [38] (Figure 2 and Table 1). For example, white-tailed deer (*Odocoileus virginianus*) in Minnesota, USA avoid foraging in areas scent-marked by wolves only during times when wolves actively hunt (dawn/dusk) [38]. By visiting these areas during safer times of the day, deer maintain access to the entire landscape, curtailing behaviorally mediated trophic cascades on vegetation. If responses to the spatial patterning of risk alone had been examined, then risk-sensitive foraging would not have been detected, possibly leading to the false conclusion that prey did not perceive or respond to risky places. In this way, divorcing space from time can mischaracterize risk effects [11,13,14].

By understanding predation risk as variable in both space and time, we can better predict the effects of predators on prey behavior, non-consumptive effects, and trophic cascades across species and systems, from aquatic microinvertebrates to terrestrial megaherbivores (Table 1). Next, we consider two broad questions: First, why and under what circumstances should actual risk, perceived risk, and prey response vary spatiotemporally, and at what scale(s)? Second, what behavioral responses should emerge in a dynamic LOF, and how do these predictions differ from those predicted by a model that ignores time?

When do risk and response vary across space and time?

Predators with particular hunting modes (e.g., ambush hunting) and behaviors (e.g., territoriality) should generate more predictable spatial patterns of risk and therefore be easier for prey to proactively avoid in space [23,39]. Similarly, predators should be more predictable, and hence avoidable, in times when the timing of their foraging/hunting activities is constrained by physiological, morphological, and/or ecological factors [40] (Figure 1). Prey likewise face spatial and temporal constraints that affect the risk–resource trade-offs that dictate their ability to respond to risk. Spatial heterogeneities in risk and response are reviewed thoroughly elsewhere [2,3]; next, we briefly outline how predator activity/hunting success and the ability of prey to respond to perceived predation risk can vary across a finite number of predictable temporal cycles that arise from Earth's rotation and Earth's and Moon's orbits.

Tidal cycles

Hourly changes in currents and tidal forces (turbidity, salinity, velocity, depth) impose functional and mechanical constraints, modulating sensory capabilities, locomotor performance, and thermoregulation [41,42], and predictably altering local predator and prey abundance, hunting success, and prey vulnerability [43]. For example, tidal oscillations in estuarine and intertidal environments can periodically trap predators and prey together (e.g., in tide pools) and regulate access to resources or spawning opportunities. Marine currents can interact with spatial heterogeneity (e.g., in reefs) to create hotspots of risk strong enough to generate behaviorally mediated trophic cascades [44].

Diel cycles

Earth's rotation affects light, temperature, and other factors on hourly timescales. Predator hunting mode interacts with photoperiods (e.g., ambush predators hunt better in low light [33]) or temperature (e.g., pursuit predators overheat at midday [45,46]) to determine capture efficiency. During predictable daily periods when predators are inactive or have low hunting success, prey can access resources in otherwise dangerous areas (temporal refuges). These factors also affect prey's ability to detect [47] or respond [48,49] to risk.

Glossary

Consumptive effects: also known as 'lethal effects'; effects that predators exert on prey populations by killing individuals (i.e., directly reducing prey density).

Dynamic landscapes of fear (dynamic LOFs): variation in perceived predation risk across space and time simultaneously.

Landscape of fear (LOF): spatial variation in perceived predation risk.

Non-consumptive effects: also known as 'risk effects' or 'non-lethal effects'; effects of predators on prey individuals and/or populations arising from behavioral and/or other phenotypic trait changes that entail fitness costs (e.g., reduced survival or reproduction).

Predation risk: chronic/long-term/ 'risky places'; the underlying risk of injury or mortality associated with a particular location generated by predictably high levels of predator activity and/or prey vulnerability (e.g., high predator density, areas where predators are predictably present and/or hunting success is consistently high). Acute/short-term/ 'risky times'; an actual and/or probable adverse encounter with a predator (e.g., predator presence, predators active within a particular distance of prey); predators may or may not be predictable in space and/or time.

Schedule of fear: cyclical temporal variation in perceived predation risk.

Table 1. Evidence for spatially and temporally predictable risk operating simultaneously across diverse systems[a]

| System	Predator	Prey	Cycle(s) of risk	Cycle(s) of constraint	Spatiotemporal response	Refs
Marine	Carnivorous zooplankters, fish, birds (various species)	Zooplankton (various species)	Lunar (light levels)	(Not measured)	Alter habitat use to use dangerous resource-rich places during safe times ('lunar vertical migration')	[52,53]
	Sharks, fishes, marine mammals (various species)	Fishes, krill, copepods, jellyfish, zooplankton (various species)	Diel (light levels)	(Not measured)	Alter habitat use to use dangerous resource-rich places during safe times ('diel vertical migration')	Reviewed in [88,89]
	White sharks (*Carcharodon carcharias*)	Cape fur seals (*Arctocephalus pusillus*)	Diel (light levels), tidal (water depth), seasonal (weather, reduced availability of alternative prey)	Seasonal (reproduction, vulnerable juveniles)	Employ group swimming, reduce surfacing, increase vigilance in risky times and places, and alter time and duration of foraging to minimize risk exposure	[108,109]
	Shark species (various), killer whales (*Orcinus orca*)	Elephant seal (*Mirounga angustirostris*)	Diel (light levels) x seasonal (photoperiod)	Seasonal (migration, resources)	Alter habitat use to use dangerous resource-rich places during safe times; are more risk-adverse during periods of better body condition	[36]
	Whitetip reef sharks (*Triaenodon obesus*), tawny nurse sharks (*Nebrius ferrugineus*)	Bony herbivorous fishes (various)	Tidal (water levels)	(Not measured)	Behaviorally mediated trophic cascade occurs due to interactions between reef topography, tidal oscillations, and shark hunting behavior, creating predictable 'hot spots' of fear on the reef where herbivores refrain from feeding	[44]
	Tiger sharks (*Galeocerdo cuvier*)	Loggerhead turtles (*Caretta caretta*)	(Not measured)	Seasonal (reproduction, temperature, foraging)	Did not alter activity to reduce risk as constrained by biotic and abiotic factors	[12]
	Tiger sharks (*G. cuvier*)	Dugongs (*Dugong dugon*); bottlenose dolphins (*Tursiops aduncus*); green sea turtles (*Chelonia mydas*)	Seasonal (migration)	Body condition (turtles)	Alter habitat use to use dangerous resource-rich places during safe times; for turtles, degree of risk-taking was mediated by body condition	[75,110,111]
Fresh water	Carnivorous zooplankters, fish, birds (various species)	Zooplankton (various species)	Diel (light levels)	(Not measured)	Alter habitat use to use dangerous resource-rich places during safe times ('diel vertical migration')	Reviewed in [112]
	Fishes (various species); predacious invertebrates (various species)	*Daphnia*, cladocerans (various species)	Diel (light levels)	(Not measured)	Alter habitat use to use dangerous resource-rich places during safe times ('diel horizontal migration')	[113]
	Bluegills (*Lepomis macrochirus*)	Dragonfly larvae (Odonata: Anisoptera)	Diel (light levels)	(Not measured)	Alter habitat use to use dangerous resource-rich places during safe times; reduced foraging in dangerous situations	[114]

Table 1. (continued)

System	Predator	Prey	Cycle(s) of risk	Cycle(s) of constraint	Spatiotemporal response	Refs
Terrestrial	Beetle larvae (*Drilus* species)	Land snails (*Albinaria* species)	(Not measured)	Seasonal (estivation)	Increased mortality during periods of estivation	[115]
	Golden eagles (*Aquila chrysaetos*)	Sage grouse (*Centrocercus urophasianus*)	Diel (light levels)	Seasonal (reproduction, lekking)	Male and female lek attendance depends on interaction between risky times and social and environmental conditions	[116]
	Red foxes (*Vulpes vulpes*); northern goshawks (*Accipiter gentilis*)	Grey partridge (*Perdix perdix*)	Diel (light levels)	(Not measured)	Alter habitat use to avoid risky places during risky times; roost in tighter groupings in risky situations	[28]
	Birds and weasels (various species)	Common voles (*Microtus arvalis*)	Diel (light levels)	(Not measured)	Avoid being and foraging in dangerous areas during dangerous times; life expectancy increased with temporal opportunism	[117]
	Various species	Small mammal species (various)	(Not measured)	Seasonal (hibernation)	Reduced activity levels increased survival	Reviewed in [61]
	Various	Apennine hare (*Lepus corsicanus*)	Diel (light levels), lunar (light levels), seasonal (temperature)	(Not measured)	Alter habitat use to use dangerous resource-rich places during safe times of diel and lunar cycles	[118]
	Multiple	Snowshoe hare (*Lepus americanus*)	Lunar cycle (light levels)	Seasonal (snowpack)	Activity levels around new moon increase in snowy (dangerous) season but not in (safe) snow-free season; no temporal change in habitat use	[119]
	Wolves (*Canis lupus*)	White-tailed deer (*Odocoileus virginianus*)	(Not measured)	Seasonal (resources)	Alter habitat use relative to avoid risky places during risky times; responsiveness to risk varies seasonally with resource constraints	[94]
	Wolves (*C. lupus*), black bears (*Ursus americanus*)	Moose (*Alces alces*)	(Not measured)	Seasonal [reproduction (rut, calving); snow cover; vegetation (forage/cover)]	Altered landscape use across reproductive cycle to optimize finding mates/caring for young, obtaining resources, and mitigating predation; habitat use varied across diel cycle to minimize use of dangerous areas in dangerous times	[120]
	Wolves (*C. lupus*), cougars (*Puma concolor*)	Elk (*Cervus elaphus*)	Diel (light levels)	(Not measured)	Occupy vacant habitat domains, use time to niche partition activity to reduce overlap with predators	[78]
	Black bears (*U. americanus*)	Coyotes (*Canis latrans*), bobcats (*Lynx rufus*), foxes (*Urocyon cinereoargenteus*)	Seasonal (hibernation)	(Not measured)	Alter competitive interactions and space use to mitigate risk from bears when not hibernating	[60]

Table 1. (continued)

System	Predator	Prey	Cycle(s) of risk	Cycle(s) of constraint	Spatiotemporal response	Refs
	Cougars (*P. concolor*)	Vicuñas (*Vicugna vicugna*)	Diel (light levels)	(Not measured)	Alter habitat use to avoid risky places during risky times; alter movement speed/direction in risky situations	[33]
	Lion (*Panthera leo*)	African wild dog (*Lycaon pictus*)	(Not measured)	Seasonal (reproduction, vulnerable juveniles)	Shift patterns of space use to minimize overlap with predators during periods with vulnerable young	[63]
	Lion (*P. leo*)	Plains zebra (*Equus quagga*)	Diel (light levels)	(Not measured)	Alter habitat use to use dangerous resource-rich places during safe times, more erratically during risky situations	[29]
	Lion (*P. leo*)	African large herbivore species (various)	Lunar (light levels)	Seasonal (resources)	Shift patterns of vigilance, grouping, and space use relative to patterns of spatial risk across time; responsiveness to risk varies seasonally with resource constraints	[35]
	Large carnivores (various species)	African large herbivore species (various)	Diel (light levels)	(Not measured)	Vulnerable species alter habitat use to use dangerous resource-rich places during safe times	[30]
	Large carnivores (various species), humans	African large herbivore species (various)	Diel (light levels)	(Not measured)	Reduced spatiotemporal niches as 'squeezed' between natural (active at night) and human (active during day) predators	[121]
	Humans, European lynx (*Lynx lynx*)	Roe deer (*Capreolus capreolus*)	Diel (light levels) × seasonal (hunting season)	(Not measured)	'Squeezed' between natural (active at night) and human (active during day) predators; altered temporal activity patterns across areas of variable human versus lynx activity	[122]
	Humans	Lion (*P. leo*)	Diel (light levels) × lunar (light levels)	(Not measured)	Use dangerous areas (near humans) during safe times (dark nights)	[93]
	Humans	Wild boar (*Sus scrofa*)	Diel (light levels) × seasonal (hunting season)	(Not measured)	Shift habitat use on two temporal scales to minimize risk from hunters outside protected areas	[31]
	Humans	Chimpanzees (*Pan troglodytes*)	(Not measured)	Seasonal (resources)	Increase spatial overlap with humans when resources are limiting	[104]

[a]A broad range of studies across systems suggest that perception of a spatiotemporally dynamic landscape of fear is pervasive across the animal kingdom. Here, we highlight examples illustrating the diversity of temporal cycles of predation risk and prey constraints that can structure prey behavioral decision-making relative to patterns of spatial risk (see 'Risk is predictable both in space and time'). This list underscores metrics that require future evaluation, such as examination of more diverse schedules of risk and constraints (e.g., cycles of temperature, hibernation, weather), monitoring for multiple types of antipredator responses (i.e., vigilance and grouping in addition to spatial redistribution), and further in-depth evaluation of downstream effects (e.g., individual-, population-, community-level consequences) of prey behavioral decision-making.
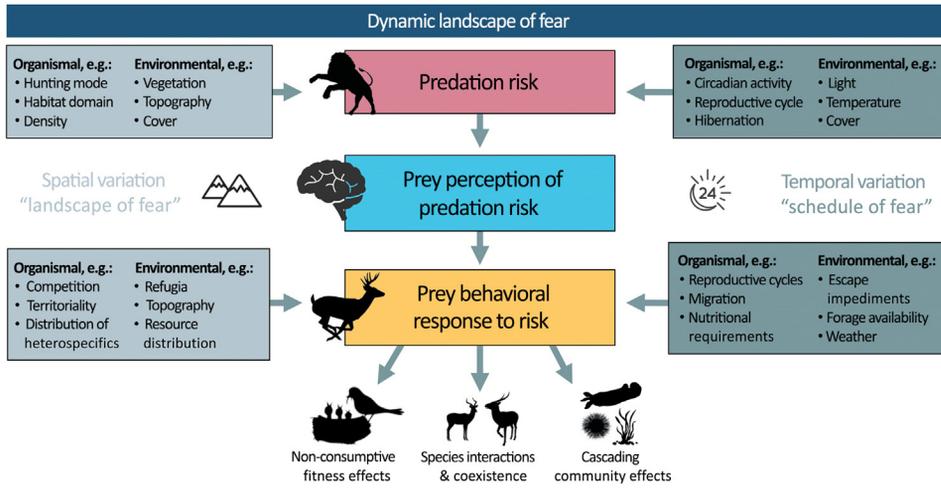
Figure 1. Schematic diagram of the dynamic landscape of fear. In a traditional, static 'landscape of fear', prey perception of predation risk is shaped by spatially varying factors that influence chronic predation risk by constraining predator activity, predator hunting success, and prey vulnerability. How prey respond to the landscape of fear is modulated by the pattern of spatial features that affect decisions prey make to optimize fitness. A 'schedule of fear' describes temporally structured patterns of perceived predation risk. Prey's ability to respond to the schedule of fear is also affected by temporally varying fitness trade-offs. Together, these two components combine to create a 'dynamic landscape of fear' that prey behaviorally navigate to survive in real ecosystems, with downstream consequences for individual fitness, species interactions and coexistence, and cascading effects on broader ecological processes.

Lunar cycles

Lunar cycles moderate nocturnal predator success and prey vulnerability via light levels [50]. For visual animals, full-moon nights can aid predators in detecting prey [47] and/or prey in detecting predators [35]. Periodicity in nocturnal brightness can affect predator space use, activity, and hunting success; for example, noctule bats (*Nyctalus noctula*) hunt in forests on dark nights and open grasslands on bright nights [51]. Furthermore, lunar phase can predictably influence daily [52,53] or seasonal [54,55] prey migration and distribution patterns.

Seasonal cycles

Seasonal periods of vegetation growth or snowfall provide concealment or present obstacles dependent on predator hunting (e.g., ambush versus pursuit) and prey escape (e.g., runner versus hider) strategies [56,57]. Prey and predator migrations may facilitate seasonal relief through predator evasion [34,58] or satiation [59]. Other temporal refuges manifest when predators or prey enter periods of dormancy [60,61].

Seasonal cycles of resource availability and reproduction also shape prey vulnerability and alter risk–foraging trade-offs [56,57]. Pregnant or lactating females engage in more risky behavior to increase energy intake [62,63], females with vulnerable offspring seek safer habitats [64], and males prioritize mating opportunities over risk mitigation [65]. Predators likewise face higher nutritional demands during their reproductive cycles, while also being restricted in movement when rearing young, creating periods of risk and safety for prey [66].

Predictions from a dynamic LOF

Considering both spatial and temporal dimensions of risk and response simultaneously generates a set of predictions that differ from those put forth using an exclusively spatial lens. Next, we propose a set of testable predictions to stimulate future research.
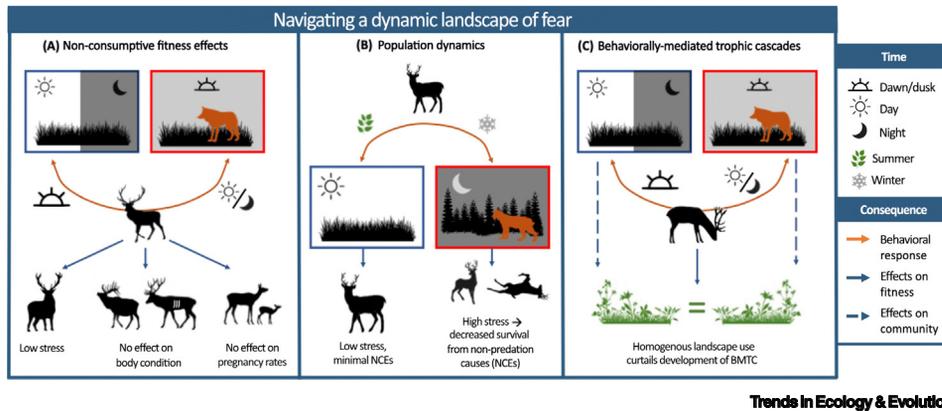
Figure 2. Consequences of navigating a dynamic landscape of fear. Case studies demonstrating how sensitivity to dynamic predation risk alters predicted non-consumptive effects on prey and the broader ecological system. Here, we focus on a single temporal cycle of risk (diel changes in luminosity), using Northern Hemisphere carnivore–ungulate systems as an example. Orange lines represent behavioral responses to each risk scenario ('safe' scenarios boxed in blue; 'risky' scenarios in red) by time period (time of day or season). Unbroken and dashed blue lines indicate non-consumptive effects on prey fitness and lower trophic levels, respectively. (A) Gray wolves (*Canis lupus*) hunt crepuscularly. Elk (*Cervus elaphus*) enter risky places during the day or night, which are wolf 'downtimes'; this may explain observed minimal effects of predation risk on elk stress levels, body condition, or pregnancy rates [11]. (B) Eurasian lynx (*Lynx lynx*) are nocturnal and hunt most successfully in forested habitats. During summer, European roe deer (*Capreolus capreolus*) avoid high-risk forests at night, instead utilizing these areas during safe daytimes, incurring minimal costs. However, when winter limits resource availability, deer must use high-risk areas day and night. Constant risk exposure increases deer stress levels, potentially increasing non-consumptive mortality [32]. (C) White-tailed deer (*Odocoileus virginianus*) avoided locations where gray wolf presence was simulated during periods when wolves would be active (dawn/dusk) but foraged in 'risky' patches during the day (safe times). Subsequently, deer landscape use was homogeneous and there were no cascading effects on plant biomass or community composition between safe or dangerous locations [38]. Abbreviation: BMTC, behaviorally mediated trophic cascade.

Interactions between spatially and temporally predictable risk

As noted earlier, predictability enables prey to anticipate and proactively mitigate predation risk [2,3,28]. Risk is predictable if it is chronic in space or periodic in time; the degree of predictability in either dimension varies from totally unpredictable to highly regular. Risk may vary predictably in one, both, or neither dimension (space and time), depending on interactions between organismal and environmental processes. Here, we consider scenarios arising at the four extremes of low and high risk predictability in space and time (Figure 3).

Risk is predictable in space but unpredictable in time (static LOF)

In this scenario, prey can reduce predation risk by proactively avoiding predators in space and/or by increasing antipredator behaviors such as vigilance or grouping in risky locations, but cannot change the timing of their landscape use to more safely access risky places (Figure 3). This situation should arise when predators rely on static landscape features to ambush prey or are constrained to certain portions of the landscape by competition or risk from their own predators [67]. Responses to fixed spatial patterns of risk have been documented in diverse circumstances (e.g., [2,13,68,69]). Where risk avoidance has costs (e.g., costly mitigation behaviors such as vigilance, or when resource scarcity in safe places forces prey to use risky ones), these behavioral decisions can result in non-consumptive effects on prey fitness [70,71]. Where prey distribution is restricted in space by predators, prey impacts can likewise become spatially constrained, resulting in altered foraging patterns (e.g., [69]) or behaviorally mediated trophic cascades (e.g., [72–74]).

Many studies documenting spatial patterns of predation risk and prey response have often been conducted over short timeframes, potentially falling within windows of elevated predation risk (e.g., during periods when migrating predators are present [34,73,75]) or reduced risk–resource

> **Box 1. Caveats and further considerations**
>
> The range of fitness-enhancing activities that are possible within spatiotemporal refuges from predation risk depends on the length and frequency with which refuges manifest. For instance, foraging can occur within hourly or daily spatiotemporal refuges, whereas reproductive opportunities may manifest on monthly or seasonal scales. Prey may not be able to exploit spatiotemporal refuges if they are too narrow or infrequent (e.g., in multipredator systems [108,123]), such that strong non-consumptive effects may still occur. Overall, the costs associated with temporal responses to risk are not well explored under field conditions, which currently limits our ability to predict downstream consequences on individual fitness, population dynamics, and community structure (e.g., [10,99,105]).
>
> While spatiotemporal partitioning of activity presents opportunities for prey to mitigate risk, evolutionary and ecological constraints likely limit the ability of prey to 'reschedule' their activity patterns to optimize fitness trade-offs (see Outstanding questions). This may occur, for example, where spatial or temporal activity shifts to avoid predation result in increased overlap with competitors. Prey may also lack the morpho-physiological flexibility to adjust activity patterns to avoid predators, incurring additional costs (e.g., thermal stress) [47,49]. In addition to the predictability of risk, the choice of whether to rely on proactive or reactive antipredator behaviors is modulated by prey traits, such as relative body size and morphology (e.g., weapons that improve outcomes in direct interactions with predators reduce the need for proactive avoidance) and escape tactics, as well as the frequency and lethality of predator encounters (e.g., if the risk of encountering or being killed during an encounter with a predator is low, then prey may rely less on proactive avoidance [67]).
>
> Furthermore, adjustments by prey should encourage counter-adjustments by predators, both ecologically and evolutionarily (e.g., [91]). The ability for prey to use spatiotemporal refuges to enhance their own fitness should, for instance, select for predators to become less predictable, potentially leading to arms races.

trade-offs (e.g., within a single season [21]). Spatial patterns of risk and the resulting strength of predator effects may exhibit more pronounced temporal variation when examined across longer timescales.

Risk is predictable in time but not in space (schedules of fear)

Here, prey can more safely use the same areas as their predators by proactively avoiding risk in time. Prey should increase their activity levels or reduce risk-mitigating behaviors during safe periods when predators are resting [28,40,47], hibernating [60], migrating [34,75], or have lower hunting success [45,46,50]. By accessing heterogeneously distributed resources within temporal refuges, prey may reduce exposure to dangerous risk–resource trade-offs (Figure 3); however, they lack safe predator-free spaces. The strength of resulting predator effects should then be modulated by the length and frequency of temporal refuges (e.g., [17,18,27]). We expect this scenario in comparatively spatially homogeneous environments (e.g., pelagic systems [76]) or where prey experience relatively uniform spatial risk (e.g., from some active-pursuit predators [23,77]; but see [11]). Prey may also modulate their activity levels through time to minimize predator encounters in multipredator systems where predators are ubiquitous and prey lack spatial refuges (e.g., [78,79]). While little is currently known about the downstream effects of temporal shifts in behavior under field conditions, prey should in principle incur fewer costs and distribute their ecological impacts across broader areas by accessing fitness-enhancing opportunities during temporal windows of lower risk.

Spatial and temporal predictability are both low

Under these circumstances, prey are unable to avoid risk in space or time, or to proactively modulate risk-mitigating behaviors (Figure 3). Prey should instead rely almost exclusively on reactive antipredator behaviors to escape from predator encounters [1,80]. Low spatiotemporal predator predictability may occur where multiple predators occupy all spatial and temporal niches [81,82] or in spatially homogeneous systems occupied by pursuit predators [83]. The inability of prey to proactively respond to predictable risk may also manifest where prey simply lack the capacity to perceive or recall predator cues (see Outstanding questions). If predator encounters are frequent, reactive antipredator behaviors can reduce individual fitness through physiological responses such as heightened stress [84,85] and reduced food intake [1,70,85]. Some studies suggest
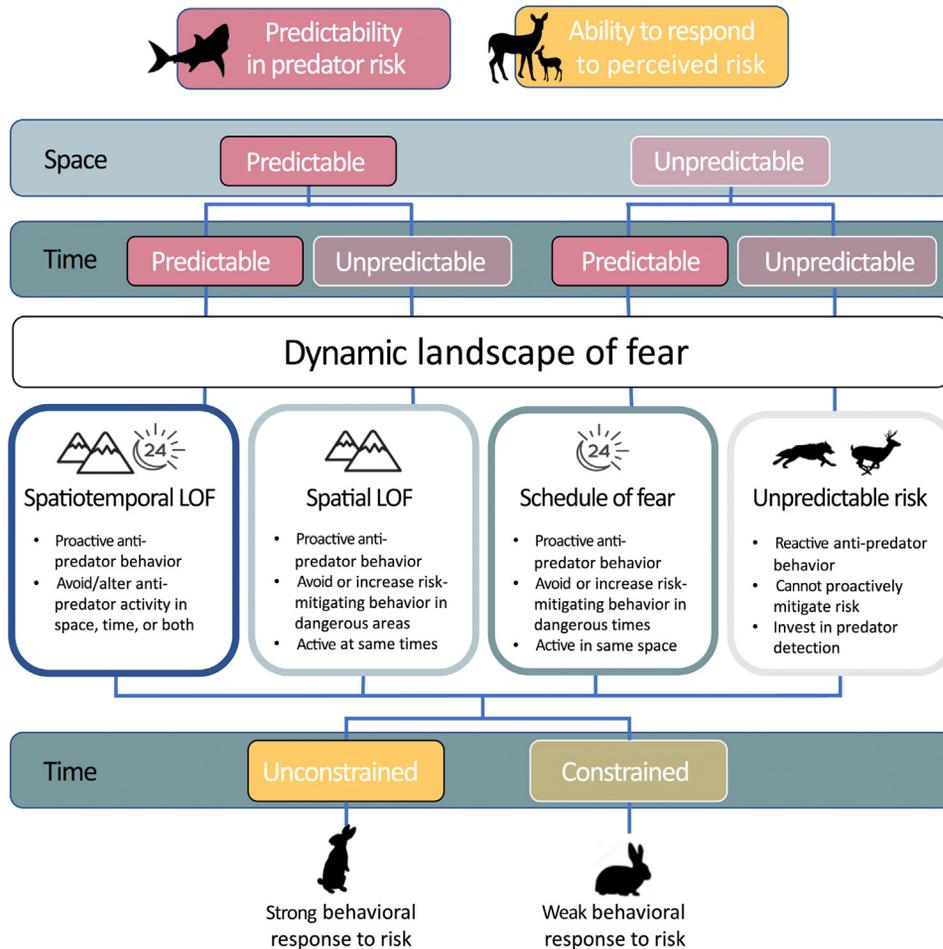
Figure 3. Predictions from a dynamic landscape of fear (LOF) framework. Perceived predation risk may vary predictably in space, time, both, or neither, with implications for the dynamics of prey response. Here, we consider four scenarios and accompanying predictions at the extremes of low and high risk predictability in space and time. When predation risk is predictable in space and time, prey can use spatial and/or temporal refuges to proactively mitigate risk. For instance, prey access otherwise dangerous areas during safe predator 'down-times,' such that antipredator behavior has minimal fitness costs. When risk is predictable in space but not time, prey proactively should adjust their spatial activity (e.g., alter distribution patterns or increase location-based vigilance or grouping) to minimize risk, but should not change their temporal activity. Prey are restricted to portions of the landscape and, if spatial risk avoidance is costly, there may be fitness consequences (i.e., non-consumptive effects). When risk is predictable in time but not space, prey should proactively adjust their temporal activity (e.g., alter activity levels or timing of vigilance or grouping) but use the same areas as their predators. Prey access all of the landscape, but incur costs if the frequency or length of temporal refuges is insufficient to enable fitness-enhancing activities. When risk is unpredictable in either dimension, prey cannot proactively minimize predator risk by changing their activity or distribution. Instead, prey rely on reactive antipredator behaviors to escape predator encounters. The strength of prey response to perceived risk is further modulated by temporal cycles of constraints such as reproductive cycles, seasonal weather patterns, or periodic increases in competition. During times when prey are unconstrained, they are able to respond strongly to mitigate risk; when prey are constrained, they may react less to spatiotemporally structured predation threats.

that **consumptive effects** (rather than non-consumptive effects) dominate when predators are unpredictable in space and time [77,86]. As such, while behaviorally mediated effects on the wider community might be limited if prey use the landscape without regard for predator activity, density-mediated cascades may still occur (e.g., [87]).

Risk is predictable both in space and time

As spatial patterns of predator activity fluctuate across temporal cycles, prey should proactively minimize risk exposure by using spatiotemporal refuges to forage and mate (Figure 3). A growing body of evidence documents prey antipredator responses to spatiotemporally predictable patterns of predator activity across a wide variety of environments and taxa (Table 1). A flagship example is diel migration, which occurs in animals ranging from zooplankton [88,89] to zebra *Equus quagga* [29], where prey move from low-risk/low-resource areas to high-resource but otherwise risky areas when sunlight conditions create temporal refuges from visually hunting predators. In addition to avoiding dangerous places at dangerous times, prey may also modulate activity levels [90,91], speed and direction of movement [33], and vigilance and group size [35] to reduce predator-encounter probabilities when they are forced to enter risky situations. Similar patterns of spatiotemporally variable antipredator decision-making occur across tidal [41,43,44], lunar [35,53,92], and seasonal or reproductive [34] cycles of predator activity and many prey modify spatial activity in response to simultaneous cycles of risk with different periodicities (e.g., diel/lunar cycles [93]; diel/seasonal cycles [31]) or created by multiple predators [78,94] (see 'When do risk and response vary across space and time?').

Given that risk is often predictable in both space and time, the dynamic LOF framework suggests that the effects of spatial variation in perceived risk on prey populations and communities (via behaviorally mediated trophic cascades) may be less pervasive than commonly assumed [9,95–97]. This is because behavioral responses to spatially and temporally varying predation risk can modulate cascading effects, as exemplified by temperate carnivore–ungulate systems (Figure 2). In these systems, multiple studies have found that prey sensitivity to spatially and temporally predictable risk results in negligible net effects on body condition and pregnancy rates [11] and nonpredation deaths (e.g., from stress, starvation) [32], while also curtailing cascading ecosystem effects [38]; this is perhaps because prey are able to utilize both spatial and temporal refuges to access fitness-enhancing opportunities at low risk [11]. The paucity of clear tests of this proposition from other systems and organisms, however, emphasizes the need for more work on the topic.

Temporal constraints on prey antipredator response

As the spatial structure of risk can vary across time, so too can prey's ability to proactively mitigate risk. Prey may be temporally constrained in their ability to respond to risk, which can predictably influence antipredator decision-making (and the downstream consequences of these actions) during certain periods (Figures 1 and 3 and Table 1). Cyclical changes in physiological (e.g., reproductive periods), community (e.g., migrations), or environmental (e.g., seed masts) factors that affect prey condition can therefore affect behavioral responses to predation risk (i.e., state-dependent decision-making [36,75,98,99]). For example, loggerhead turtles (*Caretta caretta*) take few discernible actions to minimize risk in tiger shark (*G. cuvier*) home ranges, due in part to life-history trade-offs involving foraging and nesting, environmental conditions (water temperature), and human activity [12]. Similarly, roe deer (*Capreolus capreolus*) are unable to avoid areas of high predator activity in the winter due to thermal and nutritional constraints [81].

As environmental or social conditions change, so too should prey resource–risk trade-offs and, therefore, their response to perceived risk. Elephant seals (*Mirounga angustirostris*), for example, prioritize safety (resting in dark lower ocean levels) over energy intake (foraging in more dangerous upper ocean levels) when fat stores are high but switch tactics when body fat is low [36]. African ungulates seasonally alter the magnitude of their responses to risk, avoiding risky areas to a higher degree during the wet season when forage is widely available but

prioritizing forage acquisition over minimizing risk exposure during the lean dry season [35]. Without an understanding of these cyclical temporal constraints, ecologists may mistakenly predict strong risk effects where none occur [3].

Applying the dynamic LOF framework for ecological insights

Logistical constraints have made it difficult to incorporate both spatial and temporal dimensions in empirical studies, contributing to the prevalent conceptualization of static spatial patterns of real and perceived predation risk. Large mammals are particularly intractable for experimentation in the wild, leaving open questions about the extent to which research on smaller organisms 'scales-up' to large animals and landscapes. With technical advances, ecologists are able to collect data on ever-more granular scales, allowing researchers to better match the resolution of sampling with the biological rhythms and patterns of risk–resource trade-offs [100]. Continually improving tools (e.g., GPS telemetry, accelerometers, biologgers, camera traps, drones, acoustic recorders) also expand the breadth of data, for example, by capturing the behavior of multiple interacting species simultaneously [101–103]. Novel experimental approaches are expanding the scales at which strong inference is possible [21,72] and sophisticated statistical methods increasingly enable investigators to surmount the complexity inherent in large observational datasets [36,83,104]. These and future advances will enhance investigators' ability to parse spatial and temporal dimensions of risk and response and test the predictions outlined earlier. Development of a body of formal quantitative theory would help to further define the dynamic LOF, probe its premises, and refine its predictions for different organismal and environmental contexts.

Concluding remarks

Predation risk is dynamic in both time and space and there is a rich tradition of studying each axis of variation separately. As a rapidly growing literature attests, however, synthesizing the temporal and spatial perspectives on predation risk may account for much of the observed diversity and contingency of risk responses [10,11,105]. Here, we offer a framework to guide research, outlining how an integrated spatiotemporal approach to risk and response clarifies and nuances predictions about predator effects on prey behavior and its potential population- and community-level consequences.

Many questions remain regarding risk–resource trade-offs in natural systems (Box 1 and see Outstanding questions). Given evolving technologies and global change, understanding spatial and temporal patterns of predation risk and prey response has never been more possible [101,102], or more necessary. Elimination of native predators, restoration and recolonization of historical predators, human-driven changes in species distributions, and the increasing intensity and reach of human exploitation are rapidly reshaping ecological communities and altering patterns of spatial and temporal activity for both prey and predators [93,106,107]. Understanding and mitigating the impacts of these transformations to the risk landscape is crucial for protecting animal populations and the ecosystems they inhabit.

Declaration of interests
No interests are declared.

Outstanding questions

What trade-offs constrain the evolution of predator and prey strategies? Prey should be under strong selection to avoid risky places and times, while predators should seek to overcome spatial and temporal constraints on hunting behavior. Prey and predators are undoubtedly limited in their ability to overcome these constraints by countervailing selective pressures, but these trade-offs are poorly understood.

How do prey perceive and process information about risk? How do prey acquire knowledge needed to navigate a dynamic LOF? To what extent is it innate or learned, either individually (from experience) or socially (by observing con- and heterospecifics)? What is the role of complex cognitive processes such as learning and memory?

What spatiotemporal scales govern prey behavior? Prey are often exposed to multiple trade-off cycles simultaneously (e.g., diel and lunar patterns of predator activity with seasonal resources constraints). Moving forward, we need to examine trade-offs across multiple interacting spatiotemporal scales to understand prey behavior.

How do prey respond to multiple simultaneous risk cycles? Prey often coexist with multiple predators, each generating unique dynamic LOFs. Does increasing the diversity of predator species concentrate prey into more restricted spatiotemporal refuges and/or change their antipredator responses from proactive to reactive? Is the dynamic LOF less detectable in multipredator systems? Can differential sensitivity to layered dynamic LOFs contribute to predator–prey coexistence?

How do prey respond to novel predation? Humans are decimating native predator communities and introducing new predators (including humans). Is there sufficient plasticity in evolved prey responses to avoid novel predators and how do these tactics differ from those used against native predators? Are risk landscapes becoming more homogeneous as humans replace native predators? Does this destabilize coexistence, contributing to species loss?

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