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# The role of habitat in predator–prey dynamics with applications to restoration

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**Habitat is a powerful force in ecosystems, and the quantity and quality of habitat can shape ecosystem structure and function. Among the many important roles that habitat plays is as a mediator of ecological interactions, including predator–prey dynamics. In the context of ecosystem restoration, there is great potential to better understand how predator–prey dynamics are influenced by habitat and whether this has implications for how ecosystems are managed. We consider the ways in which habitat serves as an important mediator of interactions between predators and their prey and present four ways in which habitat acts as an intermediary that enhances or diminishes this relationship. We found that habitat provides refuge from predators and shapes the physical traits of prey as they use their surroundings to protect themselves. We also discuss how habitat creates physical resistance and sets the cost of predation for predators and how habitat facilitates apparent competition within a community context. These roles of habitat are well established in ecology, but we believe they are underdeveloped from an applied perspective. We conclude that habitat must be appropriately considered in the context of how it mediates predation. Given the ways that habitat influences predation, restoration efforts should consider if and how physical measures may positively or negatively affect species interactions and whether this could lead to success or failure of overall programs.**

**Key words:** ecosystem restoration, functional response, landscape of fear, predator–prey, refuge, rewilding

## Implications for Practice

- Habitat plays an intricate role as an intermediary between predators and their prey.
- Loss of habitat can exacerbate predator–prey conflicts; therefore, restoration may mitigate such conflicts.
- Habitat restoration can be key to ecosystem-based management.
- Practitioners should consider how habitat loss and gain may contribute to diverse management aims at an ecosystem scale.

## Introduction

Habitat is a core concept in ecology that describes the physical environment that contributes to the abundance and diversity of life in space and time. Habitat includes the abiotic and biotic features of a landscape, which are dynamic and confer costs and benefits to animals (Fig. 1). Habitat is dynamic because landscapes change through successional processes and natural disturbances (Bhaskar et al. 2014) and more recently, due to anthropogenic changes that cause fragmentation, homogenization, and change or loss of habitat (Fahrig 2001). A habitat can be high quality for one animal but low quality for other species or even individuals within species, depending on the size, coloration, metabolism, stress responsiveness, and other traits. Importantly, individuals may not always occupy their optimal habitat, using also secondary habitats as part of an optimality (Rosenzweig 1981) or due to competition or fear effects (DeCesare et al. 2014). Habitat can be measured at different

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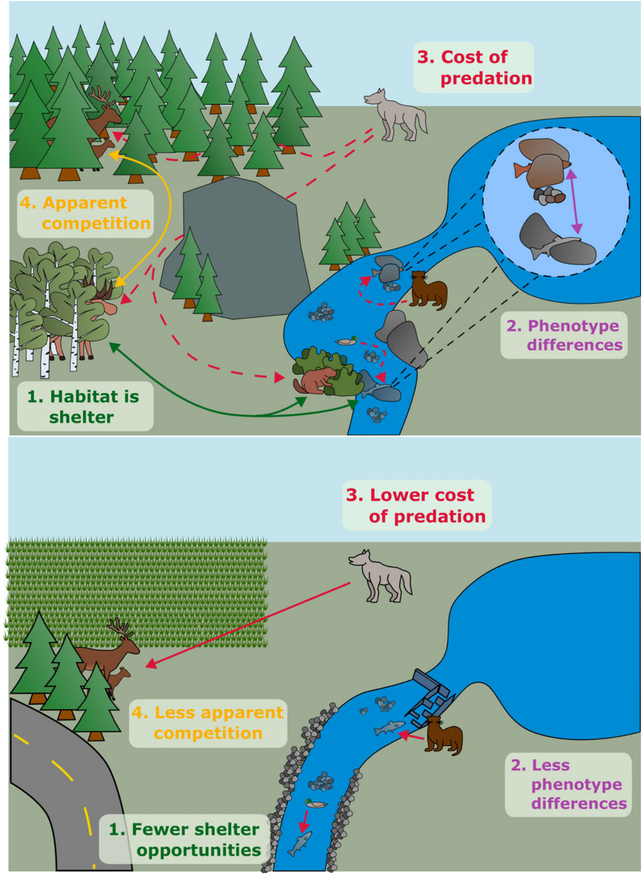



Figure 1. Conceptual diagram of habitat as an intermediary in predator–prey systems.

scales (i.e. microhabitat; Price 1978), and a landscape can contain many different habitats and microhabitats, creating heterogeneity that is important to the maintenance of biodiversity (Morris 1987). Importantly, habitat can be used by multiple species (i.e. an assemblage) and their interactions may converge in specific locations that yield predictable patterns in how species interact (Kauffman et al. 2007).

Habitat is fundamental to effective species conservation and to successful ecosystem restoration (Young 2000). Quality habitat tends to confer proximate individual condition and ultimate fitness benefits; therefore, animals benefit from the availability of habitat that they consider to be high quality (Johnson 2007). Habitat is not only important for its own sake, but for the roles that it plays in the lives of animals. One of the most important of these roles is how habitat keeps animals safe and how it serves as a buffer against predation risk. Although it will not be controversial to many readers that habitat plays a role in the dynamics between predators and their prey, we believe that the importance of habitat has not been fully integrated into conservation planning or ecosystem restoration, particularly where indirect pathways exist. In this essay, we describe the role of habitat in (1) providing refuge, (2) shaping prey phenotypes, (3) the energetics of predation, and (4) mediating apparent competition. In doing so, we discuss how the relationship among habitat, prey, and predators can contribute to restoration. We conclude by discussing both the realized and potential applications and limitations of this hypothesis, particularly with respect to conservation and restoration where habitat may play an indirect role.

## Evidence

We propose four key ways in which habitat is important to predator–prey dynamics, and in this section, we collate evidence supporting our hypothesis that habitat sets the cost of predation. Firstly, habitat is refuge for prey species and is a spatial area where individuals can rest, develop, digest, and recover from stress. In addition to providing hiding places and serving as refuge, habitat shapes animal coloration/pigmentation and morphological traits (Huey 1991; Sultan 2015). Natural selection will shape the bodies of prey species in ways that match their phenotypes to the environment, shaping the needs of animals to match their size and shape for maximum reproductive potential while also limiting visibility to predators via camouflage. Third, habitat rugosity and complexity determine the energy costs of locomotion and establish the costs and benefits of hunting prey for predators (Huey 1991). Finally, a more complex habitat further has the ability to sustain a more diverse prey community that can buffer the impacts of predation on a single species (Kovalenko et al. 2012). These four concepts are explored in more detail with specific reference to how this knowledge can be applied to restoration below.

### Habitat Is Refuge

A primary service provided by habitat is to create refuge areas where prey can limit their visibility and vulnerability to stressors, especially predators (Eggleston & Lipiscus 1992). Refuge is therefore key to limiting encounters with predators. Physical refuge for prey has long been recognized as reducing the risk of predator-induced extinctions, as well as dampening oscillations in predator–prey cycles (McNair 1986; Sih 1987). Refuge areas are also part of the natural habitat for ambush predators to conceal themselves from their prey and increase their hunting success. Predation success for sculpin (*Cottus gobio*) on salmon (*Salmo salar*) eggs depended on how effectively habitat could be used as refuge; smaller substrate sizes sheltering the eggs provided better protection from the predators compared to larger substrate sizes that yielded greater access for the sculpins to capture eggs (Palm et al. 2009). Habitat complexity is also an important feature of nursery areas such as mangroves, whose roots protect juvenile fishes and crustaceans from predation (e.g. lemon sharks; Franks 2007). Kamal et al. (2014) demonstrated that mangrove root habitat appears more complex to larger fish than to smaller counterparts given their space restrictions to maneuver within the entanglements.

Restoration efforts therefore need to consider how the available habitat can be enhanced to provide sufficient refuge. Landscapes that have been simplified for human convenience are the most likely to require consideration of the refuge needs of constituent species. Anthropogenic alteration of refuge habitats can increase predation rates; for example, construction of linear features in peatlands, previously a refuge for Caribou (*Rangifer tarandus*), increased the presence of wolves

(*Canis lupus*) in peatlands and reduced the value of these habitat features as refuge areas (DeMars & Boutin 2018). In the opposite direction, increasing the habitat complexity by adding structure like vegetation can create hiding places that reduce predation vulnerability (Stansfield et al. 1997; Ranåker et al. 2012). Two experiments demonstrate different outcomes of predator–prey interactions at varying habitat complexity that could inform restoration: Swisher et al. (1998) found that mayfly larvae escaped dragonfly larvae attacks but became vulnerable to Bluegill sunfish (*Lepomis macrochirus*) predation when macrophyte density was low, whereas Warfe and Barmuta (2004) demonstrated that macrophyte shape affected the relationship between Damselfly larvae (*Ischnura heterosticta*) and Pygmy perch (*Nannoperca australis*), reducing overall rates of mosquito larvae predation. Alternative aspects of habitat, like water turbidity, may have more nuanced effects; turbidity could provide refuge, but may also reduce visibility, rendering unexpecting prey more vulnerable. Pied kingfishers (*Ceryle rudis*) had much greater prey capture success when diving into turbid waters, perhaps due to low predator detectability by fish (Holbech et al. 2018). In another study, turbidity did not change patterns of predation, though structural complexity significantly reduced predation (Figueiredo et al. 2014) (Box 1).

**Implications for Restoration.** Habitat simplification in urbanized or developed landscapes can reduce refuge quality and increase the vulnerability of animals to predation; restoration can improve refuge quality and decrease the vulnerability of animals to predators. Norman et al. (2024) demonstrated how a pumping station in a river provided poor refuge for fish sheltering from predators, a clear target for restoration efforts that introduce habitat complexity and refuge for fish. Fortunately, in altered habitats where there is reduced refuge for prey, there is evidence that predation rates can be stabilized by restoration that focuses on increasing prey refuge. Radinger et al. (2023) emphasized this in an experiment demonstrating that habitat improvements were much more successful than fish stocking for enhancing fish populations in the lake. Similar studies are lacking for other interventions such as predator removal, but there is clearly value in focusing on habitat as an intervention to address productivity at an ecosystem scale. Researchers and practitioners may wish to characterize refuge as a fundamental aspect of the landscape and consider whether degradations or planned enhancements will serve as effective refuge from predation.

### Habitat Is the Canvas of Phenotypic Variation in Prey Populations

Habitat drives variation in prey phenotypes and makes it difficult for predators that have to adapt their prey picture. Many animals have evolved to match their phenotypes to the habitat that they frequent, based in large part on selective pressures that they encounter from predators (e.g. Boratyński et al. 2017), which can change via plasticity (e.g. chromatophores; Hanlon 2007) and natural selection driven by predation in response to habitat changes (e.g. Peppered moth [*Biston betularia*]; Berry 1990). Linnen et al. (2009) showed that a novel mutation arose in deer mice living in sandy habitat, and the mutation spread rapidly to create lighter-colored mice in the lighter-colored habitat. Winemiller et al. (1990) also found evidence supporting habitat and predation as drivers of phenotype in guppies, indicating that showiness (coloration pattern) varied with habitat, and resulted in greater risks of predation. Specifically, showy males that were too conspicuous (highly contrasting to their habitats) were more likely to be predated. Physical phenotypic alterations can include body shape and appendage length to camouflage; the Leafy seadragon (*Phycodurus eques*) is a notable example of camouflage to blend in with seagrass (Randall 2005). Alternatively, morphological features can evolve to meet the demands of the habitat, like the body shape of male Sockeye salmon (*Oncorhynchus nerka*), which is selected in part by female choice, in part by predation vulnerability, and in part by the characteristics of the habitat that they must navigate in order to spawn. All three selective pressures will have different benefits for large versus small sockeye, but if the individual is too deep-bodied to get into a small spawning stream, it will be unsuccessful in passing on its genes (Hamon & Foote 2005; Carlson et al. 2009).

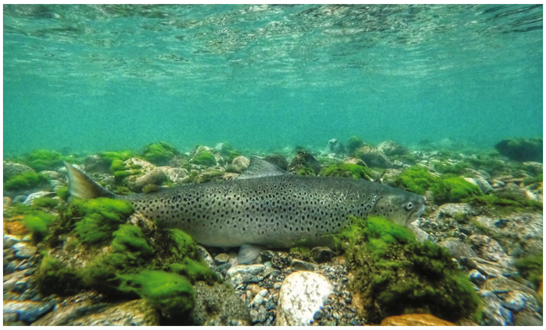
Anthropogenic changes to habitat due to climate change and land use change are among the most pressing threats to biodiversity in most biomes (Sala et al. 2000). Species that live in altered habitats are often more vulnerable to predators, because the anti-predation adaptations (e.g. camouflage) they have evolved are not serving the same benefits as in their natural habitats (Atmeh et al. 2018). Animals may have evolved a range of phenotypes for coloration, body shape, or behavior to reduce predation risk in the habitat they live in, but as this habitat continues to change, the existing range of phenotypic variability may no longer serve to avoid predators. For example, Pedersen et al. (2017) showed that mountain hares were more vulnerable to predation in areas where snow cover duration had decreased because of a climate change-induced molting mismatch. Concurrently, the existing genetic variability in a prey population may not be sufficient for new adaptations to arise, or the rate of evolution may not keep up with the speed of habitat changes (Gibert et al. 2019), particularly if the structural aspects of the habitat that served as shelter are no longer available. Thus, adapting to changes in temperature, food availability, and altered competition may not be enough for animal populations to endure climate change and land use change together. The capacity to alter anti-predation phenotypes is also a key part of adapting to changing habitats (e.g. Jones et al. 2020), and may ultimately determine which species survive the Anthropocene.

**Implications for Restoration.** Restoration can consider the role of phenotypic match and mismatch in animal populations. Recognition of mechanisms that may be challenging species can assist in making informed decisions for restoration. Baling et al. (2016) released Shore skinks (*Oligosoma smithi*) into novel habitats and found rapid selection for changes in the coloration, likely reflecting predation risk of mismatched phenotypes; they recommended considering camouflage requirements when conducting rewilding, and practitioners can see the value in considering this in restoration as well. In practice, this might look like prioritizing breeding or releasing phenotypes that are likely to match with

**Box 1 Visual summary of the theoretical framework in which habitat influences the vulnerability of species to predation in four ways.**

Coral reef habitats provide refuge for species such as this Moorish idol (*Zanclus cornutus*) in the tropical Pacific.

This sea-run Brown trout (*Salmo trutta*) has coloration and patterning shaped by the river habitat where it has returned to reproduce following a period at sea. The shape and pigmentation of these animals have been molded by their habitat to avoid being visible to birds, otters, and other potential predators (photo: Terje Andrè Skjolda).



Reindeer (*Rangifer tarandus*) and Caribou (*R. tarandus tarandus*) can select high rugosity habitat that sets the cost of cursorial predation for species like wolves.

Habitat selection by species such as Impala (*Aepyceros melampus*) affects their exposure to predators such as Lions (*Panthera leo*). Apparent competition with other plains ungulates is governed by dynamics in habitat selection and vulnerability across space and time.

the available environment; alternatively, planting vegetation or installing cover that will provide opportunities for natural camouflaging. For snowshoe hares that are increasingly vulnerable to predation because they are not molting their winter fur fast enough to track with accelerated springtime, alternative actions may be effective for their conservation, such as planting tree stands that buffer predation and buy time for the animals to molt and match the summer vegetation (Wilson et al. 2019).

### Habitat Sets the Energetic Cost of Predation

Predator and prey performance depends on the environment that they encounter, with varying energetic costs of activity in different environments (i.e. energy landscape). A complex habitat makes it challenging for predators to capture prey, thus reducing predation pressure while sustaining a more diverse species assemblage, although the movement between diverse habitat types can be costly in itself (Hammerschlag et al. 2010). Predators exhibit different hunting strategies, which likely affect habitat selection of prey to modulate their vulnerability to predation. Cursorial predators like wolves excel on flat ground where the energetic cost of pursuing or capturing prey is lower than on slopes (e.g. Kauffman et al. 2007), whereas ambush predators like Lions (*Panthera leo*) will thrive in environments where they can conceal themselves in structure, avoiding hunting in open plains where the energetic costs of predation are high. In Hwange National Park, several herbivore species preferred open areas of the landscape where they could better detect and escape Lions, compared to edges where lion ambushes would be more likely (Valeix et al. 2009).

Prey that encounter predators can avoid them or must escape if they are to survive an attack (Guiden et al. 2019). Complex habitats can provide prey better opportunities to evade a predator for agile animals and thus reduce their own exposure to predators so that predators must invest more time in searching (Johnson et al. 2019). Landscape heterogeneity also affects the energetic and temporal costs of predation and can make escape easier for prey that encounter predators. Furthermore, a complex habitat can reduce the probability of encounter between a predator not only by providing refuge (see above), but also by slowing predator travel speed (Diehl 1988; Johnson et al. 2019). Consequently, spatial complexity can influence predator–prey interactions by reducing predation success via energetic limitations (Dickie et al. 2022). Escaping predators can be energetically and temporally costly and may lead to exhaustion of the pursued animal (Godin 1997; Pérez-Tris et al. 2004), which subsequently demands physiological recovery (e.g. Wood et al. 1983; Portner et al. 1993). Higher landscape heterogeneity can offer more shelter that serves as a predation refuge or promotes recovery of prey after escaping a predation event. Furthermore, exhausting migration corridors such as dam tailraces may make prey vulnerable during their recovery from anaerobiosis (e.g. Sockeye salmon in challenging fish passage structures; Burnett et al. 2014). Taken together, the efficiencies of predators and the evasive mechanisms of prey are affected by the degree of structural complexity in the habitat (Eklöv 1997). A key implication is that humans, to some extent, can modulate the energetic and temporal cost dynamics between predators and prey by adding or removing structural complexity through habitat restoration or engineering measures.

**Implications for Restoration.** Structural complexity should be a priority for restoration programs to maintain the energy landscape that balances the costs of predation for predators. For many aquatic habitats, streams have been simplified by channelization and shorelines have been homogenized with seawalls; on land, much of the randomness of nature can be lost if spatially patterned methods of restoration are not implemented effectively (Shaw et al. 2020), such as planting trees in rows. Although simplification may seem to make life easier for animals that need to navigate, the shifts in the physical landscape can affect predation costs. Dickie et al. (2017) showed that linear features can reduce the costs of predation for wolves and suggested that restoration could focus on reducing this linearity. Where possible, appropriate consideration of complexity and the energy costs of landscape features should be tested with experiments or at least considered in light of the ecosystem dynamics in each area targeted for restoration.

### Habitat and Community Structure Establish Apparent Competition

Sufficient quantity and quality of habitat can support a diverse species assemblage, which creates a varied menu for a predator. However, loss or homogenization of habitat in a landscape will reduce species diversity and force predators to increase specialization on remaining constituents. When predators are focused on a smaller number of potential prey, the relative share of predation on some species may increase and become more visible or problematic. This is essentially apparent competition, in which the distribution or behavior of one prey species affects the predation rate on another species (Holt 1977). In the prairies, loss of the grassland titan American bison (*Bison bison*) as an alternative prey for wolves increased predation on elk, suggesting that more bison could reduce predation pressure on elk. However, restoration of the habitat to facilitate the return of the bison is necessary to buffer the conflicts associated with wolf-elk predation (Garrott et al. 2008). The role of habitat in apparent competition among prey species may be strong, but remains poorly studied. An alternative example is within species apparent competition, where stocked animals have repeatedly been shown to have different behavior, physiology, and life history from wild counterparts (Einum & Fleming 2001; Nilsen et al. 2022). Stocked animals may be more vulnerable to predators and therefore in apparent competition with wild individuals. Apparent competition between domesticated and wild prey has also provided evidence that maintenance of habitat supporting native prey can buffer conflicts with predators. In Portugal, Eurasian otter (*Lutra lutra*) predation in commercial fish ponds was found to increase with the distance to suitable freshwater habitats, suggesting that the presence of wild prey reduced otter disruption of fish farmers (Santos-Reis et al. 2013). Obtaining empirical evidence of apparent competition is challenging, but prey switching by predators to modulate their diet as the relative abundance of potential prey fluctuates is well established and is the primary mechanism that was used to describe Holling's type III functional response curve (Holling 1959).

**Implications for Restoration.** It is tempting, and not necessarily incorrect, to conclude that increased predation of a valued species like elk must be the result of an imbalance between that species and its predators, like wolves (e.g. Garrott et al. 2008). Because many predators have a broad diet, focusing on the ecosystem more holistically may be important to mitigating conflicts. Indeed, researchers and practitioners may consider whether the predator has lost other prey sources and whether restoration action can help to rebuild alternative prey. Poor Pacific salmon (*Oncorhynchus* spp.) runs have been connected to increased conflicts between humans and bears (*Ursus arctos*; Artelle et al. 2016), and restoration of Roe deer (*Capreolus capreolus*) was suggested as a solution to reduce Lynx (*Lynx lynx*) predation on farms. These examples suggest that restoration of alternative prey can be a key mechanism by which management intervention can affect conservation efforts, as also suggested by Frenette et al. (2020), who noted that declining Moose (*Alces alces*) numbers affected Endangered Gaspesie caribou predation by Coyotes (*Canis latrans*). If habitat quality has been reduced and can be restored to increase the local biological diversity, apparent competition can distribute predation and reduce the pressure on focal species, potentially with better outcomes for conservation than culling the predator would yield.

## Habitat Is Important, But Not a Panacea

Having established multiple pathways via which habitat serves as an intermediary with predation, we consider what limitations should be considered in applying this concept in practice. Indeed, the narrative would not be complete without addressing shortcomings of our hypothesis and acknowledging that habitat is not the only mechanism by which prey can avoid predation.

### Ecological and Perceptual Raps

Ecological traps attract animals to areas that are deceptively poor in quality, for example, areas that they will be vulnerable to predation (Dwernychuk & Boag 1972). Hale and Swearer (2017) described how perceptual traps can lead animals to avoid restored habitats, and ecological traps can cause animals to prefer restored habitats that are lower quality and thereby compromise fitness. Ultimately, traps arise because humans fail to effectively understand the habitat needs of the focal species, leading to ineffective interventions and unintended consequences. Given most circumstances, the presence of a trap in a landscape will drive a local population to locally altered abundance, if not extinction (Battin 2004). Anthropogenic alterations to habitat are a common mechanism underlying ecological traps (Robertson & Hutto 2006), but climate change may also be creating ecological traps for species that aggregate in thermal refuge where they become vulnerable to predators (Sullivan et al. 2023). Restoration efforts to create migration corridors for terrestrial animals may seem helpful to facilitate movement and connectivity, but these may also act as predation hotspots (Ohms et al. 2022). Wildlife corridors across roads and railways have frequently been found to be used by a range of terrestrial predators, to their advantage over their prey species that are attracted to such structures by the habitat created for them there by humans (Little et al. 2002). Fish passage structures in rivers that similarly provide upstream passage at dams may also become areas where predators can hide and ambush fish attempting to pass (Agostinho et al. 2012; Boulêtreau et al. 2018). Creating or protecting small pockets of thermal refuge for animals to shelter from climate-related impacts of warming may also influence predation, and this consideration should be integrated in environmental designs. Habitat that is not well designed by restoration practitioners, especially engineered habitat, can therefore have the opposite effect on prey species and interactions between predators and prey. Examples of design shortcomings include wildlife overpasses that are not wide enough (Brennan et al. 2022), simplification of aquatic ecosystems using unsustainable materials like plastic and concrete to create artificial habitat (Cooke et al. 2020, 2023), or the aforementioned creation of predation hotspots (Boulêtreau et al. 2018).

### Biological Invasions

Invasive species can greatly alter the relationship between native predators and their prey and can also disturb the role that habitat plays as an intermediary in predator–prey relationships. For restoration, this means that the presence of invasive species may complicate efforts (D'Antonio et al. 2016) and make it challenging to address predation via restoration explicitly. Protection of quality habitat is itself important to resist biological invasions, and restoration plays a role when there are invasive species present. However, invasive species can offset the benefits of restoration targeting native species recovery, for example. This is the case for invasive Lionfish (*Pterois* spp.); one reason why lionfish tends to be so problematic as an invasive species is that they use much broader habitat domains than native predators that they are competing with in areas like the Caribbean Sea and are therefore able to have a wider resource base upon which to thrive compared to the native species whose dietary options are more restricted (Jud et al. 2015; Benkwitt 2016). Lionfish and other invaders can be damaging to the ecosystem function, as well as the structure that native species rely on for foraging and refuge seeking (Gallardo et al. 2016). Pacific oyster (*Crassostrea gigas*), for example, is an invasive species that creates hard reef structures, altering the structure and complexity of native habitats, with an impact on soft substrate habitats like mudflats by creating areas that can be effectively used by predators (Mortensen et al. 2018). *Juncus bulbosus* is also an ecosystem engineer that has many damaging effects on habitats, but also some benefits to native species, such as providing refuge for juvenile salmonids and macroinvertebrates, so the impacts of the invasive species depend on what impact is being studied (Velle et al. 2022). Similarly, invasive amur honeysuckle in Missouri, United States, were preferred by white-tailed deer and could be perceived to be creating habitat; however, this native-invasive association comes with a major cost, because the honeysuckles have high loads of deer tick infected with the bacterium causing ehrlichiosis in humans (Allan et al. 2010).

Invasive species can also greatly increase competition for available habitats (Dunoyer et al. 2014; Wang et al. 2021), reducing the amount of refuge available to native prey and making them more vulnerable to predation. This has been shown in lakes where introduced crayfish kept native crayfish out of refugia when refuge habitat was limited, making them more vulnerable to predation by Largemouth bass (*Micropterus salmoides*; Garvey et al. 1994). However, when crayfish refuge habitat was not limiting, both native and invasive crayfishes increased their use of refuge and reduced their risk of bass predation, highlighting that habitat refuge availability can mediate the consequences of invasive species on predator–prey interactions. The effect of habitat modification on predator–prey interactions may also differ between native and invasive species. In Ireland, successful recovery of the native predator Pine marten (*Martes martes*) increased suppression on the invasive Gray squirrel (*Sciurus carolinensis*; novel predator–naïve prey), which in turn favored recovery of the native Red squirrel (*Sciurus vulgaris*; native coevolved prey) through competitive release (Twining et al. 2022). However, this predation effect was only observed in native broadleaf woodlands, and not in non-native conifer plantations where both squirrel species were suppressed equally by the marten. This suggests that effective predator control of invasive prey species may be less dependent on habitat than native prey scenarios, but that anthropogenically modified habitats may cancel out potential benefits of such control programs on native prey species.

### Depensation and Predation Pits

Largely, one cannot simply restore one's way out of all conservation challenges. This is the case when there are not enough reproductive individuals to use the available habitat to its full potential. When populations spiral toward critically low densities, they are unable to increase their abundance via expected density-dependent population growth, owing to relatively high predation rates at low or medium prey densities. This is called a "predation pit" (Bakun 2006), a type of depensation dependent on predators displaying a type III functional response (Gascoigne & Lipcius 2004). A change in a lake-dwelling Kokanee salmon (*Oncorhynchus nerka*) population to an alternative, low-abundance state was described as a predator pit by Warnock et al. (2022) based on dramatic reductions in juvenile kokanee survival that never recovered. Schrott et al. (2005) also demonstrated with simulations that habitat restoration would do little for the recovery of depleted songbirds if initiated too late in the decline of the birds, particularly for species whose reproductive success declines with increasing edge habitat, which is a common symptom of anthropogenic fragmentation. However, the "depth" of the predation pit may be assumed to depend on habitat heterogeneity, because predators may lose interest in the rare prey and switch to alternative species (if available) in a complex landscape with much more refuge than in a homogenous landscape with little refuge. If this is the case, habitat restoration may yet play a role in increasing prey populations after they have fallen into a predation pit. Furthermore, increasing refuge may reduce the risk of Allee effects (i.e. the correlation or dependence of [mean] individual fitness to population size or density) and extinction of prey populations in cases when predators have a type I or type II functional response (Gascoigne & Lipcius 2004).

### Nonconsumptive Effects

Habitat is not the only mechanism controlling the distribution of prey species, and there have been other works advocating for how trophic interactions could be considered in ecosystem restoration (Fraser et al. 2015). Nonconsumptive effects occur when predators influence the behavior, physiology, or life history of prey species and can create what is termed a "landscape of fear," in which the distribution of animals is constrained by the invisible but very real influence of predators on the decisions of prey species (Laundré et al. 2010). For example, Thomson et al. (2006) found that Pied flycatchers (*Ficedula hypoleuca*) preferentially occupied, and had the largest clutch sizes in, nest boxes at intermediate distances from predatory sparrowhawk nests, demonstrating how there can be more to habitat quality than the physical structure alone. Living in the presence of predators may induce a stress response, another nonconsumptive effect that can distract energy and reduce growth or reproduction (Sheriff et al. 2009), but animals may compensate by adjusting spatial or temporal activity as demonstrated by Kohl et al. (2018).

## Discussion

We develop a hypothesis in this paper that habitat modulates the relationship between predators and prey. It follows that the loss of quality or quantity of habitats can be an underlying mechanism or aggravating factor in predator–prey conflicts. The role of habitat in ecosystem interactions is not novel, but there are important advances in our ability to directly observe, quantify, and test the role of habitat that have made a significant contribution to understanding how this dynamic is shaped in nature (Gable et al. 2020; Dickie et al. 2022). We describe habitat as a force that shapes animal phenotypes, a feature that protects them from being vulnerable, a relief that buffers the efficiency of their predators, and a mosaic that supports a community of diverse prey sources for predators. These four aspects of habitat are all critical to understanding how the physical landscape can intervene and mediate the interactions between predators and prey. Moreover, many conservation efforts are focused on single species, and an increased understanding of the habitat requirements of both predator and prey is crucial to mitigate human–wildlife conflicts. We argue that humans can play a direct or indirect role in mediating the interactions between predators and prey through (1) actions that cause habitat loss or degradation, (2) habitat management and conservation, and (3) habitat restoration.

We are in the early phases of the UN Decade for Ecosystem Restoration. Although the Decade has been critiqued for being "just about planting trees" (lots of trees), more focused restoration actions that strategically target key habitat features and consider both habitat structure and function are essential for achieving restoration success (Banks-Leite et al. 2020). Effective habitat restoration requires complexity, including physical heterogeneity that creates shelter, microhabitats, and allows co-existence of predators and a diverse prey community (Palmer et al. 2010). Restoration already considers the community and ecosystem contexts that habitat needs to serve, but how habitat plays a role in the relationships among species and the demographic tables of animals can be more thoroughly studied and applied to enhance restoration efforts. As such, it is important to recognize that restoration should not focus on the needs of single species (Lindenmayer et al. 2002). Restoration must also focus on environmental design that creates sufficient quality habitat to buffer the synergistic risks of ecological traps that can emerge from restoration, such as aggregation of fish in thermal refugia where they are more vulnerable to predation (Sullivan et al. 2023). Moreover, restoration must race against evolutionary clocks because predator–prey relationships evolve over long time scales, whereas habitat is being altered much too rapidly for these relationships to keep pace.

As much as our position provides some insights into the role of habitat in predator–prey dynamics, this paper also revealed some new questions that can be asked and a lack of a thorough understanding of the limits of habitat in mediating predator–prey interactions. Research should expand in this area to attempt to: (1) determine how habitat restoration drives evolution of prey phenotypes; (2) quantify the effects of shelter on prey demography and predation rates before and after restoration; (3) identify how restoration alters the cost of predation for predators; (4) assess whether restored habitats may form ecological traps in a fragmented landscape; (5) ask under which conditions habitat restoration may reduce the risk or severity of Allee effects and predation pits; and (6) evaluate the effect of habitat restoration and conservation in situations where predators target both an invasive species and its native competitors. Ultimately, more manipulative work that adopts an ecosystem (habitat restoration and conservation) approach to address human–wildlife conflicts has the potential not only to de-escalate some (but not all) conflicts, but could be an actionable alternative to removing predators, which is generally counterproductive (Lennox et al. 2018) for achieving long-term success. Efforts including co-production, where scientists, community members, and other relevant actors work together to define research questions, secure funding, collect data, and interpret results, must be adopted to generate mutual understanding, engage in respectful knowledge exchange, and build trust across interest groups working toward protection and restoration of habitat, species interactions, and biodiversity (Metzger et al. 2017). It may well be that a consistent approach will require a combination of interventions that includes habitat restoration as part of an integrated strategy to overcome challenging conflicts that threaten conservation and biodiversity objectives.

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