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Patchy indirect effects of predation: predators contribute to landscape heterogeneity and ecosystem function via localized pathways

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Predators are widely recognized for their irreplaceable roles in influencing the abundance and traits of lower trophic levels. Predators also have irreplaceable roles in shaping community interactions and ecological processes via highly localized pathways (i.e. effects with well-defined and measurable spatio–temporal boundaries), irrespective of their influence on prey density or behavior. We synthesized empirical and theoretical research describing how predators – particularly medium- and large-sized carnivores – have indirect ecological effects confined to discrete landscape patches, processes we have termed 'patchy indirect effects (PIEs) of predation'. Predators generate PIEs via three main localized pathways: generating and distributing prey carcasses, creating ecological hotspots by concentrating nutrients derived from prey, and killing ecosystem engineers that create patches. In each pathway, the indirect effects are limited to discrete areas with measurable spatial and temporal boundaries (i.e. patches). Our synthesis reveals the diverse and complex ways that predators indirectly affect other species via patches, ranging from mediating scavenger interactions to influencing parasite/disease transmission risk, and from altering ecosystem biogeochemistry to facilitating local biodiversity. We provide basic guidelines on how these effects can be quantified at the patch and landscape scales, and discuss how predator-mediated patches ultimately contribute to landscape heterogeneity and ecosystem functioning. Whereas density- and trait-mediated indirect effects of predation generally occur through population-scale

Synthesis

Understanding the role of predation in ecosystems is key to the research, conservation, and management of predators. We synthesized the many ways predators drive landscape heterogeneity via the creation, and sometimes the prevention, of ecological hotspots within ecosystems. The indirect effects of predators on ecosystem dynamics through population-level changes to prey abundance or behavior are widely recognized, but we show how predators also have "patchy indirect effects" on other species via patch-scale pathways with ecosystem-level consequences. This concept moves us toward a more holistic view of predation by providing a multi-scale perspective on the importance of predators to functioning ecosystems.

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changes, PIEs of predation occur through individual- and patch-level pathways. Our synthesis provides a more holistic view of the functional role of predation in ecosystems by addressing how predators create patchy landscapes via localized pathways, in addition to influencing the abundance and behavior of lower trophic levels.

Keywords: density-mediated indirect effects, ecosystem engineering, nutrient cycling, predator–prey interactions, trait-mediated indirect effects, trophic cascade

Introduction

Predators are important contributors to ecosystem structure and function through consumptive (Glossary) and non-consumptive effects (Ripple et al. 2014). Consumptive effects occur when predators have a lethal effect on lower trophic levels. If predation rates are high enough to affect the abundance (density) of lower trophic levels, this top–down limitation may then have cascading, indirect effects on other species (i.e. density-mediated indirect effects; Paine 1980, Carpenter et al. 1985, Polis et al. 2000, Terborgh and Estes 2010); for example, predators can alter plant communities through top–down control of herbivores (Estes and Palmisano 1974), or influence predation rates on other prey by limiting subordinate predator density (Elmhagen et al. 2010, Levi and Wilmers 2012). Non-consumptive effects occur through non-lethal changes in prey traits, broadly categorized as predation-risk effects (Creel and Christianson 2008, Peacor et al. 2020). Predation risk elicits changes in flexible prey traits such as foraging preferences or space use (Lima and Dill 1990, Lima 1998) that, in turn, indirectly affect other species (i.e. trait-mediated indirect effects; Abrams et al. 1996). Predators are typically assumed to alter ecosystem structure and function primarily through density- and trait-mediated indirect effects, which have both been well-documented and synthesized in the literature (Lima 1998, Schmitz et al. 2000, Werner and Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005, Ripple et al. 2014, Say-Sallaz et al. 2019, Wirsing et al. 2021). However, there is growing recognition predators can have outsized ecological effects via additional mechanistic pathways (Bump et al. 2009a, Schmitz et al. 2010, Gable et al. 2020, Monk and Schmitz 2022).

One such pathway is the redistribution of nutrients by predators through their movements. Many animals – herbivores and carnivores alike – act as mobile links that connect separate habitats/ecosystems through their movement (Lundberg and Moberg 2003). These movements help maintain ecosystem function and resilience through processes like dispersal, migration, and nutrient transportation (Polis et al. 1997, McCann et al. 2005, Bauer and Hoye 2014, Doughty et al. 2016, Schlägel et al. 2020). Recent work has demonstrated that mobile links are a key component of meta-ecosystem dynamics (Massol et al. 2011) – a conceptual framework concerned with studying the flow of energy and organic material among ecosystems (Loreau et al. 2003, Leroux and Loreau 2008, Gounand et al. 2018). Ellis-Soto et al. (2021) showed that the meta-ecosystem framework provides a useful roadmap for studying animal-transported nutrient dynamics, as it allows researchers to examine how landscape attributes and animal movement traits interact to influence spatiotemporal patterns of nutrient deposition. Although these concepts can be applied to the many species that act as nutrient vectors (Schmitz et al. 2018, McInturf et al. 2019, Subalusky and Post 2019, Schmitz and Leroux 2020), predators are particularly important vectors because they transport resource subsidies high in limiting nutrients (e.g. calcium, nitrogen, phosphorous) (Schmitz et al. 2010, Monk and Schmitz 2022). When predators transport these limiting nutrients into concentrated locations, they can create biogeochemical hotspots on the landscape (Gharajehdaghipour et al. 2016, de Miranda et al. 2023). Notably, these predator-mediated nutrient patches occur separate from whether or not predators alter the density or traits of prey.

Here, we synthesize the diverse ways predators indirectly affect ecosystems in a localized manner by creating or altering patches on the landscape – processes we term patchy indirect effects (PIEs) of predation. We define PIEs as *indirect consumptive effects of predation that are restricted to landscape patches with measurable spatial and temporal boundaries*. Although the term patch may be defined differently depending on the scale or system of interest (Leibold et al. 2004), we define patch here as a discrete microsite that contrasts with the surrounding landscape matrix.

We begin our synthesis by providing an overview of the three main pathways by which predators have PIEs within ecosystems: 1) creating and distributing carcasses across the landscape, 2) creating biogeochemical hotspots by repeatedly transporting nutrients derived from prey to discrete areas, and 3) by killing ecosystem engineers that create patches. For each pathway, we synthesize numerous examples from empirical studies, and provide a case study that collectively demonstrate how each pathway indirectly affects other species, irrespective of changes to the density or traits of lower trophic levels. We then provide some guidance on how to quantify the effects of each pathway at the patch and landscape scales, provide predictions about when and where PIEs are likely to be relatively more or less important, and finally discuss how our synthesis provides a more holistic view of the functional role of predation in ecosystems. Our synthesis focuses on predators of medium and large body size because the patches they create/interact with are larger, but the concepts can be extended to smaller species. Although our synthesis is embedded within theoretical concepts, we also summarize empirical research that highlights the variety and complexity of ways predators influence ecosystem dynamics via localized pathways.

Carcass pathway: prey carcasses are ephemeral ecological hotspots

Carrion is an essential yet often-overlooked ecosystem component that drives myriad inter-specific interactions between predators, scavengers, and local invertebrate, plant and soil communities (DeVault et al. 2003, Wilson and Wolkovich 2011, Barton et al. 2013a, 2019). And predators, particularly large carnivores, play a key role in generating carrion within ecosystems through predation (Box 1).

Predators positively affect a wide range of scavengers by provisioning carrion (Moleón et al. 2014, Pereira et al. 2014), a resource subsidy many species rely upon as an important (and sometimes essential) food resource (Prugh and Sivy 2020). Carcasses may become sites of 'fatal attraction' (Sivy et al. 2017) where smaller scavengers are killed by larger animals while competing for the same carcass. Ephemeral landscapes of fear and disgust may establish around carcasses as well (Moleón and Sánchez-Zapata 2021, Newsome et al. 2021): smaller animals may be at risk of predation and thus avoid carcasses to reduce fatal encounters with larger scavengers ('landscape of fear'; Cunningham et al. 2018), while other species may avoid carcasses to prevent parasitism and infection risk ('landscape of disgust'; Buck et al. 2018, Muñoz-Lozano et al. 2019). Opportunistic scavengers attracted to carcasses may even kill other prey near carcasses (Cortés-Avizanda et al. 2009a, b, Spencer et al. 2021).

Prey carcasses release a pulse of nutrients into the soil that affect local invertebrate, soil, and plant communities. Individual invertebrates are larger and invertebrate assemblages are different at carcasses compared to adjacent areas (Barton et al. 2013b). High arthropod abundance may in turn attract other species to carcasses (Moreno-Opo and Margalida 2013, Morris and Bump 2020). While flesh remains on carcasses, invertebrates, particularly fly larvae and beetles (Coleoptera), play a key role in converting flesh into nutrients (e.g. nitrogen, phosphorous) and regulating the rate these nutrients are delivered to belowground communities (Ilardi et al. 2021). Consequently, as carcasses putrefy, the biogeochemistry of soils under carcasses change (Keenan et al. 2018). This nutrient influx is readily taken up by fungi, microbes, and plants, resulting in unique species compositions at carcass sites (Bump et al. 2009b, Barton et al. 2016, Risch et al. 2020). Changes in phosphorous concentration and plant composition may persist for a long time and leave distinct patches decades after carcass decomposition (Danell et al. 2002, Bump et al. 2009b, Barton et al. 2016). Because most studies evaluating carcass effects on soils, plants and invertebrates come from experimentally-placed carcasses rather than depredated animals (Bump et al. 2009a, Barry et al. 2019, Risch et al. 2020), expanding research on the similarities and differences between carcasses created through predation vs other mortality sources will be beneficial for understanding when and how prey carcasses uniquely alter ecosystems (Bump et al. 2009a, Ellis-Soto et al. 2021).

The ecological importance of individual prey carcasses does not necessarily depend on whether the traits or population density of the prey are substantially altered by the predator. Rather, individual predation events can produce important PIEs at each kill site. Carcasses are continuously deposited within ecosystems through numerous sources of mortality (e.g. disease, starvation, human hunting), but predators distinctively influence the timing, spatial distribution, and rates of carcass deposition (Wilmers et al. 2003b, Ellis-Soto et al. 2021). Indeed, predators help stabilize carrion abundance in ecosystems by reducing the temporal variation of carrion (Wilmers and Getz 2004), which may even buffer the effects of climate change on scavengers (Wilmers and Getz 2005). On Isle Royale, carcasses of moose *Alces alces* killed by wolves *Canis lupus* were deposited in some areas up to 12× more often than other areas (Bump et al. 2009a), creating heterogeneity in the distribution of carcass-mediated effects across the landscape.

The unique spatiotemporal distribution of prey carcasses implies that predators drive landscape heterogeneity from the top–down (Wilmers et al. 2003a, Bump et al. 2009a, Schmitz et al. 2010, Monk and Schmitz 2022). However, environmental characteristics also have an influence on the spatiotemporal distribution of prey carcasses. Landscape features such as topography influence spatial patterns of predation risk (Gaynor et al. 2019), whereas phenological drivers like vegetation green-up can influence the spatiotemporal distribution of prey (Merkle et al. 2016). Ultimately, these environmental characteristics help shape when and where prey are killed (Kauffman et al. 2007), and, consequently, all of the PIEs associated with prey carcasses. From a meta-ecosystem perspective, prey carcasses can be viewed as predator-mediated nutrient inputs influenced by environmental conditions. These nutrient inputs, in turn, indirectly affect both above- and below-ground communities in unique spatiotemporal patterns.

Nutrient accumulation pathway: predators create biogeochemical hotspots by concentrating prey-derived nutrients into patches

As discussed earlier, animals are important nutrient vectors because they often deposit nutrients at different rates, locations, and directions (i.e. against natural gradients) than passive resource subsidy sources (McInturf et al. 2019, Subalusky and Post 2019). When predators concentrate nutrients derived from prey remains (prey-derived nutrients) into certain areas, they can generate biogeochemical hotspots with PIEs on other species.

Predator home sites (i.e. where predators raise offspring) often become biogeochemical hotspots (Box 2). Adults repeatedly bring prey remains to home sites to provision offspring, and as breeding seasons progress the accumulation of prey remains, coupled with excrement from the predators, increases nutrient content around home sites. For instance, nutrient concentrations are elevated within top soils under ground-nesting eagle owl *Bubo bubo* nests, enhancing grass

Box 1. Case study: the ecological importance of puma-killed carcasses

Pumas *Puma concolor* are apex predators with the widest geographic range of any terrestrial mammal in the Western Hemisphere. They have an important ecological role by regulating prey density, affecting prey behavior through predation risk, and generating carrion (LaBarge et al. 2022). Pumas predominantly kill large ungulates but because pumas are solitary predators it often takes them a long time to fully consume prey, which means other scavengers may have time to locate and respond to puma-killed carcasses. Indeed, a greater diversity of scavengers are found at puma kills than from any other predator studied (Elbroch et al. 2017), which often results in complex interspecific interactions at kill sites.

Pumas face direct competition at carcasses from other dominant scavengers, i.e. wolves and bears (Fig. 1B), which may result in fatal encounters or force pumas to abandon their kills. Kleptoparasitism by black bears *Ursus americanus* can occur often enough that pumas increase their kill rates to compensate for food losses (Elbroch et al. 2015a, Allen et al. 2021), thereby increasing carcass availability. Smaller scavengers tend to exhibit species-specific responses to kill sites. Some species, like coyotes *Canis latrans*, incur both costs and benefits by interacting with puma kills. In Oregon, USA, coyotes scavenged nearly every puma kill, resulting in high diet overlap between coyotes and pumas (Ruprecht et al. 2021). Coyotes showed a strong response in their space use towards kill sites, but they avoided pumas to presumably reduce fatal encounters; pumas killed ~ 23% of the coyote population annually (Ruprecht et al. 2021). Other species such as bobcats *Lynx rufus* and birds show more limited responses to puma-killed carcasses (Allen et al. 2015, Ruprecht et al. 2021), whereas red fox *Vulpes vulpes* responses vary depending on the season (O'Malley et al. 2018). In South America, puma-killed carcasses subsidize and help structure sex-specific dietary partitioning of Andean condors *Vultur gryphus* (Perrig et al. 2017, Barceló et al. 2022), scavengers that preferentially feed on carcasses in low vegetation and flat areas to reduce predation risk from other predators near kill sites (Perrig et al. 2022).

Puma-killed carcasses provide a unique, ephemeral habitat for beetles. Relative to control sites, puma-killed carcasses support a greater abundance, species richness, and diversity of beetles (Fig. 1C) (Barry et al. 2019). Carcasses also release limiting nutrients into soils (Fig. 1D), leading to greater nitrogen concentrations in soils and plants at puma kill sites relative to control areas (Peziol et al. 2023). Landscape-scale biogeochemical effects of puma-killed carcasses were quantified by multiplying individual kill rates by puma density, concluding that pumas contribute 44.1 kg of carrion per km^2 annually (Peziol et al. 2023). Puma-killed carcasses thus represent a comprehensive example of how predators can generate PIEs via the carcass pathway by influencing spatiotemporal interactions among scavengers and facilitating local plant, invertebrate and soil communities.

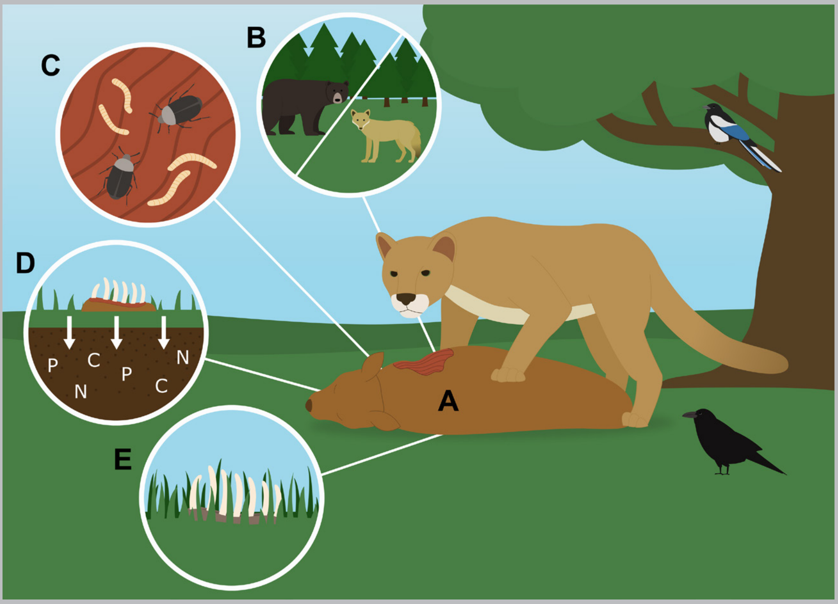

Figure 1. Patchy indirect effects (PIEs) that occur at puma-killed carcasses. Once a puma makes a kill (A), scavengers like corvids, bears, and coyotes may quickly respond to the carcass site (B). Since pumas often cache their prey, unique beetle communities develop on carcasses (C). As the carcasses decompose, nutrients like carbon, nitrogen, and phosphorous leach into the soil (D), which increases soil nutrient content and enhances plant growth in the immediate vicinity as the carcass decomposes entirely (E).

Box 2. Case study: Arctic fox dens are ecological hotspots on the tundra

Arctic foxes give birth during spring while the tundra is still covered in snow and ice, which restricts their ability to excavate new dens. They instead re-use the same dens for decades – even centuries – to raise pups (Macpherson 1969). For instance, in Manitoba, Canada, Arctic foxes re-use the same dens year after year presumably because suitable den sites are restricted to elevated beach ridges that are easy to excavate and prevent the den from flooding during snowmelt (Johnson-Bice et al. 2023). As foxes repeatedly occupy the dens, the decay of accumulated prey remains and fox excrement increases soil nutrient concentration and plant production (Smith et al. 1992, Gharajehdaghipour et al. 2016), resulting in nutritionally enriched, and locally diverse, plant communities on Arctic fox dens (Bruun et al. 2005, Fafard et al. 2020). Throughout much of the Arctic, Arctic fox dens are characterized with lush, atypical vegetation that stands in stark contrast to the surrounding landscape (Fig. 2A), earning them the nickname 'gardens of the tundra.' Arctic fox dens are large enough that the productivity and phenology of den vegetation can be studied from satellite imagery (Johnson-Bice et al. 2023).

Wildlife from across the tundra are attracted to Arctic fox dens for both food and shelter. Predators and scavengers are detected far more frequently on Arctic fox dens than similar tundra areas (Zhao et al. 2022), likely attracted by the prey remains found on dens. Indeed, numerous species have been observed consuming or removing prey remains from Arctic fox dens including ravens *Corvus corax*, eagles (*Haliaeetus* spp.), sandhill cranes *Antigone canadensis*, and polar bears *Ursus maritimus* (Fig. 2C–E; Mallory 1987, Zhao et al. 2022). Caribou *Rangifer tarandus* also visit Arctic fox dens twice as often as reference sites, likely to forage on the enhanced vegetation (Fig. 2F; Zhao et al. 2022). Perhaps counterintuitively, Arctic fox dens even attract their main prey, lemmings. Tall vegetation on dens traps snow and provides suitable winter habitat for lemmings (Gharajehdaghipour and Roth 2018). Observations of greater wildlife occurrence at fox dens relative to comparable areas suggests that these other animals adjust their space use toward den sites across the landscape. When wildlife visit Arctic fox dens they may also excrete nutrients at or near the dens (Fig. 2B), creating a positive feedback that further enriches den sites. Through both direct (provisioning prey remains) and indirect (vegetation changes from nutrient deposition) pathways, Arctic fox dens have substantial PIEs on other tundra species that are spatially constrained by landscape characteristics.

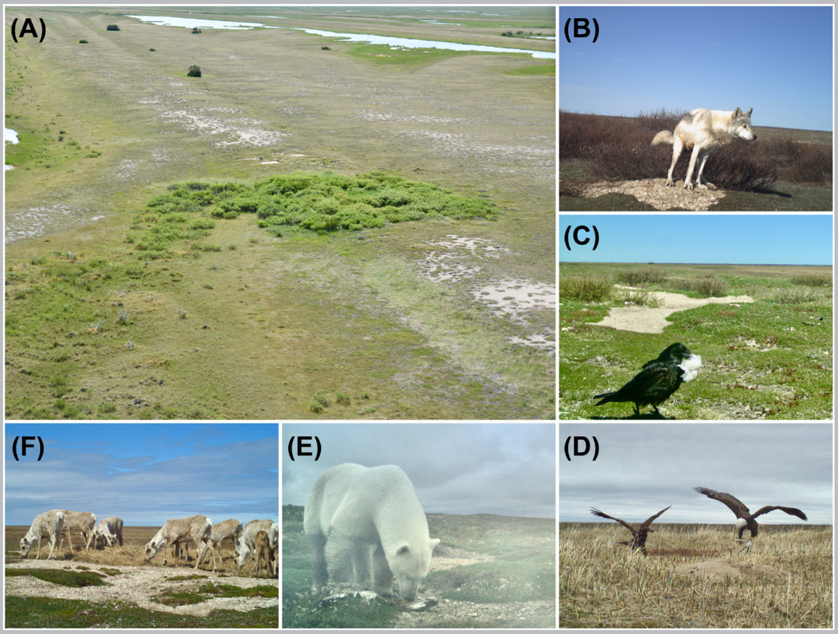

Figure 2. A collection of photos from Arctic fox dens near Churchill, Manitoba, Canada. Arctic fox dens are distinct biogeochemical patches with lush vegetation that stands out prominently on the tundra (A). (B)–(F) are all photos taken with remote cameras placed on Arctic fox dens: a wolf defecating on a fox den (B), a raven stealing feathers from a goose carcass off a den (C), a juvenile and adult bald eagle sparring over prey remains from a den (D), a polar bear consuming prey remains on a den (E), and a small group of caribou foraging on a den in late spring (F).

seedling growth (Fedriani et al. 2015). Home sites perennially used by predators may have long-lasting PIEs. Red fox *Vulpes vulpes* dens in the subarctic are used for decades or longer, resulting in greater nutrient concentrations at den sites (Lang et al. 2021) and greater annual growth and reproductive output of nearby mast-seeding trees (Kucheravy et al. 2021, Lang et al. 2022). Some PIEs associated with predator home sites may be due to disturbance behavior (e.g. burrowing activities; Kurek et al. 2014, Gharajehdaghipour et al. 2016, Lang et al. 2021), but experiments could disentangle the relative influence prey-derived nutrients and bioturbation have on generating biogeochemical hotspots.

Predators that socialize or breed in aggregations can alter local environments by transporting huge quantities of prey-derived nutrients into localized areas, often coupling separate ecosystems in the process. Seals and other marine mammals aggregate in haul-outs on land and concentrate marine prey-derived nutrients via excretion and transported prey (Fariña et al. 2003), which can influence terrestrial herbivore space use and foraging dynamics by enriching vegetation near the haul-outs (McLoughlin et al. 2016). In Antarctic ecosystems, nutrients around seal haul-outs and penguin colonies drive the abundance and richness of terrestrial plants and invertebrates (Bokhorst et al. 2019). Many seabirds, through colonial nesting, transform terrestrial ecosystems by depositing marine nutrients in and around their colonies (Polis and Hurd 1996, Clyde et al. 2021). Studies evaluating the disruption of seabird-mediated nutrients by other predators have revealed the extent to which seabird colonies affect island ecosystems (Croll et al. 2005, Fukami et al. 2006, Maron et al. 2006, Towns et al. 2009, Graham et al. 2018, Benkwitt et al. 2021). Prey-derived nutrients from seabird colonies can, in turn, subsidize fish (Benkwitt et al. 2019), mangrove (Adame et al. 2015), and coral communities (Lorrain et al. 2017) in marine habitats in the colony's immediate vicinity through runoff.

Predators also create nutrient patches through localized, repeated activities like scent-marking. Arctic foxes *Vulpes lagopus* repeatedly scent-mark to demark territory boundaries, creating a string of conspicuous vegetative 'islands' on the tundra (Goltsman et al. 2005). River otters *Lutra canadensis* are semi-aquatic predators that transport nutrients from aquatic prey onto land through scent-marking behavior (i.e. latrines). Soil and plant nutrient content and plant growth are greater at latrines than control sites (Ben-David et al. 1998, Crait and Ben-David 2007), but variation in the frequency otters use latrines creates heterogeneity in their relative importance (Ben-David et al. 2005). Predator latrines also concentrate parasites, which can indirectly affect other animals. For instance, parasite-vulnerable species avoid raccoon *Procyon lotor* latrines but disease-tolerant species are attracted to them (Weinstein et al. 2018).

Repeatedly-used predator resting and foraging sites may also generate PIEs. In coral reef systems, schooling fish concentrate nutrients derived from prey *off* the reef into patches *on* the reef, which enhances coral growth and promotes grazing by herbivorous fish (Shantz et al. 2015). Studies have also demonstrated plant productivity is greater under common seabird perches (Powell et al. 1991, Herbert and Fourqurean 2008). Perhaps the best-known example of PIEs from predator foraging comes from salmonid systems: bears, in particular, are key predators that create biogeochemical hotspots along streams by transporting salmon-derived nutrients onto land (Helfield and Naiman 2006, Levi et al. 2020). Bear-transported salmon, in turn, benefit riparian soils (Holtgrieve et al. 2009), invertebrates (Hocking and Reimchen 2006), and plants, including enhancing the growth of old-growth conifers (Reimchen and Fox 2013).

The distinguishing characteristic between patches generated from prey carcasses and patches generated from nutrient accumulation is that in the latter pathway predators deposit the nutrients at different sites from where prey are killed. Moreover, PIEs from the carcass pathway occur through individual predation events whereas effects via nutrient transport occur through frequent, repeated nutrient deposits that have compounding effects. Relative to carcasses, patches created from nutrient accumulations also tend to be larger and have spatiotemporal boundaries that may be more challenging to delineate. For instance, prey-derived nutrients may be detected hundreds of meters from predator colonies (Bokhorst et al. 2019, Benkwitt et al. 2021). Nonetheless, the effects from these ecological hotspots are still limited in space and time and occur largely independently of prey density or behavior.

Predator movement and resource selection traits are the primary drivers of the spatiotemporal distribution of patches generated via nutrient accumulation. Predators transport prey-derived nutrients from one site to another, the location of which is often influenced by environmental characteristics: coastal topography influences the site selection of marine mammal haul-outs and seabird colonies, tree availability influences roosting sites, and habitat characteristics influence predator home site selection. Thus, the nutrient accumulation pathway demonstrates how predator behavior and movements work in tandem to link donor and recipient nutrient sites, and ultimately influence where patches are created.

Ecosystem engineer removal pathway: predators alter ecosystems by killing ecosystem engineers that create and maintain patches

Ecosystem engineers are organisms that influence the availability of resources to other species by physically modifying their environment (Jones et al. 1994). Ecosystem engineers can be found throughout most biomes on earth and they exhibit considerable variation in the magnitude of their ecological impact (Hastings et al. 2007). Although some engineering species have more diffuse ecological effects, engineers that build structures or create patches indirectly affect other species in a localized manner. For instance, termites build mounds and underground cavities that indirectly affect soil microbiota communities, nutrient cycling, and vegetative production at mound sites (Dangerfield et al. 1998, Jouquet et al. 2011). Some birds build large, perennially used nests (e.g. eagles) that can become biodiversity hotspots (Maciorowski et al. 2021). Despite the fact that most ecosystem engineering species occupy mid-trophic levels (Coggan et al. 2018), surprisingly few studies have evaluated how predators indirectly affect other species by hunting ecosystem engineer prey.

We draw upon what few studies have been conducted on predator–ecosystem engineer interactions to suggest that predators have PIEs on ecosystems by killing ecosystem engineers that create and maintain patches. The effects follow a logical succession: 1) engineers create and maintain patches that indirectly affect organisms, 2) predators remove the engineer(s), resulting in no animals left to maintain patch functionality, and 3) over time the ecological effects of the engineered patch diminish and the environment reverts to its pre-engineered state. In these scenarios, predators have PIEs limited to the spatial boundaries of the engineered patch and the length of time it takes for the environment to recover at the patch site.

One empirical example of this pathway comes from mound-building ants (*Atta* sp.). *Atta* are leaf-cutter ants that build huge nest mounds (up to 250 m^2) that affect surrounding plant assemblages and soil characteristics (Corrêa et al. 2010, Meyer et al. 2013). Armadillos *Dasypus novemcinctus* and army ants *Nomamyrmex esenbeckii* are both predators of *Atta* colonies capable of destroying young and mature colonies (Rao 2000, Powell and Clark 2004). Although more often recognized for their top-down control of *Atta* population density (Terborgh et al. 2001), predators that destroy these colonies also alter the manner in which the colony mounds affect other species by initiating the mounds' return to their pre-engineered state. Strong evidence that predators generate PIEs by killing ecosystem engineers comes from a case study on wolf predation of dispersing beavers *Castor canadensis*, whereby wolves directly affect beaver pond dynamics and indirectly affect the wide variety of species that thrive in beaver-altered environments (Gable et al. 2020, detailed in Box 3).

Few studies have directly evaluated the indirect effects of predator–ecosystem engineer interactions (Sanders and Van Veen 2011, Dunoyer et al. 2020), making it difficult to estimate how frequently predators alter ecosystems by killing engineers. However, we suggest it likely occurs anywhere predators kill patch-creating ecosystem engineers. The lack of examples is likely not a reflection of the frequency that this pathway occurs in nature but rather the amount of research on predator-ecosystem engineer dynamics.

The ecological implications of predator–ecosystem engineer dynamics are best understood from the engineer's perspective. Because patches created by engineers often persist beyond the death of the engineer, engineered patches go through periods of occupation, abandonment, and recolonization that are influenced by population dynamics of the engineers and the rate(s) of decay/recovery of the patches (Wright et al. 2004). Thus, the processes underlying engineered patch dynamics – mortality, immigration, persistence – are similar in many ways to metapopulation or source–sink dynamics (Fryxell 2001). At a landscape perspective, these demographic and ecological processes lead to a mosaic of patches at various stages of occupation/abandonment that increase heterogeneity (Remillard et al. 1987). This process parallels the classic patch dynamics concept from landscape ecology whereby disturbance events drive heterogeneity (Bormann and Likens 1979, Pickett and White 1985). Although evaluations of ecosystem engineer-patch dynamics rarely incorporate predation into their models, predators will be inherently linked to the dynamics of engineered patches and all effects associated with the patches when predation is a substantial source of mortality for the engineer populations.

Predicting where and when patchy indirect effects are important

We can make some general predictions about the relative importance of PIEs in ecosystems based on patch size and density/frequency, predator community dynamics, and ecosystem productivity. Here, we define importance generally to represent the relative magnitude of the PIEs, or the capacity for the resultant patch to affect ecological processes of interest.

First, logically, larger patches or patches with long-lasting effects are going to be more ecologically important, relatively speaking, than smaller or shorter-lasting patches (Fig. 4). Consider the disparity in ecological effects from small vs large predator-killed carcasses. Smaller carcasses have less carrion, which may be quickly consumed by scavengers and, in turn, have reduced effects on plants due to fewer nutrients leaching into soils. This size difference is likely, in part, why predator-killed roe deer *Capreolus caprelous* (20–30 kg mass) have no detectable effects on soil or plants (Teurlings et al. 2020) but predator-killed large ungulates do (Bump et al. 2009a, Risch et al. 2020, Peziol et al. 2023). Second, the relative ecological importance of PIEs in an ecosystem will often be related to their density and frequency on the landscape. Patches that occur more frequently are likely more important from a cumulative, landscape–scale perspective (Fig. 4). For example, the greater the density of predator-created biogeochemical hotspots, the greater the likelihood that these patches influence ecosystem dynamics. Similarly, despite the small size of salmon carcasses, they can have large effects on ecosystems because they occur in such large numbers (Helfield and Naiman 2001, 2006, Holtgrieve et al. 2009). Third, ecosystems that support greater predator diversity likely support a greater diversity of PIEs (Fig. 4). In ecosystems with diverse predator guilds, interspecific competition for prey may cause dietary (Elbroch et al. 2015b) or spatial partitioning (Vanak et al. 2013), which likely affects the spatiotemporal patterns of PIEs (i.e. variation in carcass type and kill site locations). Finally, ecosystem productivity and rates of ecosystem recovery and turnover likely also influence the

Box 3. Case study: wolves alter ecosystems by killing pond-creating beavers

Beavers are renowned ecosystem engineers that create and maintain ponds by constructing dams. Beaver ponds alter the hydrologic, geomorphic and vegetative characteristics around the dammed site (Naiman et al. 1988), providing numerous ecological benefits to plant, fish, amphibian, reptile and mammal species (Rosell et al. 2005, Brazier et al. 2021).

In the Greater Voyageurs Ecosystem (GVE) in Minnesota, USA, wolves have an outsized effect by altering the creation and recolonization of ponds by killing dispersing beavers (Gable et al. 2020). Juvenile beavers typically disperse during spring and establish a new colony by either constructing a new pond, or recolonizing an abandoned pond by repairing an old dam (Fig. 3A). When wolves kill a beaver in the process of creating or recolonizing a pond, the pond fails to persist into the fall (Gable et al. 2020). Occupancy rates of 'wolf-altered' ponds are substantially lower compared to reference ponds in the same year the predation event occurs (0 versus 84%), and there is some evidence that indicates these effects may last for several years (Gable et al. 2020). Thus, wolves, by killing dispersing beavers, directly alter the ecological trajectory and fate of individual ponds, indirectly affecting other species that benefit from beaver-altered environments. To date, there is no evidence that wolf predation limits beaver abundance in this system (Gable and Windels 2018, Johnson-Bice et al. 2021). Instead, wolves appear to be a top–down force that influences the spatial distribution and temporal occupancy of beaver ponds, rather than the number of ponds (Gable et al. 2020).

Put differently, the broader-scale effects of wolf predation on beavers are not mediated through changes in beaver density, but rather through changes in individual ponds distributed across the landscape. Like other engineered patch types, beaver ponds go through periods of occupation and abandonment, resulting in a mosaic of ponds at different ecological states that increases landscape heterogeneity and promotes ecosystem resilience (Remillard et al. 1987, Johnson-Bice et al. 2022). As a force influencing the spatiotemporal distribution of ponds, wolves are thus connected to this landscape mosaic. Using data on wolf density and kill rates, beaver dispersal, and the number of ponds maintained per beaver colony, Gable et al. (2020) estimated wolves alter the fate of 88 ponds annually (95% CI: 36–162). Considering ~ 120 ponds are created annually in the study area (Johnson-Bice et al. unpubl.), wolf predation appears to be an important influence of broader beaver pond dynamics (though individual variation in kill rates of beavers means there is likely intraspecific variation in how wolves affect pond dynamics; Bump et al. 2022). Because wolves and beavers co-occur across a large portion of the Northern Hemisphere, this mechanism is likely widespread (Gable et al. 2018). And although wolves are the dominant predator of beavers, there is little reason to suspect this mechanism is unique to wolves as a variety of other large predators such as pumas, bears, coyotes and lynx also kill beavers (Kertson et al. 2011, Lowrey et al. 2016, Gable et al. 2018).

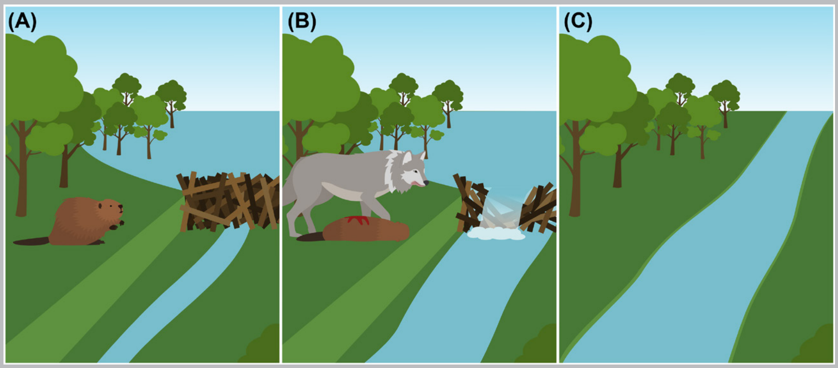

Figure 3. Dramatic representation of PIEs that occur within riparian ecosystems when predators kill dispersing beavers. Juvenile beavers disperse and create a new pond or recolonize an old pond (A). When a predator kills the dispersing beaver, the dam and pond begin to degrade over time (B). Eventually the dam may collapse, causing the riparian site to revert to its pre-engineered state (C).

magnitude of PIEs (Fig. 4). PIEs in ecosystems with slower recovery and turnover rates will have greater relative ecological importance compared to ecosystems with faster recovery and turnover rates. In general, the effects of above-ground animals on nutrient cycling are expected to be more pronounced in environments with abiotic constraints on nutrient cycling (Malhi et al. 2022). For instance, seabird-transported nutrient subsidies have a weaker relative impact on local terrestrial communities in highly-productive, tropical islands compared to high-latitude islands (Steibl et al. 2021), whereas prey carcasses can affect plants on the Arctic tundra for a decade or more (Danell et al. 2002).

These general factors (patch size, frequency/density, diversity, and ecosystem productivity) may have context-dependent

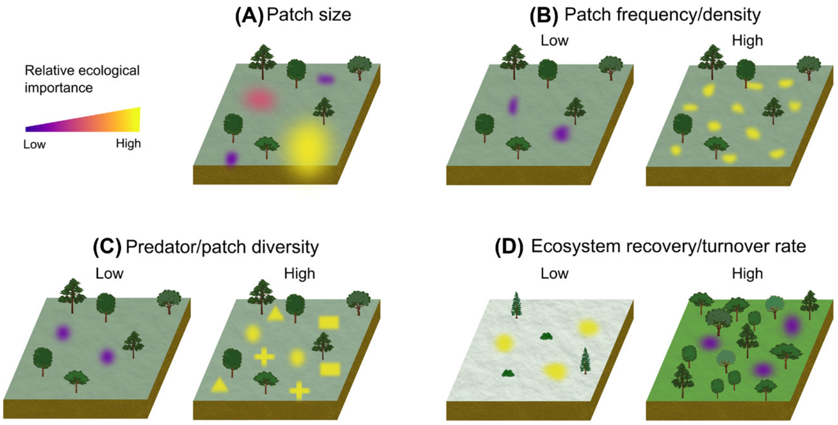

Figure 4. Conceptual diagram of ecological conditions that may influence the relative magnitude or ecological importance of patchy indirect effects (PIEs) of predation in ecosystems. Larger patches will generally have a larger ecological impact than smaller patches (A). Similarly, from a cumulative, ecosystem-level perspective, predator-altered patches that occur more frequently in time or space should be relatively more important than infrequent patches (B). Ecosystems that support a greater diversity of predators should likewise support a greater diversity of PIEs (e.g. unique spatial patterns of home sites and carcasses) (C). Finally, PIEs should be relatively more important in ecosystems that have a slow recovery or turnover rate (e.g. Arctic tundra) because the effects will generally persist longer in these ecosystems (D).

effects within any given system. For example, patches that occur at a low density in tundra ecosystems could have a greater capacity to influence other species than patches that occur frequently in tropical forest ecosystems due to the predicted longevity of effects in ecosystems with low recovery/turnover rates. Ultimately, what we may identify as relatively more/less important will depend on the question and system of interest – are we interested in understanding conditions that predict the importance of prey carcasses for scavenger dynamics, or conditions that predict the importance of prey carcasses for soil and plant species? These conditions may or may not be the same. We expect considerable variation in how the general factors mentioned earlier affect PIEs, often depending on the question, scale, and system of interest.

Finally, although PIEs are better studied and likely more common in terrestrial ecosystems, we contend this mechanism has often been overlooked in aquatic ecosystems. From a nutrient deposition standpoint, PIEs are likely more important for terrestrial ecosystems because nutrients can get distributed widely by water in aquatic ecosystems (Monk and Schmitz 2022). Nonetheless, PIEs are probably more common than assumed in aquatic ecosystems, particularly when predators kill large marine mammals. For instance, hundreds of vertebrate scavengers may respond to, and benefit from, large whale carcasses killed by orcas *Orcinus orca* (Totterdell et al. 2022), before the carcasses fall to the sea floor where a unique scavenger community awaits (Roman et al. 2014). Orcas will also sometimes cache whale carcasses along the sea floor, providing carrion for benthic and even terrestrial scavengers when pieces of the carcass wash ashore (Barrett-Lennard et al. 2011). Though not yet extensively examined, we predict depredated marine mammals are distributed in different spatiotemporal patterns compared to other sources of mortality, similar to depredated carcasses in terrestrial ecosystems.

Quantifying patchy indirect effects of predation at local and landscape scales

Here, we provide some approaches for quantifying PIEs of predation at both local and landscape scales. There is considerable variation and flexibility in the methods available to researchers depending on the system, but our point in illustrating numerous examples here is to demonstrate the efficacy and feasibility of quantifying PIEs of predation at multiple scales.

Quantifying PIEs at the local (patch) scale is relatively straightforward since, by our definition, the indirect effects are generally constrained within patch boundaries. A paired reference-treatment approach is often the most effective method for delineating the patch boundary and quantifying effects at this scale (Ellis-Soto et al. 2021), particularly for patches created via the carcass and nutrient accumulation pathways. Reference sites can be paired adjacent to the patch, ideally matching characteristics between the sites to be better able to attribute any differences to the predator(s). For instance, invertebrate and plant characteristics can be directly compared at a carcass or nutrient accumulation patch with nearby reference sites (Ben-David et al. 1998, Bump et al. 2009b, Barton et al. 2016, Gharajehdaghipour et al. 2016, Barry et al. 2019). Alternatively, quantitative models based on the characteristics of carcass or nutrient patches could be used to generate reference locations matching the nutrient patch characteristics for comparison (Johnson-Bice et al. 2023). Manipulative experiments or remotely sensed trail cameras can be used to evaluate food web-related effects that occur in and around patches (Cortés-Avizanda et al. 2009a, Ruprecht et al. 2021, Spencer et al. 2021, Zhao et al. 2022). Similarly, remote cameras can be used to estimate rates of nutrient accumulation by recording the rate, type, and quantity of prey remains brought to and concentrated at specific locations (de Miranda et al. 2023).

Knowledge about the ecology of predator–prey interactions is needed to quantify the landscape-scale effects of patches created through carcass deposition. The number of carcasses generated for each prey species in a system can be estimated by multiplying predator kill rates (prey killed/predator/unit time) by predator density to yield per capita carcass density estimates (carcasses/km^2/unit time) (Barton et al. 2019, Morant et al. 2022). Prey density estimates may also be needed to estimate large-scale prey carcass abundance if predator kill rates vary based on prey abundance (Vucetich et al. 2002, Morant et al. 2022). The amount of carrion available to scavengers can be estimated by multiplying carcass density by the average proportion of carcasses left by predators (Allen et al. 2015, Prugh and Sivy 2020, Peziol et al. 2023). Through time, carcass deposition patterns can provide spatially explicit estimates of areas that receive higher/lower nutrient inputs (Bump et al. 2009a, Ellis-Soto et al. 2021, Peziol et al. 2023 for methods and detailed examples), including insight on how environmental features influence spatiotemporal patterns of carcass deposition.

Information and methods needed to quantify the landscape-scale effects of patches created through the nutrient accumulation pathway depend on the patch type of interest. Surveys are likely one of the easiest ways to quantify home site density. For instance, census survey methods have been used to quantify Arctic fox den density (Johnson-Bice et al. 2023), and thus the landscape–scale impact fox denning behavior has on other tundra species. If predator home sites (or colonies, haul-outs) vary in size, these size-dependent effects can be accounted for when quantifying their broader scale impact (Bokhorst et al. 2019). Individual-based data collection methods can also be used to estimate patch density at the landscape scale if predator density is known (e.g. num. latrines per individual × individuals km^{-2}). For instance, biologging devices can be used to identify scent-marking and foraging behaviors (Bidder et al. 2020, Clermont et al. 2021), which, when combined with location data, may be used to identify and quantify nutrient deposition hotspots. With knowledge of the rate of nutrient deposition at each nutrient hotspot (e.g. g/m^2/unit time of nitrogen), estimates of the landscape-scale magnitude of predator nutrient deposition can be quantified (Ellis-Soto et al. 2021).

Measuring patch-scale effects from the ecosystem engineer removal pathway – if they occur at all – is more challenging, since the natural periods of occupation, abandonment, and recolonization of patches by other engineers obscures the effects of direct predation. After a predator kills an engineer, it may be difficult to determine whether changes to the patch are a direct result of predation as opposed to alternative explanations. Consider possible scenarios that may occur after a predator kills a dispersing beaver: if a second beaver occupies the affected pond shortly after the first beaver dies, then the predation event had little ecological effect. Despite the simple chain of events (predator kills engineer, engineered patch changes), careful study designs are needed to demonstrate predators cause any changes to the engineered patch.

One general approach that may be useful is to repeatedly monitor patches affected by the predator (i.e. where predators kill engineers) and also reference patches that provide baseline information on the occupancy dynamics of engineer-created patches (Gable et al. 2020). The approach involves: 1) identifying predation events where predators killed engineers that occupied or were creating a patch, 2) documenting how each patch was or was not changed by other engineers after predation, 3) identifying reference patches to assess expected conditions at patches if engineers were not killed and 4) comparing differences between reference and predator-altered patches. Any meaningful differences could then be plausibly attributed to predators. Researchers could also experimentally simulate ‘predation events’ on the engineer prey via non-lethal methods, such as removing or translocating engineers, and compare ecological patterns at the manipulated patches versus reference patches. Depending on the species or systems of interest, there may be other approaches that are simpler or more appropriate for similar evaluations.

Gauging the landscape-scale effects of predator–engineer interactions is similarly difficult. As discussed earlier, occupancy dynamics of engineered patches are influenced by both patch characteristics and the demography of the engineer. Specifically, not all engineers are successful in creating patches and/or the engineer(s) may be responsible for +/− one patch per individual. These factors (engineer mortality, patch creation/recolonization rate, and the number of patches affected per engineer) affect landscape-scale patch dynamics (Wright et al. 2004), and must be accounted for. Individual-based designs that assess both the creation and recolonization of patches, and the proportion of engineer mortality due to predation, can reveal these landscape-scale effects. Alternatively, Gable et al. (2020) demonstrated the feasibility of quantifying landscape-scale effects using a predator-centric study design by combining data on predator density, kill rates of engineers, and data on the engineered patch dynamics. Generalizing the approach from Gable et al. (2020), we can estimate the number of patches (P) predators affect:

$$P = N_{\text{pred}} \times \text{KR}_{\text{pred}} \times P_{\text{established}} \times P_{\text{individual}} \times P_{\text{occupancy}} \qquad (1)$$

where N_{pred} is the number (or density) of predators, KR_{pred} is the kill rate of engineers, $P_{\text{established}}$ is the proportion of engineers that successfully establish patches, $P_{\text{individual}}$ is the number of patches established per engineer and $P_{\text{occupancy}}$ is natural occupancy rate, all measured over a time period of interest. Together, these metrics account for the proportion (or number) of patches predators affect in relation to the occupancy dynamics of the engineered patch mosaic.

Perhaps the most straightforward method to assess large-scale predator–engineer dynamics is to use a paired approach that compares patch dynamics in similar landscapes with and without predators (or before and after predator introduction). However, this approach is likely most feasible for systems where the engineered patches are small and easy to monitor. The take-home message is that because engineered patch dynamics are affected by the ecology and movements of engineers themselves, resolving the role predators play is difficult and requires study designs that can decompose the relative influence of predators and engineers.

By quantifying PIEs at both the local and landscape scales, researchers can obtain not only a more thorough and multi-scale perspective of predators' impacts on ecosystems, but this process can also help identify larger spatiotemporal patterns of PIEs. For instance, several studies have demonstrated that patches of enhanced vegetation created through predator-mediated nutrient deposition can affect the foraging dynamics and space use of herbivores at larger spatial scales (Shantz et al. 2015, McLoughlin et al. 2016, Zhao et al. 2022). Landscape (or spatial) heterogeneity is widely recognized as a key driver of numerous ecological patterns and processes, including species biodiversity and richness (Tews et al. 2004 Stein et al. 2014), space use and dispersal patterns (Gustafson and Gardner 1996, Pyke et al. 1977, Avgar et al. 2013, Davies et al. 2021), and the dynamics and persistence of populations (Hanski 1999). Research efforts that quantify predator-mediated landscape heterogeneity will further elucidate the unique role predators play in these broader ecological processes that help govern ecosystem structure and function.

Interaction, co-occurrence, and distinction of patchy, density-mediated and trait-mediated mechanisms

PIEs are a distinct mechanism from density- or trait-mediated mechanisms because 1) they do not require predators to substantially alter the population density or behavior of prey and 2) they are limited to the spatial and temporal boundaries of the created patch (carcass pathway, nutrient accumulation pathway) or affected patch (engineer removal pathway). This does not mean the mechanisms cannot co-occur in predator–prey systems, as is often the case with density- and trait-mediated indirect effects (DMIEs and TMIEs) (Peacor and Werner 2001, Werner and Peacor 2003, Preisser et al. 2005, Pruett and Weissburg 2021).

Consider predator–prey systems where predators influence the spatial distribution of their prey. In these systems, predation risk (a non-consumptive/trait-mediated mechanism) alters the spatial (and likely spatiotemporal) distribution of where prey congregate on the landscape. As a consequence of the altered prey distribution, when predators kill these prey the resulting carcass locations will have, in turn, been influenced by non-consumptive mechanisms that altered the prey's distribution in the first place. Thus, there is an interaction (or feedback) between patchy and trait-mediated mechanisms that occurs within these predator–prey systems. Moreover, when predators affect the abundance of their prey, there will be a similar feedback between the predators' effects on prey density and the number of carcasses generated (lower density of prey, lower density of carcasses).

We can see evidence of the co-occurrence and interaction of these mechanisms in a system like Yellowstone National Park. Wolves in Yellowstone affected both the population density (Peterson et al. 2014, Metz et al. 2020) and, to a lesser degree, space use of elk *Cervus canadensis* (Kohl et al. 2018, Cusack et al. 2019), which has had a weak but measurable cascading effect on tree recruitment (DMIEs and TMIEs; Brice et al. 2022). But wolf-killed elk carcasses also have PIEs on local plant and soil communities separate from DMIEs and TMIEs (Risch et al. 2020); the number and location of these carcasses are nonetheless influenced by wolves' ability to alter the traits and regulate the abundance of elk. Similarly, expanding on our earlier example of how predators have PIEs by destroying leaf-cutter ant (*Atta* sp.) colonies, predators may also have co-occurring DMIEs by reducing *Atta* colony abundance, thereby preventing the transformation of tropical forest communities through their herbivory (Terborgh et al. 2001). Thus, although PIEs are a distinct mechanism by which predators alter ecosystems, they certainly can operate simultaneously and in tandem with density and trait-mediated mechanisms.

Distinguishing between PIEs, DMIEs and TMIEs requires examining the indirect effects of the predator–prey interaction(s), identifying the mechanism(s) that led to the effects, and defining the scale (spatial and temporal) of interest. For instance, although indirect non-consumptive effects of predation may be confined to the boundaries of a patch, these effects are not PIEs. In the Andes, puma predation risk influences the diel migration patterns of vicuñas *Vicugna vicugna*, resulting in patches of nutrients in the lower-risk areas (Monk et al. 2023). Although these nutrients are spatially confined, the mechanism shaping the spatial patterning of nutrient deposition – predation risk – would fall under the umbrella of TMIEs because it is non-consumptive (expanded in greater detail in Monk and Schmitz 2022). In a system where predators limit the abundance of patch-creating ecosystem engineers (e.g. the *Atta* leafcutter system described above), distinguishing between PIES and DMIEs may depend upon viewing these effects at different spatial scales. Density-mediated mechanisms may influence the density of patches on the landscape, whereas patchy mechanisms drive the indirect effects on other species at the patch scale. If there are characteristics of individual patches created by engineers that make these patches more/less prone to being affected by predators, then we could reasonably conclude density-mediated mechanisms have a greater influence on the total number of patches but patchy mechanisms influence the spatial distribution of patches through variation in the susceptibility of each patch being affected by the predator(s).

These examples demonstrate how, in many ways, disentangling the relative effects of patchy, density-mediated, and trait-mediated mechanisms is challenging in natural systems, and may require approaching the same question from different angles. We do not see this difficulty of distinguishing between the various predator-mediated mechanisms as a weakness, but rather as an accurate reflection that indirect effects resulting from predator–prey dynamics within natural systems are often complex, nuanced, and may not fall neatly within our pre-defined categories.

Concluding remarks

Through our synthesis and case studies, we demonstrated the diverse ways predators indirectly affect other species via highly localized pathways limited to the boundaries of a patch – whether the patch is a carcass, a homesite or latrine, or a patch created by ecosystem engineer prey. The carcass distribution and nutrient accumulation pathways have been previously discussed both empirically and theoretically (Schmitz et al. 2010, Leroux and Schmitz 2015, Schmitz and Leroux 2020, Ellis-Soto et al. 2021, Newsome et al. 2021, Monk and Schmitz 2022), which helped lay the foundation for part of our synthesis. However, these previous studies have largely focused either on just one pathway (Newsome et al. 2021) or on the nutrient cycling/deposition aspects of the pathways (Schmitz et al. 2010, Monk and Schmitz 2022), and thus do not account for the multitude of other interspecific interactions and indirect effects that occur at these patches (e.g. scavenger interactions, opportunistic predation, parasite risk/transmission).

Our synthesis builds upon this previous body of work by defining and linking together all of these different ways predators affect ecosystem dynamics via a unifying element, a discrete *patch*. We provided examples of PIEs that spanned a wide diversity of taxa and ecological disciplines – studies on mammalian, avian, invertebrate, and fish predators that incorporated elements from plant and soil ecology, behavioral ecology, spatial ecology and food web dynamics. We offered explicit predictions of when and where these patches are likely to be important, and provided numerous different approaches researchers could take to quantify PIEs of predation at both the patch and landscape scales. Although most of the research on these topics (and thus the examples we provided) are biased towards large terrestrial mammals in the Northern Hemisphere, by providing specific terminology for these processes (*PIEs of predation*) we hope that the concepts discussed here will be more broadly recognized and appreciated.

As predator populations decline globally (Estes et al. 2011, Ripple et al. 2014), there is a need for a broader, more holistic understanding of the functional roles of predators in order to manage and conserve their populations – actions that can have wider benefits for the ecosystems they inhabit (Sergio et al. 2014, Natsukawa and Sergio 2022). To date, the justification for conserving, managing, and reintroducing predators frequently hinges on their ability to influence ecosystems through changes to the abundance and traits of lower trophic levels at the population scale (i.e. density- and trait-mediated indirect effects; Sergio et al. 2008, Ritchie et al. 2012, Blossey and Hare 2022). However, our synthesis demonstrates predators also have important ecological effects that function at the individual or patch scale regardless of whether the predator(s) substantially affect prey populations. We have clearly shown that predators, through PIEs, have *irreplaceable ecological roles within ecosystems that influence nutrient cycling, community interactions, local species biodiversity, and myriad other ecological processes that ultimately increase landscape heterogeneity and contribute to ecosystem functioning*. Predators' ability to create patchy landscapes through these localized pathways adds to the growing evidence that they affect ecosystem structure and function in ways that are not easily replicated by humans (Lennox et al. 2022). We therefore see the PIEs concept as a step towards a unified view of predation in ecosystems by providing a spatially-explicit, multi-scale perspective of how predators affect ecosystems through patch-scale pathways. Considerable theoretical and empirical research has demonstrated that ecological patterns and processes can vary or be linked across multiple spatial scales (Levin 1992), and our synthesis demonstrates that predation is yet another ecological process that can be better understood through this multi-scale perspective.

Glossary

Carrion: the decaying flesh of dead animals

Consumptive effects: lethal effects of predators on their prey due to predation mortality

Density-mediated indirect effects: indirect effects of predation on other species that are mediated through reducing the population density of prey (or subordinate predators)

Ecosystem engineer: organisms that alter the flow of resources for other species through physical modifications of their environment

Ecosystem recovery rate: the rate at which an ecosystem returns to its pre-disturbance state following disturbance

Ecosystem turnover rate: the rate at which nutrients or other variables of interest flow through ecosystems

Meta-ecosystem theory: a theoretical framework centered around understanding how ecosystems are connected by spatial flows of organisms, organic matter, and nutrients across ecosystem boundaries

Mobile links: actively moving organisms that connect habitats and ecosystems in space and time

Non-consumptive effects: nonlethal effects of predation due to changes in prey behavior or other flexible prey traits in response to predation risk

Patchy indirect effects: indirect consumptive effects of predation on other species that are restricted to landscape patches with measurable spatial and temporal boundaries

Predation-risk effects: effects of predation risk on prey or other species that arise due to changes in flexible prey traits

Resource subsidy: energy resources transported from a donor habitat by either natural gradients (such as gravity, ocean currents; passive subsidy) or vectors (such as animals, humans; active subsidy), which alters the dynamics of a consumer in the recipient habitat

Trait-mediated indirect effects: indirect effects of predators on other species that are mediated through altering the behavior or other flexible traits of prey (or subordinate predators)

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Author contributions

Sean M. Johnson-Bice: Conceptualization (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Thomas D. Gable**: Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **James D. Roth**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Joseph K. Bump**: Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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