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

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Abstract

Predators are widely recognized for their irreplaceable roles regulating the abundance and altering the traits of lower trophic levels. Predators also have irreplaceable roles in shaping community interactions and ecological processes via highly localized pathways, irrespective of their influence on prey density or behavior. We synthesized empirical and theoretical research describing how predators have indirect ecological effects confined to discrete patches on the landscape, processes we have termed patchy indirect effects of predation. Predators generate patchy indirect effects via three main pathways: generating and distributing prey carcasses, creating biogeochemical hotspots by concentrating nutrients derived from prey, and killing ecosystem engineers that create patches. In each pathway, the indirect ecological 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 discrete patches, ranging from mediating scavenger interactions to interspecific parasite/disease transmission risk, and from altering ecosystem biogeochemistry to facilitating local species biodiversity. We also show how existing multi-scale ecological frameworks (metapopulation, meta-ecosystem, and patch dynamics concepts) offer insight into the mechanisms underlying the formation of these patches within ecosystems. We then provide basic guidelines on how these effects can be quantified at both the patch and landscape scales, and discuss how these predator-mediated patches ultimately increase landscape heterogeneity and contribute to ecosystem functioning. Whereas density- and trait-mediated indirect effects of predation generally occur through population-scale changes, patchy indirect effects 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.

Introduction

Predators are important contributors to ecosystem structure and function through **consumptive** (see 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**; (Carpenter et al. 1985; Hoeks et al. 2020; Paine 1980; Polis et al. 2000; Ripple et al. 2016; Terborgh & Estes 2010); for example, predators can structure plant communities through top-down control of herbivore populations (Estes & Palmisano 1974), or influence predation rates on other prey through top-down control of subordinate predators (Elmhagen et al. 2010; Levi & Wilmers 2012). Non-consumptive effects (Creel & Christianson 2008; Peacor et al. 2020). The risk (or fear) of predation elicits changes in flexible prey traits (e.g., foraging preferences, space usage; (Lima 1998; Lima & Dill 1990)

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 (e.g., (Lima 1998; Peacor et al. 2022; Preisser et al. 2005; Ripple et al. 2014; Say-Sallaz et al. 2019; Schmitz et al. 2000; Schmitz et al. 2004; Werner & Peacor 2003; Wirsing et al. 2021; Wootton 1994). However, there is growing recognition predators can have outsized ecological effects on ecosystems via additional mechanistic pathways (Bump et al. 2009a; Gable et al. 2020; Monk & Schmitz 2022; Schmitz et al. 2010).

Here, we synthesize the diverse ways that predators indirectly affect ecosystem dynamics in a highly-localized manner by creating or altering discrete patches on the landscape—processes we have termed **patchy indirect effects** (PIEs) of predation. We define PIEs as *indirect 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 metapopulation, metacommunity, and meta-ecosystem concepts – the conceptual framework(s) that allow us to understand the mechanisms underlying the formation and larger ecological implications of PIEs of predation. We then provide a detailed 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 detailed case study that collectively demonstrate how each pathway indirectly affects other species, irrespective of whether the density or traits of lower trophic levels are altered. 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 ecologically important, and finally discuss how our synthesis provides a more holistic view of the functional role of predation in ecosystems. Although our synthesis is embedded within theoretical concepts, we focus on summarizing empirical research that highlights the variety and complexity of ways predators influence ecosystem dynamics via localized pathways.

Frameworks for multi-scale ecological effects

Considerable theoretical and empirical research has demonstrated that ecological patterns and processes can vary or be linked across multiple spatial scales (Levin 1992). Although much of the original theoretical work focused on the assumption that populations, communities, and ecosystems are isolated from one another, it is now widely recognized that, in fact, they are often interconnected and exhibit important spatial properties (Leibold et al. 2004; Loreau & Holt 2004). Metapopulation theory posits that disconnected populations of a species are linked through dispersal events (immigration, emigration), which directly influence the probability of persistence or extinction of each population (Hanski 1998). The metacommunity concept extends this general theoretical approach to whole communities, whereby metacommunities consist of communities linked by the dispersal of multiple interacting species (Leibold et al. 2004). The combined effects of organismal dispersal and environmental heterogeneity, in turn, shape multi-scale patterns of species coexistence and biodiversity (Holyoak et al. 2005). Meta-ecosystem theory takes an even broader approach: it is concerned with the spatial coupling of ecosystems linked by the movement of species and organic matter (nutrients), and how environmental conditions (e.g., topography) influence these movements (Gounand et al. 2018; Leroux & Loreau 2008; Loreau et al. 2003). Notably, a major component of meta-ecosystem theory is that the spatial scales at which organisms and nutrients flow across and through ecosystems are flexible and often variable (Gounand et al. 2018). Although these conceptual frameworks focus on different levels of organization and spatial scales, they are linked by the common notion that movement and environmental conditions collectively shape multi-scale ecological dynamics.

Recent work has extended these concepts, particularly meta-ecosystem theory, towards understanding how

animals play a key role in generating landscape heterogeneity through the deposition of nutrients. Metaecosystem theory originally focused on understanding how existing environmental features regulate spatial nutrient flows (e.g., how rivers transport nutrients into recipient aquatic ecosystems) (Loreau et al. 2003), but there is now widespread appreciation that animals are also important nutrient vectors and regulators of ecosystem biogeochemistry (McInturf et al. 2019; Schmitz & Leroux 2020; Schmitz et al. 2018; Subalusky & Post 2019). Ellis-Soto, Ferraro et al. (2021) demonstrated the meta-ecosystem concept could be used to quantify animal-transported nutrients within ecosystems by examining how landscape structure influences animal movement ecology and the associated nutrient deposition patterns resulting from these movements. Monk and Schmitz (2022) provided an additional perspective on how predators influence ecosystem spatial biogeochemistry through both consumptive and non-consumptive mechanisms. Collectively, this previous body of work examining the importance of multi-scale ecological effects to landscape heterogeneity and ecosystem function provides the theoretical foundation for quantifying and describing the ecological importance of PIEs of predation. The next three sections provide detailed overviews and in-depth case studies of each pathway, and how each pathway relates to current multi-scale ecological frameworks.

Carcass pathway: prey carcasses are ephemeral ecological hotspots

Carrion is an essential vet often-overlooked ecosystem component that drives a myriad of inter-specific interactions between predators, scavengers, and local invertebrate, plant, and soil communities (Barton et al. 2013a; 2019; DeVault et al. 2003; Wilson & Wolkovich 2011). And predators, particularly large carnivores, play a key role in generating carrient within ecosystems through predation. Predators positively affect scavengers by provisioning carrion, a **resource subsidy** many species rely upon as an important (and sometimes essential) food resource ((Prugh & Sivy 2020). The nutritional value of carrier attracts a wide range of competitive scavengers (Moleón et al. 2014; Pereira et al. 2014). 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 & Sánchez-Zapata 2021; Newsome et al. 2021): smaller animals may be at risk for predation and thus avoid carcasses to reduce fatal encounters with larger scavengers ("landscape of fear"; (Cunningham et al. 2018; Frank et al. 2020), 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 in the carcass vicinity (Cortés-Avizanda et al. 2009a; Cortés-Avizanda et al. 2009b; Spencer et al. 2021). This web of trophic interactions is further influenced by seasonality (Peers et al. 2020), scavenger and carrier abundance (Mellard et al. 2021), and scavenger guild traits (Sebastián-González et al. 2021), highlighting the complex yet important role carrier plays in vertebrate community dynamics.

Prey carcasses release a pulse of nutrients into the surrounding soil that affect local invertebrate, soil, and plant communities. While flesh remains on carcasses, invertebrates, particularly fly larvae and beetles (Coleoptera), play a key role in converting flesh into nutrients. Individual invertebrates are larger and invertebrate assemblages are different at carcass sites compared to adjacent areas (Barton et al. 2013b). High arthropod abundance may in turn attract other species such as passerine birds to carcasses (Moreno-Opo & Margalida 2013; Morris & Bump 2020). Recent research suggests beetles even regulate the rate nutrients are delivered to below ground communities (Ilardi et al. 2021). As carcasses putrefy, limiting nutrients such as nitrogen and phosphorous discharge into the soil, substantially changing soil biogeochemistry relative to pre-carcass conditions (Keenan et al. 2018). The nutrient influx is readily taken up by fungi, microbes, and plants, resulting in unique species compositions at carcass sites (Barton et al. 2016; Bump et al. 2009b; Risch et al. 2020). Although soil nitrogen concentration may return to background levels within a few years, changes in phosphorous concentration and plant composition may last longer (Barton et al. 2016; Bump et al. 2009b) and leave distinct patches decades after carcass decomposition (Danell et al. 2002; Towne 2000). Most studies evaluating carcass effects on soils, plants, and invertebrates come from experimentally placed carcasses rather than depredated animals (but see (Barry et al. 2019; Bump et al. 2009a; Risch et al. 2020). Expanded research exploring the similarities and differences between carcasses created through predation vs.

other mortality sources will be beneficial for understanding when and how predator-killed 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 uniquely influence the timing, spatial distribution, and rates that carcasses are deposited (Ellis-Soto et al. 2021; Wilmers et al. 2003b). Indeed, predators help stabilize carrion abundance in ecosystems by reducing the temporal variation of carrion (Wilmers & Getz 2004), which may even buffer the effects of climate change on scavengers (Wilmers & Getz 2005). On Isle Royale, moose (*Alces alces*) carcasses killed by wolves (*Canis lupus*) were deposited in some areas up to 12x more often than other areas (Bump et al. 2009a).

The unique spatiotemporal distribution of prey carcasses implies that predators drive landscape heterogeneity from the top-down (Bump et al. 2009a; Monk & Schmitz 2022; Schmitz et al. 2010; Wilmers et al. 2003a). 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.

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 (Sunquist & Sunquist 2002). They play numerous roles within ecosystems, including regulating prey density, affecting prey behavior through fear, and generating carrion (LaBarge et al. 2022). Pumas predominantly kill large ungulates but because pumas are solitary predators they require more time to consume large prey relative to social apex predators. The slower rate of carcass use means other scavengers have more time to locate and respond to puma-killed carcasses: a greater diversity of scavengers are found at puma-killed carcasses than from any other predator studied (Elbroch et al. 2017), which often results in complex interspecific interactions at puma kill sites.

Pumas face direct competition at carcasses from other dominant scavengers, i.e., wolves and bears (Fig. 1B), which may result in fatal interspecific encounters or force pumas to abandon their kills. Kleptoparasitism by black bears (*Ursus americanus*) can occur frequently enough that pumas must increase their kill rates to compensate for food losses (Allen et al. 2021; Elbroch et al. 2015a), thereby potentially increasing prey carcass availability. Smaller scavengers tend to exhibit species-specific responses to kill sites. Some species, like coyotes (*C. latrans*), incur both costs and benefits from interactions at puma-killed carcasses. In Oregon, USA, coyotes scavenged nearly every puma kill, resulting in remarkable diet overlap between coyotes and pumas (Ruprecht et al. 2021). Although coyotes adjusted their space use towards kill sites, they actively 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 help structure sex-specific dietary partitioning of Andean condors (*Vultur gryphus*) by providing a source of vegetation from the stomachs of killed prey to the obligate scavengers (Barceló 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 2020). 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.

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

As discussed earlier, animals are important nutrient vectors that often deposit nutrients at different rates, locations, and directions (i.e., against natural gradients) than passive resource subsidy sources (McInturf et al. 2019; Subalusky & Post 2019). Predators are particularly important subsidy vectors because they transport prey remains high in limiting nutrients (e.g., calcium, nitrogen, phosphorous) (Monk & Schmitz 2022; Schmitz et al. 2010). When predators concentrate nutrients derived from prey remains (prey-derived nutrients) into certain areas, they can generate biogeochemical hotspots with patchy indirect effects (PIEs) on other species.

Predator home sites (where predators raise offspring; e.g., dens, nests) often become biogeochemical hotspots through the steady accumulation of prey-derived nutrients. Adults repeatedly bring prey remains to home sites to provision their offspring, and as breeding seasons progress the accumulation of prey remains, coupled with excrement produced by the predators, increases soil nutrient content around home sites. For instance, nutrient concentrations are elevated within top soils under ground-nesting eagle owl (*Bubo bubo*) nests, enhancing grass 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; (Gharajehdaghipour et al. 2016; Kurek et al. 2014; 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 different ecosystems in the process. Seals and other marine mammals aggregate in haul-outs on land and concentrate marine prey-derived nutrients via excretion and transporting prey remains (Fariña et al. 2003), which can influence the foraging dynamics of terrestrial herbivores 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 concentrating marine nutrients in and around their colonies (Anderson & Polis 1999; Clyde et al. 2021; Polis & Hurd 1996). Studies evaluating the disruption of seabird-mediated nutrients by other predators have revealed the importance and extent to which seabird colonies affect island ecosystems (Benkwitt et al. 2021; Croll et al. 2005; Fukami et al. 2006; Graham et al. 2018; Maron et al. 2006; Towns et al. 2009). Prey-derived nutrients from these 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 aquatically-derived nutrients onto land by consistently scent-marking locations with urine and feces (i.e., latrines). Soil and plant nutrient concentration and plant growth are greater at otter latrines than control sites (Ben-David et al. 1998; Crait & Ben-David 2007), but variation in the frequency that otters use latrines creates heterogeneity in their relative ecological importance (Ben-David et al. 2005). Predator latrines also concentrate parasites, which can indirectly affect other animals. For instance, parasite-vulnerable species like birds and some small mammals avoid raccoon (*Procyon lotor*) latrines, while

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 prey-derived nutrients from *off* the reef into patches *on* the reef, which enhances coral growth and promotes grazing by herbivorous fishes (Shantz et al. 2015). Experimental studies have also demonstrated plant productivity is greater under common seabird perches (Herbert & Fourqurean 2008; Powell et al. 1991). Perhaps the best-known example of PIEs created through predator foraging comes from salmonid systems: black and brown bears (*U. arctos*), in particular, are key predators that generate biogeochemical hotspots along streams by transporting salmon-derived nutrients onto land (Helfield & Naiman 2006; Levi et al. 2020). Bear-transported salmon nutrients, in turn, benefit riparian soils (Holtgrieve et al. 2009), invertebrates (Hocking & Reimchen 2006), and plants (Helfield & Naiman 2001), including enhancing the growth of ecologically valuable old-growth conifers (Reimchen & Arbellay 2019; Reimchen & 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 the nutrient transport pathway occur through frequent, repeated nutrient deposition in a localized area that has compounding effects on local communities. 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, marine prey-derived nutrients may be detected hundreds of meters from the edges of predator colonies (Benkwitt et al. 2021; Bokhorst et al. 2019). Nonetheless, the ecological effects from these biogeochemical hotspots are patchy because the effects are limited in space and time and they 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 the nutrient accumulation pathway. Predators transport prey-derived nutrients from one site to another, the location of which is often influenced by environmental characteristics: coastal topography influences site selection characteristics of marine mammal haul-outs and seabird colonies, tree availability influences roosting site selection, and habitat characteristics influence predator home site selection. Meta-ecosystem theory provides a useful framework for understanding how landscape features and predator behavior and movement ecology work in tandem to link donor and recipient nutrient sites, and ultimately influence where patches are created via recurring nutrient deposition.

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

Arctic foxes are top predators throughout the circumpolar tundra. While they are well-known for their influence on prey population dynamics, Arctic foxes also have outsized effects on tundra communities by creating biogeochemical hotspots via their denning activity.

Arctic foxes give birth during spring while the tundra is still covered in snow and ice, which restricts their ability to excavate new dens and leads them to re-use the same dens for decades—even centuries—to raise pups (Macpherson 1969). For instance, in northeastern Manitoba, Arctic foxes re-use the same dens year after year presumably because suitable den sites are restricted to elevated, sandy beach ridges that are easy to excavate and promote water drainage during snowmelt to prevent the den from flooding (Johnson-Bice et al. 2022b). As foxes repeatedly occupy the dens, the decay of accumulated prey remains and fox excrement increases soil nutrient concentration (nitrogen, phosphorous) at dens (Gharajehdaghipour et al. 2016; Smith et al. 1992), which is advantageous to local plants; vegetative production on fox dens can be nearly three times greater than nearby control sites (Gharajehdaghipour et al. 2016). Moreover, plant composition on Arctic fox dens is unique for the area, which facilitates species richness and biodiversity (Bruun et al. 2005; Fafard et al. 2020). Throughout many parts of the Arctic, well-established Arctic fox dens have lush patches of enriched, atypical vegetation that stand in stark contrast to the surrounding barren 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. 2022b).

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 compared to similar tundra areas (Zhao et al. 2022), likely attracted by the prey remains littered on dens. Indeed, numerous species have been observed consuming or removing prey remains from Arctic fox dens including gulls (*Larus* spp.), ravens (*Corvus corax*), eagles (*Haliaeetus* spp.), sandhill cranes (*Antigone canadensis*), and polar bears (*Ursus maritimus*) (Fig. 2C-E; (Mallory 1987; Stempniewicz & Iliszko 2010; Zhao et al. 2022). Caribou (*Rangifer tarandus*) also visit Arctic fox dens twice as often as reference sites, likely to forage on the enhanced den 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 & Roth 2018). 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 by functioning as ecological hotspots, the locations of which are constrained by landscape characteristics.

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; Wright & Jones 2006). Ecosystem engineers can be found throughout most biomes on earth and they exhibit considerable variation in the spatial and temporal magnitude of their ecological impact (Hastings et al. 2007). Although some engineering species have more diffuse effects on ecosystem dynamics (e.g., crayfish bioturbation effects on water sedimentation; (Statzner et al. 2003), 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 (see (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 m²) that affect surrounding plant assemblages and soil characteristics (Corrêa et al. 2010; Meyer et al. 2013). Armadillos (Dasypus novemcinctus) and army ants (Nomamyrmexesenbeckii) are both predators of Atta colonies capable of destroying young and mature colonies. 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 the creation, recolonization, and spatial distribution of beaver ponds and indirectly affect the wide variety of species that thrive in beaver-altered environments (Gable et al. 2020), detailed in the next section). Few studies have directly evaluated the indirect effects of predator-ecosystem engineer interactions (but see (Dunoyer et al. 2020; Sanders & Van Veen 2011), making it difficult to estimate how frequently predators alter ecosystems by killing engineers. However, given that the pathway is straightforward, 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 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 ecosystem 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 (e.g., mortality, immigration) of the engineers and the rate(s) of decay/recovery of the patches (Wright et al. 2004). In other words, engineered patches are abandoned when resources around the patch are depleted or when the engineer(s) die, and they are recolonized through dispersal/immigration once the resources recover or when a vacant patch becomes available. Thus, the processes underlying engineered patch dynamics-mortality, immigration, persistence-are similar in many ways to metapopulation dynamics (Fryxell 2001). When viewing engineered patches from a landscape perspective, these demographic and ecological processes lead to a mosaic of patches at various stages of occupation/abandonment that increase heterogeneity due to patches often having different impacts depending on their ecological state (Remillard et al. 1987). This process parallels the classic patchy dynamics concept from landscape ecology, whereby disturbance events are recognized as key drivers of spatial and temporal heterogeneity within ecosystems (Bormann & Likens 1979; Pickett & White 1985). Although to our knowledge evaluations of ecosystem engineer-patch dynamics have not incorporated predation into their models, it seems clear that if predation is a substantial source of mortality for the ecosystem engineer population then predators are inherently linked to the dynamics of engineered patches and all of the ecological effects associated with the mosaic of engineered patches. Notably, these indirect effects from predation occur regardless of whether predators substantially alter the population density of the ecosystem engineers, as we show in the last case study.

Case study: Wolves alter ecosystems by killing pond-creating beavers

Beavers are renowned ecosystem engineers that create and maintain ponds by constructing dams. Water is impounded upstream of the dam, creating a pond that alters hydrologic, geomorphic, and vegetative characteristics of the dammed site (Naiman et al. 1988), providing numerous ecological benefits to plant, fish, amphibian, reptile, and mammal species (Brazier et al. 2021; Rosell et al. 2005).

In the Greater Voyageurs Ecosystem (GVE) in Minnesota, USA, wolves have an outsized effect on this boreal ecosystem 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 dispersing 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 these 'wolf-altered' ponds are substantially lower compared to reference ponds (i.e., ponds that are representative of the fate of all newly-created or recolonized ponds) in the same year the predation event occurs (0% vs. 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, which ultimately indirectly affects other species that benefit from beaver-altered environments. To date, there is no evidence that wolf predation limits beaver abundance in this system (Gable & Windels 2018; Johnson-Bice et al. 2021); wolf predation appears compensatory in the GVE beaver population. Instead, wolves appear to be a top-down force that influences the spatial distribution and temporal occupancy dynamics of beaver ponds, rather than the total number of ponds (Gable et al. 2020).

To put it differently, the broader-scale effects of wolf predation on beavers *are not* mediated through changes in beaver population density, but rather through changes in the creation or recolonization of individual ponds distributed across the landscape. Like other engineered patch types, beaver ponds go through periods of occupation and abandonment due to mortality, dispersal, or depletion of resources, resulting in a mosaic of ponds at varying ecological states that increases landscape heterogeneity and promotes ecosystem resilience by stabilizing ecological processes (Johnson-Bice et al. 2022a). As a predatory force influencing the spatiotemporal distribution of ponds, wolves are thus also connected to this landscape mosaic. Indeed, using information 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 (Gable and Johnson-Bice, unpublished data), wolf predation is likely an important influence on broader beaver pond dynamics. Although, recent research suggests individual variation in wolf kill rates on beavers may lead to intraspecific variation in the influence wolves have on beaver 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 across the Northern Hemisphere, 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 (Gable et al. 2018).

Predicting where and when patchy indirect effects are important

We can also draw some general predictions about the relative importance of patchy indirect effects (PIEs) in ecosystems based on patch size and density/frequency, predator community dynamics, and ecosystem productivity. First, logically, patches that cover a greater area or have effects that last longer 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 fewer scavengers and, in turn, have reduced effects on plants due to fewer nutrients leaching into soils. This 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). Second, the relative ecological importance of PIEs in an ecosystem will often be related to their density and frequency on the landscape. In other words, 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 more important they likely are for ecosystem dynamics. 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 prev selection and kill site locations). Finally, ecosystem productivity and rates of ecosystem recovery and turnover also influence the magnitude of PIEs (Fig. 4). Patchy indirect effects 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 more pronounced in environments with abiotic constraints on nutrient cycling (Malhi et al. 2022; Wall et al. 2008). 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 local plant communities on the 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 effects within any given system. For example, patches that occur infrequently in Arctic tundra ecosystems may be locally more important than patches that occur frequently in tropical forest ecosystems.

We also predict that PIEs are more common and relatively more important in terrestrial ecosystems, but contend this mechanism has often been overlooked in aquatic ecosystems. From a nutrient deposition stand-point, PIEs are likely more important for terrestrial ecosystems because nutrients are likely to get distributed widely by water current in aquatic ecosystems (Monk & 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 to continue feeding on them for days, providing carrier 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 basic approaches for quantifying patchy indirect effects (PIEs) of predation at both local and landscape scales. There is considerable variation and flexibility in the methods available to researchers depending on the ecology of the predator, 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 are often paired adjacently to the patch, ideally matching characteristics between the sites to be better able to attribute any differences to the predator(s). For instance, characteristics of local invertebrates and plants can be directly compared at a carcass or nutrient accumulation patch with nearby reference sites (e.g., (Barry et al. 2019; Barton et al. 2016; Ben-David et al. 1998; Bump et al. 2009b; Gharajehdaghipour et al. 2016). Alternatively, quantitative models based on characteristics of carcass or nutrient patches could be used to generate reference locations matching those characteristics (Johnson-Bice et al. 2022b). Manipulative experiments or remotely sensed trail cameras can also 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).

Knowledge about the ecology of predator-prey interactions is needed to quantify the landscape-scale effects of patches created through the carcass deposition pathway. 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/km²/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 (Morant et al. 2022; Vucetich et al. 2002). The amount of prey carcass biomass provisioned to scavengers can be estimated by multiplying carcass density by the average proportion of carcasses left by predators (Prugh & Sivy 2020), information that can be gained by placing remote game cameras next to a carcass (e.g., (Allen et al. 2015). Through time, carcass deposition patterns can provide spatially explicit estimates of areas that receive higher/lower prey carcass inputs (see (Bump et al. 2009a; Ellis-Soto et al. 2021) for detailed methods), 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, but multiple approaches are feasible. 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. 2022b), and thus the landscape-scale impact fox denning behavior has on other tundra species. If predator home sites (or colonies, haul-out sites) vary significantly in size, these size-dependent effects can be accounted for when assessing the broader scale impacts of these patches (Bokhorst et al. 2019). Surveys near home sites or along habitat features known to be preferred foraging, resting, or scent-marking sites can also determine the density of these patches (Crait & Ben-David 2007). Alternatively, individual-based data collection methods can be used to estimate landscape-

scale patch density predator density is known (e.g., number of latrines per individual * individuals/km²). 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 hotspots of predator nutrient deposition. And with knowledge of the rate of nutrient deposition at each biogeochemical hotspot (e.g., $g/m^2/unit$ time of nitrogen), estimates of the landscape-scale magnitude of predator nutrient deposition via these repeated behaviors 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 may obscure the effects of direct predation. After a predator kills an engineer, it may be difficult to determine whether changes to the engineered 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 because the second beaver maintains pond functionality. Despite the simple chain of events (predator kills engineer, engineered patch then changes), careful study designs and interpretations 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, over a temporal period of interest, 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. 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 in their lifetime and/or the engineer(s) may be responsible for +/-1 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 equation from Gable et al. (2020), we can estimate the number of patches (P) predators affect:

$P = N_{pred} \times KR_{pred} \times P_{established} \times P_{individual} \times P_{occupancy}$

where N_{pred} is the number (or density) of predators, KR_{pred} is the kill rate of engineers, $P_{established}$ is the proportion of engineers that successfully establish patches, $P_{individual}$ is the number of patches established per engineer, and $P_{occupancy}$ is natural occupancy rate, which are 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 compare patch dynamics before and after predator introduction). However, this is likely feasible only for systems where the engineered patches are relatively small and easy to continuously monitor. The take-home message here is that because engineered patch dynamics are affected by the ecology and movements of engineers themselves, resolving the role predators play in landscape patch dynamics is difficult and requires detailed study designs that can decompose the relative influence of predators and engineers.

Concluding remarks

Through our synthesis and detailed 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 den or latrine, or a patch created by ecosystem engineering prey. The carcass distribution and nutrient accumulation pathways have been previously discussed both empirically and theoretically (Ellis-Soto et al. 2021; Leroux & Schmitz 2015; Monk & Schmitz 2022; Newsome et al. 2021; Schmitz et al. 2010; Schmitz & Leroux 2020), 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 (e.g., (Monk & Schmitz 2022; Schmitz et al. 2010), which overlooks 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 the multitude of ways predators affect ecosystem dynamics via a unifying element, a discrete *patch*. We showed how multi-scale ecological frameworks, like metapopulation and meta-ecosystem theories, help us understand how these patches form and can contribute to larger ecological patterns and processes. We also offered explicit predictions of when and where these patches are likely to be important, and we provided numerous different approaches researchers could take to quantify patchy indirect effects of predation at both the patch and landscape scales. Moreover, we provided terminology, *patchy indirect effects of predation*, that we hope will result in the concepts discussed here being more broadly recognized and appreciated, rather than a tertiary focus of most predator conservation and research objectives. Our synthesis has clearly shown that predators, through patchy indirect effects (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' unique ability to create patchy landscapes via these localized pathways adds to the growing evidence that they affect ecosystems in ways humans cannot easily replicate (Lennox et al. 2022).

As predator populations decline globally (Estes et al. 2011; Ripple et al. 2014), we need a thorough understanding of the diverse functional roles of predators in order to effectively manage and conserve their populations, actions which in turn can have broader effects on the ecosystems they inhabit (Natsukawa & Sergio 2022). To date, most research on how predators influence ecosystems has focused on how they affect the abundance and traits of lower trophic levels. The justification for conserving, managing, and reintroducing predators frequently hinges on their ability to influence ecosystems via changes to lower trophic levels at the population scale (i.e., density- and trait-mediated indirect effects; (Blossev & Hare 2022; Ritchie et al. 2012; Sergio et al. 2008). Nonetheless, our PIE 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. 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 (Peacor & Werner 2001; Preisser et al. 2005; Pruett & Weissburg 2021; Werner & Peacor 2003). For example, in Yellowstone National Park, wolves affected both the population density (Peterson et al. 2014; Vucetich et al. 2005) and, to a lesser degree, space use of elk (Cervus canadensis) (Cusack et al. 2019; Kohl et al. 2018), which had a weak but measurable cascading effect on aspen (Populus tremuloides) recruitment (density- and trait-mediated effects; (Brice et al. 2022). But wolf-killed elk carcasses also have PIEs on local plant and soil communities (Risch et al. 2020) that would occur regardless of whether wolves altered elk density or traits. Thus, although PIEs are a distinct mechanism by which predators alter ecosystems, they certainly operate simultaneously and in tandem with density and trait-mediated mechanisms.

Research on predators has often focused on specialized, disconnected subfields in ecology, and there is a need for a broader, more holistic understanding of the importance of predators to ecosystem dynamics (Sergio et al. 2014). We see PIEs as a step towards a unified view of predation in ecosystems by providing a spatially explicit perspective that is rooted in current multi-scale ecological frameworks. These multi-scale frameworks provide insight into how environmental conditions work in tandem with predator and

prey movement ecology to shape the spatiotemporal distribution of predator-altered patches, and how these patch-scale pathways can have landscape-scale effects across a multitude of taxa, predator-prey systems, and environments. In this review, we provided examples of PIEs from mammalian, avian, invertebrate, and fish predators that were drawn from studies spanning plant and soil ecology, behavioral ecology, spatial ecology, and food web dynamics. Nonetheless, our examples and most of the research on these topics are biased towards large terrestrial mammals in the Northern Hemisphere. We can obtain a better cross-disciplinary understanding of predation by expanding research efforts on patch-scale predator-prey ecology across more taxa and ecosystems. Doing so will help provide a synthetic view of predation and ultimately advance the research, conservation, and management of these iconic and ecologically vital species.

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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

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 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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Figures



Figure 1: Patchy indirect effects 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), often leading to fierce interspecific interactions. 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).



Figure 2: A collection of photos from Arctic fox dens near Churchill, Manitoba, Canada demonstrating patchy indirect effects on other species. Arctic fox dens are distinct biogeochemical patches on the tundra with lush, bright green vegetation that is prominent on the landscape (A). Panels 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).



Figure 3: Dramatic representation of patchy indirect effects within riparian ecosystems that occur 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).



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).