Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry

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Abstract

Spatial heterogeneity in ecological systems can result from animal-driven top-down processes, but despite some theoretical attention, the emergence of spatial heterogeneity from feedbacks caused by animals is not well understood empirically. Interactions between predators and prey influence animal movement and associated nutrient transport and release, generating spatial heterogeneity that cascades throughout ecological systems. In this review, we synthesize the existing literature to evaluate the mechanisms by which terrestrial predators can generate spatial heterogeneity in biogeochemical processes through consumptive and non-consumptive effects. Overall, we propose that predators increase heterogeneity in ecosystems whenever predation is intense and spatially variable, whereas predator-prey interactions homogenize ecosystems whenever predation is weak or diffuse in space. This leads to several testable hypotheses: (1) that predation and carcass deposition at high-predation risk sites stimulate positive feedbacks between predation risk and nutrient availability; (2) that prey generate nutrient hotspots when they concentrate activity in safe habitats, but instead generate nutrient subsidies when they migrate daily between safe and risky habitats; (3) that herbivore body size mediates risk effects, such that megaherbivores are more likely to homogenize ecosystems; and 4) that predator loss in general will tend to homogenize ecosystems. Testing these hypotheses will advance our understanding of whether predators amplify landscape heterogeneity in ecological systems.

Keywords: landscape of fear, biogeochemistry, heterogeneity, predator-prey interactions, spatial patterning, zoogeochemistry

Introduction

Ecosystems are complex and spatially heterogeneous, and spatial heterogeneity can have decided consequences for ecosystem functioning (Chapin et al. 2011, Hunter and Price 1992, Turner and Chapin 2005). The degree of heterogeneity at the landscape scale can influence community dynamics (Hastings 1977, Turner and Gardner 2015), species coexistence (Davies et al. 2021), and resilience to environmental change (van Nes and Scheffer 2005). Much effort, especially, has been devoted to characterizing how landscape-scale spatial heterogeneity impacts wildlife population persistence and community dynamics (Hutchings et al. 2000), with the goal of understanding how habitat should be protected to best support species of conservation concern (Lovett et al. 2005). However, far less work has explored how wildlife community dynamics may impact spatial heterogeneity, and hence the potential for wildlife conservation to become a key tool for preserving ecosystem functioning and resilience (Sinclair and Byrom 2006, Schmitz et al. 2010, Bakker et al. 2016).

Variation in geomorphology, hydrology, microclimate, and microbial communities creates spatial heterogeneity in biogeochemistry from the bottom up, explaining variation in vegetation and animal communities within and among ecosystems (Turner and Chapin 2005, Chapin et al. 2011). However, animals can also have profound effects on ecosystems, reinforcing or countervailing bottom-up forces and potentially shaping spatial variation in biogeochemistry and vegetation from the top down (Pastor 2005). Animals roam widely across landscapes, all the while consuming and redistributing nutrients via egestion, excretion, and carcass deposition (Bauer and Hoye 2014, Schmitz et al. 2018, Subalusky and Post 2018, McInturf et al. 2019, Pausas and Bond 2020). Animal movement of nutrients can in turn result in knock-on feedbacks that either amplify or erode underlying spatial heterogeneity caused by geophysical setting, hydrological regimes, or microbial processes (Pastor 2005, Chapin et al. 2011, Leroux and Loreau 2015). Predators in particular can have strong cascading effects on ecosystems through their consumptive and non-consumptive effects on herbivore prey, which can control the quality and fate of nutrients in ecosystems (Schmitz et al. 2010). Nevertheless, characterization of landscape-scale biogeochemical and vegetation patterning is still largely framed by our understanding of bottom-up controls. Recent examples (le Roux et al. 2018, 2020, Edwards and Konar 2020, Mackay et al. 2021) show why bottom-up conceptual frameworks alone are insufficient to explain landscape spatial patterning.

Here we argue for a conceptual re-orientation to motivate new empirical analyses of top-down controls over landscape heterogeneity. We begin with a synthetic review of the way predator-herbivore interactions cascade to shape spatial patterning in the distribution of nutrients in terrestrial ecosystems. We identify key traits of predators and prey that shape their impacts on landscape heterogeneity. We then use these insights to generate testable predictions of how changes in predator and herbivore populations and their movement should impact biogeochemical patterning at landscape scales.

Predator impacts on ecosystem heterogeneity: review and mechanisms

Several key mechanisms by which predators can influence biogeochemical processes and vegetation have previously been identified (Schmitz et al. 2010). These mechanisms involve both consumption by predators (which determines prey carcass distribution) and non-consumptive effects of predators (which influence herbivore foraging patterns and effects on nutrient cycling). In this section, we extend this foundation to explore how consumptive and non-consumptive predator effects explicitly influence spatial processes and patterning.

Consumptive predator effects: carcass distribution

Animal carcass deposition is a natural consequence of a consumptive predator-prey interaction. Carcass decomposition, in turn, plays an important role in nutrient cycling by creating biogeochemical hotspots with higher soil nutrients, plant quality, and plant diversity than the surrounding landscape (Towne 2000, Danell et al. 2002, Moore et al. 2004, Carter et al. 2007, Parmenter and MacMahon 2009, Barton et al. 2013a, Keenan et al. 2018). Of course, all animals die, and carcasses are therefore continually deposited regardless of predator activity. But predators influence rates of prey mortality and where prey die on the landscape, thereby determining the quantity and spatial distribution of decomposing carcasses in ecosystems (Bump et al. 2009a). Predation can thus increase small-scale heterogeneity by concentrating nutrients and physical disturbance at kill sites, altering local biogeochemistry and community composition of plants and soil organisms (Holtgrieve et al. 2009, Barton et al. 2013a, 2013b, Risch et al. 2020).

While carcasses themselves are temporary, their effects may linger in landscapes for years, maintaining variation in soil conditions and plant diversity at decomposition sites (Bump et al. 2009b, Macdonald et al. 2014, Barton et al. 2016). When predation concentrates these carrion inputs in areas with high predator activity and hunting success, this process may redistribute and concentrate nutrients in patches within predator home ranges (Macek et al. 2009, Schmitz et al. 2010), *e.g.*, at predator den and nest sites, where carnivores transport small carcasses for storage or to feed their young (Fedriani et al. 2015, Gharajehdaghipour et al. 2016). At arctic fox dens, carcasses increased plant productivity to such an extent that den sites were identifiable via remote sensing (Gharajehdaghipour et al. 2016). Predator bodies, urine, and feces also contribute to nutrient cycling, and these can also be concentrated at key sites within predator home ranges.

The extent to which predators determine the spatial effects of carcasses depends on how other drivers of mortality distribute carcasses throughout the landscape. Some non-predation mortality events may also be clustered and have large, pulsed effects on ecosystems; for example, mass drownings of migrating wildebeest substantially alter nutrient budgets of the Mara River in Kenya (Subalusky et al. 2017). Nevertheless, predation often differs in spatial distribution from other causes of death. On Isle Royale, Michigan, wolf-killed moose carcasses were spatially clustered in areas distinct from starvation-killed carcasses (Bump et al. 2009a), increasing soil nutrients, microbial activity, and foliar nitrogen in areas of high wolf hunting success, with knock-on effects on seedling recruitment (Bump et al. 2009b). Furthermore, predators facilitate the transport of nutrients across ecosystem boundaries and generate nutrient subsidies by moving carcasses between habitats (Schmitz et al. 2010, Subalusky and Post 2018). These nutrient subsidies could contribute further to spatial heterogeneity in recipient ecosystems. For example, bears create biogeochemical hotspots with increased nitrogen by catching salmon in streams and littering their remains in surrounding forests (Helfield and Naiman 2006, Holtgrieve et al. 2009). These predator-driven nutrient subsidies cascade to influence plant diversity and quality along salmon-filled streams (Hilderbrand et al. 1999, Helfield and Naiman 2001, Hocking and Reynolds 2011, 2012).

Non-consumptive predator effects: the spatial distribution of herbivory

Trophic interactions in heterogeneous landscapes lie at the center of the concept of the ‘landscape of fear’, in which spatial variation in perceived predation risk drives prey behavior and habitat use as prey trade-off foraging needs against avoiding predation (Brown et al. 1999, Laundré et al. 2001, 2010, Gaynor et al. 2019). When non-consumptive predator effects play out in a heterogeneous landscape of fear, they can further influence spatial patterns of herbivory (Ripple and Beschta 2004, Acebes et al. 2013, Ford et al. 2014, Donadio and Buskirk 2016, Atkins et al. 2019). Predators induce behaviorally-mediated trophic cascades when prey alter their habitat selection and behavior in response to predation risk, shifting the intensity and spatial distribution of herbivory (Abrams 1984, Schmitz et al. 1997, 2004, Creel and Christianson 2008). Variation in habitat structure coupled with predator and prey behavior creates a gradient of predation risk across the landscape (e.g. areas with denser tree cover may provide refuge [Fortin *et al.* 2005], or alternately may increase risk by reducing visibility for prey [Riginos 2015]; rocky outcroppings with brush provide greater cover for ambush predators [Donadio & Buskirk 2016]). In such landscapes of fear, herbivorous prey may attempt to remain in 'safe' areas or may reduce feeding rates in risky areas as they increase vigilance (Sih 1980, Brown et al. 1999, Hernández and Laundré 2005, Laundré et al. 2010). Regardless, predation risk should reinforce heterogeneity as prey navigate risk by reducing grazing and browsing pressure in risky habitats and increasing herbivory in safe habitats.

These non-consumptive effects of predators have not been documented in all predator-prey systems, nor are they the only determinants of herbivory patterns in ecosystems (Middleton et al. 2013b, Kohl et al. 2018, Cusack et al. 2019, Say-Sallaz et al. 2019). The role of risk effects in determining herbivory patterns – and thus shaping landscape heterogeneity – are context-dependent (Schmitz et al. 2004, 2017b), varying with resource availability and predator and prey functional traits. Yet when risk effects do drive herbivory, they can be profound. For example, in African savannas, grazing lawns – or patches of heavily grazed, nutrient-rich, fast-growing grasses – are maintained by herbivores that concentrate in areas with high visibility as a collective antipredator strategy (McNaughton 1983, McNaughton et al. 1989, Young et al. 1995, Sinclair et al. 2003, Cromsigt and Olff 2008, le Roux et al. 2020). Concentrated grazing helps generate heterogeneity in these grasslands, as high herbivory in safe habitats selects for highly productive grasses and increases rates of nutrient cycling (McNaughton 1979; McNaughton et al. 1997). Similarly, in the central Andes vicuñas grazed less and were more vigilant in wet meadow and canyon habitats where puma predation was more frequent (Donadio and Buskirk 2016). Consequently, herbivory was significantly higher in "safe" habitats (dry, sparsely vegetated grasslands with high visibility), thereby reducing standing green biomass to 15% of that in fenced plots that excluded vicuñas. In this arid ecosystem, vicuña behavioral responses to predation risk reinforce extant heterogeneity on the landscape by reducing grass biomass in unproductive sites and relieving herbivory pressure in productive ones. Similar patterns were observed in guanacos avoiding predation during the breeding season at lower elevations (Acebes et al. 2013).

When the distribution of high-quality forage shifts over time, as in highly seasonal environments or along elevational gradients, herbivores may migrate to follow green-up and access new growth – a phenomenon known as "green-wave surfing" (Fryxell et al. 1988, van der Graaf et al. 2006, Bischof et al. 2012, Merkle et al. 2016). This phenomenon is driven by spatiotemporal heterogeneity of high-quality resources (Fryxell et al. 1988). Predators may intervene and reinforce this heterogeneity at landscape scales by impeding migratory behavior and confining migration, and herbivory, to safe corridors (Middleton et al. 2013a). For example, reindeer were constrained from following the flush of peak forage during green-up in areas with high bear densities (Rivrud et al. 2018). Consequently, reindeer herbivory was intensified in lower-quality habitats, exacerbating differences in plant composition and nutrient content between high risk, high productivity and low risk, low productivity habitats.

Non-consumptive predator effects: herbivore-mediated nutrient cycling

Herbivores mediate nutrient cycling when they alter plant nutrient content through selective foraging (Pastor et al. 1993, Augustine and Frank 2001, Wardle et al. 2002, Bai et al. 2012), process and transport nutrients through egestion and excretion (Day and Detling 1990, Seagle 2003, Abbas et al. 2012, Barthelemy et al. 2017), and physically disturb plants and the soil (Huntly and Inouye 1988, Fleming et al. 2013, Veldhuis et al. 2014, Pellegrini et al. 2016). When predators regulate prey foraging behavior and movement, they in turn can have strong, landscape-scale effects on spatial patterning due to herbivore-mediated nutrient cycling.

Any predator avoidance behavior that concentrates herbivory in safe locations can in turn create heterogeneity in biogeochemical cycling. Intensive foraging in safe habitats can generate biogeochemical hotspots wherever herbivore egestion and excretion increases plant-available nutrients by hastening rates of nutrient cycling – so-called fast cycling (McNaughton et al. 1989, Bardgett and Wardle 2003). Grazing lawns and glades in savannas provide classic examples. In these savanna hotspots, intensive localized herbivory is driven by both top-down (predator avoidance) and bottom-up (high-quality forage) controls (Anderson et al. 2010). However, these nutrient hotspots seem to be maintained, and in some cases formed, by fertilization from herbivore egestion and excretion coupled with selection for fast-growing plants with high nutrient concentrations under high grazing pressure (McNaughton 1985, McNaughton et al. 1997, Winnie et al. 2008, Anderson et al. 2008). Additionally, hotspots are formed by human predator avoidance (safeguarding of livestock in paddocks known as *kraals* and *bomas*), and wild herbivores often maintain these legacy hotspots, further increasing plant and soil heterogeneity in savannas (Augustine 2003, Augustine et al. 2003, van der Waal et al. 2011). In contrast, foraging under high predation risk may alter herbivore and plant stoichiometry as physiologically stressed prey select for carbohydrate-rich over nitrogen-rich plants, slowing decomposition and nutrient cycling (Hawlena and Schmitz 2010, Hawlena et al. 2012).

Predation risk does not just restrict prey to safe sites with high rates of herbivore-mediated nutrient cycling. Predators also influence prey movement throughout the landscape, shaping the pattern of nutrient transport as herbivores consume resources in one area and excrete and egest them elsewhere. For example, anti-predatory daily migrations (Lima and Dill 1990) may drive the redistribution of nutrients between risky and safe sites. In wooded savannahs, zebras forage in nutritious open grasslands near watering holes during the day, when lions are largely inactive, but retreat away from watering holes when lions are more active and predation risk is high (Valeix et al. 2009, Courbin et al. 2018). Similarly, elk in the Greater Yellowstone Ecosystem appear to use high-risk, forage-rich areas when wolves are resting, but avoid these areas during the morning and evening hours when the crepuscular predators tend to hunt (Kohl et al. 2018). The same pattern was observed in vicuñas avoiding puma predation at essential foraging sites in the central Andes (Smith et al. 2019b). As yet, little research has traced the importance of nutrient transport between habitats as large mammalian herbivores track risk and forage quality across the landscape (but see le Roux *et al.* 2018). However, diel migrations made by other herbivores have been shown to have substantial effects, e.g. geese driving large nutrient outfluxes from fertile feeding grounds (Kitchell et al. 1999). Thus, predation risk may be an important factor driving nutrient subsidies between high and low productivity habitats.

Toward conceptual integration of predator-prey dynamics and spatial biogeochemistry

Given known predator effects on biogeochemical cycling (Hawlena et al. 2012, Strickland et al. 2013, Leroux and Schmitz 2015, Schmitz et al. 2017a), it seems clear that both predation and perceived predation risk can drive spatial patterns of nutrient transport and accumulation. Yet despite this logical link between predator effects and nutrient distributions (Abrams 2000, Schmitz et al. 2010), the varied roles of predators as top-down drivers of landscape heterogeneity remain largely unexplored (Anderson et al. 2008). Synthesis of the evidence for predator control of nutrient distribution suggests a broad generalization about how predators structure ecosystems: direct predation and predator non-consumptive effects tend to increase patchiness and landscape-level heterogeneity in ecosystems by directing and concentrating the flow of nutrients processed by herbivorous prey. Of course, there are exceptions, and these offer opportunities to test mechanistic predictions and develop a more nuanced, context-dependent theory of the role of predators in spatial biogeochemistry. Several key principles emerge from our examination of the literature. Rigorous empirical testing of the hypotheses drawn from these principles should allow for improved prediction of predator impacts in diverse landscapes and changing environments.

Risk-resource feedback loops

We repeatedly found studies that showed that sites with high predation were often characterized by high resource availability and forage quality (Schmidt and Kuijper 2015, Donadio and Buskirk 2016, Courbin et al. 2018, Kohl et al. 2018, Atkins et al. 2019). We hypothesize that where there is strong spatial variation in risk—as in the case of sit-and-wait predators whose hunting success is facilitated by habitat structure and cover—a positive feedback between productivity, predation, and decomposition amplifies spatial heterogeneity in both predation risk and nutrient availability (Figure 1). Herbivores are often drawn to sites with abundant or nutrient-rich forage (Hopcraft et al. 2010). Where herbivores reliably forage, predators may also congregate, creating sites with high risk and high reward for herbivores. Where predation is concentrated at high-risk sites, carcass decomposition will likely generate a cluster of nutrient hotspots (Bump et al. 2009a). These nutrient hotspots may increase both the abundance and quality of plants in risky areas (Danell et al. 2002, Moore et al. 2004, Carter et al. 2007, Bump et al. 2009b, Barton et al. 2016). As a result, prey in great need of nutritious, abundant forage may be further drawn to these habitats despite high predation risk (Abrams 1992, Sih 2005, Gharajehdaghipour and Roth 2018, Smith et al. 2019a, Smith et al. 2021). Meanwhile, healthy prey may avoid such sites, allowing plant biomass to accumulate despite its high palatability. This elevated biomass could provide increased visual cover for predators, further increasing predation risk and completing the positive feedback loop (Hopcraft et al. 2010, Figure 1).

The extent to which prey avoid or are drawn to these nutrient-rich, high-risk sites likely depends upon a) prey body condition and b) the availability of resources on the landscape (McNamara and Houston 1990, Sinclair and Arcese 1995, Montgomery et al. 2014, Riginos 2015, Schmidt and Kuijper 2015, Oates et al. 2019). Optimal foraging theory and the predation-sensitive foraging hypothesis would suggest that body condition determines the threshold at which prey deprioritize predator avoidance in favor of resource acquisition (Sinclair and Arcese 1995). When prey are healthy and able to access sufficient forage in refuge habitats, they will avoid risky areas. Via this mechanism, predation risk could increase landscape heterogeneity by concentrating plant consumption in safe areas with lower plant biomass and quality – thus reinforcing differences between safe and risky sites. However, some level of herbivore activity at risky sites will be maintained by bold individuals or those in greater need of high-quality resources during periods of deprivation – enabling continued predator success and carcass decomposition in nutrient-rich, high-risk habitats (Sinclair and Arcese 1995, Hopcraft et al. 2005, Hay et al. 2008, Riginos 2015, Bonnot et al. 2018).

Additionally, prey forage in high-risk, high-reward sites more often if risky habitat contains essential resources that cannot be found elsewhere on the landscape. Thus, the positive feedback linking risk to resource quality should be strongest in nutrient- or water-limited conditions, when these essential resources are both rare and spatially concentrated (*e.g.*, during drought). Under such conditions, prey are more likely to ignore predation risk continually or periodically to forage for resources, and enough prey activity at high-quality, risky sites will continue to fuel the positive biogeochemical feedback. This tradeoff can be observed at savanna watering holes, where lion predation succeeds due to high vegetative cover and consistent prey presence when ungulates are confined to areas with water during the dry season (Hopcraft et al. 2005). Risk was also disregarded in favor of abundant forage during times of extreme drought in savannas, whereas herbivores avoided these low-visibility settings with high grass biomass when rainfall was plentiful (Riginos 2015). Similarly, elevated plant growth and nutritional quality at arctic fox dens attract lemming prey in the nutrient-limited arctic tundra (Gharajehdaghipour and Roth 2018), and vicuñas migrate daily between lush, high-risk wet meadows and arid plains refuge habitat in the alpine deserts of central Argentina (Smith et al. 2019b).

Prey may mitigate risk by engaging in vigilance, grouping, or avoidance of risky habitats at the times of day when predators are most active (Valeix et al. 2009, Makin et al. 2018, Smith et al. 2019b). However, in resource-limited ecosystems where prey must eventually spend time in high-risk, high-reward areas, predation rates at risky sites should be high enough to maintain the positive biogeochemical feedback loop. Indeed, we contend that this correlation between predation risk, nutrient availability, and forage availability is necessary for ambush predation to remain a viable strategy. For ambush predators to utilize easily avoidable areas with high cover and maintain relatively predictable sites of high predation risk, the draw of these sites must at least occasionally outweigh the risk for prey – thus, risky habitats should logically contain resources in greater abundance or of greater quality than the surrounding landscape (Sih 1980, 2005, Luttbeg et al. 2020). Accordingly, we predict that the landscape of fear – or strong spatial patterning in non-consumptive predator effects – and its associated biogeochemical legacy should be most apparent in aridlands and other ecosystems with overall low primary productivity. In ecosystems where resources are more abundant or productivity is higher, risk may be more uniform across the landscape – either because actively hunting predators dominate, or because ample structure (such as trees in a forest) exists to support ambush predation – thus rendering the correlation between risk and nutrient availability weaker.

Predator hunting mode and prey behavioral traits

The nature of predator effects on herbivore-mediated nutrient cycling and transport depends upon both predator and prey behavioral traits. Predator hunting mode (*i.e.*, active hunting vs. ambush predation) mediates the spatial response of prey to predation risk (Schmitz 2008, Thaker et al. 2011, Vanak et al. 2013, Gervasi et al. 2013, Miller et al. 2014, Makin et al. 2018, Owen-Smith 2019). We expect stronger spatial heterogeneity due to predation in systems dominated by ambush predators (predators who hide and rapidly attack prey in opportune areas, *e.g.* pumas, rather than actively chasing them down, *e.g.*, wolves), as an ambush hunting mode more firmly establishes the predictable spatial patterns of risk that define the ‘landscape of fear’ (Brown et al. 1999, Schmitz 2008, Laundré et al. 2010, Kauffman et al. 2010, Creel 2018, Gaynor et al. 2019). Stronger site-specific fear effects should elicit greater spatial variation in prey habitat use and behavior, amplifying the effects of predators on landscape heterogeneity. Developing better methods to quantify the strength of predator non-consumptive effects will be a key step in testing this hypothesis and testing the effects of predation risk on spatial biogeochemistry in the landscape of fear (Moll et al. 2017, Peers et al. 2018, Wirsing et al. 2021).

Additionally, herbivore antipredator strategies likely play an important role in nutrient redistribution. Prey species employ a wide variety of antipredator behaviors. Nevertheless, predator avoidance traits can be roughly aggregated into two main categories: habitat shifts and time budget shifts (Schmitz et al. 2017b). When a prey animal’s habitat domain (or the spatial area an individual occupies relevant to predator-prey interactions; Schmitz et al. 2004) ranges beyond the spatial extent of its predator’s habitat domain, individuals can shift habitat use and concentrate their activity in refuge habitats (Figure 2). In such cases, habitat shifts may lead to the creation and maintenance of nutrient hotspots as herbivores forage, excrete, and egest in spatially constrained “safe” habitats (Figure 2).

However, herbivore diet can also moderate the effectiveness of habitat shifts in maintaining nutrient hotspots in refuge habitats. Grazing lawns in savannas are maintained when high levels of herbivory and herbivore-mediated nutrient cycling select for fast-growing, nutrient-rich grasses (McNaughton 1979, 1985). These lawns are in turn kept short by these high levels of herbivory, maintaining visibility and openness and thus protecting herbivores from the predators who hunt best under some degree of cover (Riginos and Grace 2008). However, in savannas, this same openness can also reduce grass competition with tree seedlings, allowing trees to encroach into formerly grassy areas (Riginos 2009). Accordingly, herbivory by grazers can generate nutrient hotspots in refuge habitats, but continued grazing can also act as a negative feedback that converts refuge sites to high-risk sites by allowing tree encroachment. Conversely, if browsers are also present to consume seedlings at the edges of grazing lawns, nutrient hotspots in refuge habitats can be maintained by herbivores over longer time periods (Staver and Bond 2014). Thus, the distribution of refuge habitats and safe habitats does not always remain static, but can continually shift when different forms of herbivory modulate plant community dynamics, with herbivores engineering their own refuges but also inadvertently generating the habitat structure that leads to their demise.

When predators successfully hunt throughout a prey animal's home range, prey cannot easily seek out refuge habitats. In this case, predation may instead induce time budget shifts as prey reduce foraging time due to increased vigilance or alter daily activity patterns to minimize encounter risk (Figure 2). This antipredator strategy should have little influence on the spatial distribution of nutrients, particularly if time budget shifts are uniform across the prey habitat domain. In reality, however, herbivore antipredator strategies often comprise a mixture of habitat shifts and time budget shifts. Prey may spend more time being vigilant in risky locations than in safe habitats (Blanchard et al. 2018), and may structure their daily habitat use to forage in risky locations at safer times when predators are less active (Dröge et al. 2017, Courbin et al. 2018, Kohl et al. 2018, Smith et al. 2019b). If this combined antipredator strategy increases herbivore movement between risky habitats and safe habitats, predation risk could drive an herbivore-mediated nutrient subsidy along a gradient of high to low risk (Figure 2). This mixed habitat-time budget shift strategy and potential associated subsidy are particularly likely if risky sites are of higher forage quality or contain essential limited resources, as discussed above.

Herbivore body size

Predation risk decreases with increasing herbivore body size (Sinclair et al. 2003, Hopcraft et al. 2012, Owen-Smith 2019), and so prey body size may mediate the potential for spatial cascades from predation. We predict that medium-sized herbivores should be most likely to increase spatial heterogeneity as they evade predators, because they are large enough to transport and concentrate high nutrient loads over large distances, but susceptible enough to predators that predation may change their space use. In contrast, megafauna are more free to move and may instead homogenize landscapes (Sinclair et al. 2003, Riginos and Grace 2008, Hopcraft et al. 2012, Riginos 2015, Bakker et al. 2016, le Roux et al. 2018) as their impacts are widely distributed. For example, buffalo, which are less susceptible to predation than smaller herbivores (Hopcraft et al. 2010), were able to range widely to find and graze down nutrient-rich grass in refugia during times of drought in African savannas – taking advantage of and effectively homogenizing an otherwise patchy landscape (Abraham et al. 2019, Staver et al. 2019).

Because of this variation in vulnerability to predation, the presence of multiple herbivore species of varying body size could dampen the effects of predators on nutrient distributions (Owen-Smith 2015, Atkins et al. 2019, Owen-Smith 2019). This is exemplified by the diverse prey and predators found in African savannas. As discussed above, smaller mammalian herbivores in savannas tend to concentrate herbivory pressure, excretion, and egestion in open areas with high visibility, often generating nutrient-rich hotspots in their attempts to maintain safety from predators. Megaherbivores may similarly create and maintain these patches; in fact, white rhinos were more effective than mesoherbivores at maintaining grazing lawns in mesic regions of South Africa (Waldram et al. 2008). However, le Roux *et al.* (2018) found that megaherbivores (elephants, white rhinos, and giraffe) counteracted mesoherbivore effects on nutrient distributions by feeding in open glades but defecating uniformly across the landscape, transporting nutrients against the nutrient gradient.

Thus, predators may exert stronger effects on landscape heterogeneity in ecosystems dominated by mesoherbivores and lacking megafauna. Examples of such ecosystems are plentiful – in fact, megaherbivores are increasingly restricted to sub-Saharan African and southeast Asian fragments within their historical ranges (Owen-Smith 1988). However, prior to the Pleistocene megafauna extinctions, megaherbivores roamed every continent, and we are only beginning to understand what a world dominated by megafauna might have looked like (Owen-Smith 1988, Gill et al. 2009, Doughty et al. 2013, Bakker et al. 2016, Doughty et al. 2016b). Because megaherbivores tend to distribute nutrients more uniformly across the landscape, ecosystems may have been more spatially homogenous when megafauna were dominant (Wolf et al. 2013, Bakker et al. 2016, Doughty et al. 2016a, le Roux et al. 2018). Thus, we hypothesize that megaherbivore extinctions triggered what we term "heterogeneity cascades", allowing top-down predator control of nutrient cycling and transport to play a greater role in the configuration of modern landscape heterogeneity (Figure 3). Understanding and predicting such heterogeneity cascades, if they exist, is more than a thought exercise: large carnivore populations are in global decline, and the extirpation or functional extinction of top predators is an imminent reality in many ecosystems (Estes et al. 2011, Ripple et al. 2014). If these declines persist, we predict a fundamental change in landscape biogeochemical patterning, trending towards the homogenization of the ecosystems where these predators were once present (Figure 3). Without the spatial restrictions imposed by predation and risk, mesoherbivores may consume and transport resources more uniformly. Indeed, such restructuring of landscapes via herbivory after predator extirpation has been observed in Gorongosa National Park, Mozambique, where mesoherbivores grazed down plants in formerly risky habitats, restricting their herbivory and movement on the landscape only when predator cues were experimentally reintroduced to simulate risk (Atkins et al. 2019). As evidence of altered prey behavior in predator-free landscapes mounts (Bonnot et al. 2016, Leempoel et al. 2019, Cunningham et al. 2019), such homogenization may become more apparent, and understanding the ecosystem-wide impacts of predators on landscapes an ever more urgent necessity.

Moving Forward

The landscape of fear is a useful framework for understanding predator non-consumptive effects across space, and the concept can be extended to predator effects on biogeochemical processes. Of course, not all herbivore species will exhibit spatial responses to predators; for example, as detailed above, body size modulates herbivore sensitivity to predation risk (Figure 3). The context-dependency of herbivore effects on ecosystems – and, similarly, of cascading predator effects – has been emphasized in many studies (e.g. Anderson et al. 2008; Bai et al. 2012; Young et al. 2015; Haswell et al. 2017; Goheen et al. 2018; Forbes et al. 2019). Further progress will depend on making sense of this context-dependency based on predator and herbivore functional traits and on ecosystem characteristics. As a starting point, we offer a simple synthetic hypothesis (Figure 4): in systems with strong predator-prey trophic links and high spatial variation in predator effects, predators should be heterogenizing forces in ecosystems, whereas where trophic links are weaker and predator effects are not restricted in space, predator-prey interactions should be neutral or homogenizing forces on landscapes.

Our synthetic hypothesis can be broken down into components for testing. First, we hypothesize that where there is strong spatial variation in predation, biogeochemical hotspots at carcasses will fuel a positive feedback between nutrient availability and predation risk (Figure 1). Evaluations will need to test spatially explicit hypotheses by directly linking ecosystem measurements with animal movement data (Ellis-Soto, Ferraro et al. 2021). Specifically, the hypothesis could be tested by comparing soil and plant nutrient data at carcasses (*sensu* Bump et al. 2009a; Keenan et al. 2018) vs. at non-carcass sites. These biogeochemical data can be compared with spatially explicit measures of risk (*sensu* Kauffman et al. 2007, Smith et al. 2019a, b) to test for spatial correlation between risk, carcass hotspots, and nutrient-rich patches across the landscape.

Second, we hypothesized that, when prey employ a combination of habitat and time budget shifts as part of their antipredator strategy, this cyclic movement between high- and low-quality sites will drive nutrient subsidies from risky to safe habitats (Figure 2). Stable isotopes or environmental DNA offer an opportunity to test this by evaluating whether nutrients in prey feces deposited in safe habitats originated in risky areas, thereby representing a nutrient subsidy. Where there is variation in risk, or where some herbivore populations exhibit cyclic migrations and others do not, animal movements and patterns of egestion and excretion can be compared across a gradient of risk to determine the full impacts of predator avoidance strategies on nutrient transport.

Finally, we hypothesized that megaherbivores potentially homogenize landscapes by evenly distributing nutrients over large distances (le Roux et al. 2018), whereas predators should increase heterogeneity in systems dominated by susceptible mesoherbivores. Thus, in systems dominated by mesoherbivores, the loss of apex predators should initiate heterogeneity cascades, homogenizing landscapes as mesoherbivores are released from the spatial restrictions imposed by predator avoidance (Figure 3). Large-scale exclosure experiments, such as the KLEE, GLADE, and UHURU exclosure projects in Laikipia, Kenya (Goheen et al. 2018) or the dingo fence in New South Wales, Australia (Morris and Letnic 2017), provide the ideal settings in which to test such a hypothesis.

The fields of animal movement ecology and biogeochemistry are both experiencing a methodological renaissance. Portable, affordable technology facilitating rapid data collection has proliferated, allowing for large-scale GPS tagging of animals of all sizes (Kays et al. 2015, Wilmers et al. 2016) and quick, in-field assessment of biogeochemical conditions (e.g. Kane et al. 2019). Furthermore, remote sensing techniques are becoming ever more sophisticated, enabling real-time tracking of animal movement (Wilmers et al. 2016, Harvey et al. 2016, Steenweg et al. 2017) and hyperspectral analysis of plant and soil properties (Asner and Vitousek 2005, Wang et al. 2009). These new tools can and should be combined to conduct research on the relationship between animal movement and biogeochemical cycling (Ellis-Soto, Ferraro et al. 2021). By combining experimental studies with large-scale, landscape-level observations, researchers should be able to uncover how interactions between predators and prey can play a role in shaping the spatial heterogeneity of the ecosystems they inhabit.

Conclusion

Ecologists have long recognized the importance of bottom-up factors, such as geophysical variation and climate, in determining the biogeochemical and vegetational diversity of earth's ecosystems. However, the top-down effects of biotic interactions also have profound impacts on ecosystems, and consideration of these factors can improve our understanding of the generation and maintenance of landscape heterogeneity and diversity (Pausas and Bond 2019). Indeed, recognizing the ways in which organisms alter and construct their environments can help explain variation that cannot be attributed to climatic and other abiotic differences (*e.g.*, the coexistence of savanna and forest ecosystems within the same climatic zone [Staver et al. 2009, 2011; Staver & Bond 2014; Pausas & Bond 2019]). The evidence presented here enhances the call for new empirical analysis of animal-driven, spatially explicit biogeochemistry, aka zoogeochemistry (Pastor 2005, Turner and Chapin 2005, Schmitz et al. 2018). This call is not just academic, but will also deepen our understanding of the conservation value of predator and large herbivore species beyond their charisma. Predators may have pivotal roles in regulating ecosystem functioning and merit attention even when conservation strategies are geared towards a whole-ecosystem perspective (Sinclair and Byrom 2006, Schmitz et al. 2010).

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References

Abbas, F. et al. 2012. Roe deer may markedly alter forest nitrogen and phosphorus budgets across Europe. - Oikos 121: 1271–1278.

Abraham, J. O. et al. 2019. Drought-response strategies of savanna herbivores. - Ecol. Evol. 9: 7047–7056.

Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. - Am. Nat. 124: 80–96.

Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. - Am. Nat. 140: 573–600.

Abrams, P. A. 2000. The impact of habitat selection on the spatial heterogeneity of resources in varying environments. - Ecology 81: 2902–2913.

Acebes, P. et al. 2013. Trade-offs between food availability and predation risk in desert environments: the case of polygynous monomorphic guanaco (Lama guanicoe). - J. Arid. Environ. 97: 136–142.

Anderson, T. M. et al. 2008. Generation and maintenance of heterogeneity in the Serengeti ecosystem. - In: Sinclair, A. R. E. et al. (eds), Serengeti III: Human Impacts on Ecosystem Dynamics. University of Chicago Press, in press.

Anderson, T. M. et al. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. - Ecology 91: 1519–1529.

Asner, G. P. and Vitousek, P. M. 2005. Remote analysis of biological invasion and biogeochemical change. - Proc. Natl Acad. Sci. 102: 4383–4386.

Atkins, J. L. et al. 2019. Cascading impacts of large-carnivore extirpation in an African ecosystem. - Science 364: 173–177.

Augustine, D. J. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. - J. Appl. Ecol. 40: 137–149.

Augustine, D. J. and Frank, D. A. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. - Ecology 82: 3149–3162.

Augustine, D. J. et al. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. - Ecol. Appl. 13: 1325–1337.

Bai, Y. et al. 2012. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. - J. Appl. Ecol. 49: 1204–1215.

Bakker, E. S. et al. 2016. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. - Proc. Natl Acad. Sci. 113: 847–855.

Bardgett, R. D. and Wardle, D. A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. - Ecology 84: 2258–2268.

Barthelemy, H. et al. 2017. Urine is an important nitrogen source for plants irrespective of vegetation composition in an Arctic tundra: insights from a 15N-enriched urea tracer experiment. - J. Ecol. 106: 367–378.

Barton, P. S. et al. 2013a. Species traits predict assemblage dynamics at ephemeral resource patches created by carrion. - PLoS ONE 8: e53961.

Barton, P. S. et al. 2013b. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. - Oecologia 171: 761–772.

Barton, P. S. et al. 2016. Substantial long-term effects of carcass addition on soil and plants in a grassy eucalypt woodland. - Ecosphere 7: e01537.

Bauer, S. and Hoye, B. J. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. - Science 344: 1242552.

Bischof, R. et al. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? - Am. Nat. 180: 407–424.

Blanchard, P. et al. 2018. Coping with change in predation risk across space and time through complementary behavioral responses. - BMC Ecol. 18: 60.

Bonnot, N. C. et al. 2016. Sitka black-tailed deer (Odocoileus hemionus sitkensis) adjust habitat selection and activity rhythm to the absence of predators. - Can. J. Zool. 94: 385–394.

Bonnot, N. C. et al. 2018. Who's afraid of the big bad wolf? Variation in the stress response among personalities and populations in a large wild herbivore. - Oecologia 188: 85–95.

Brown, J. S. et al. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. - J. Mammal. 80: 385–399.

Bump, J. K. et al. 2009a. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. - Ecology 90: 3159–3167.

Bump, J. K. et al. 2009b. Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. - Ecosystems 12: 996–1007.

Carter, D. O. et al. 2007. Cadaver decomposition in terrestrial ecosystems. - Naturwissenschaften 94: 12–24.

Chapin, F. S. et al. 2011. Landscape Heterogeneity and Ecosystem Dynamics. - In: Chapin, F. S. et al. (eds), Principles of Terrestrial Ecosystem Ecology. Springer, pp. 369–397.

Courbin, N. et al. 2018. Zebra diel migrations reduce encounter risk with lions at night. - J. Anim. Ecol. 88: 92–101.

Creel, S. 2018. The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. - Ecol. Lett. 21: 947–956.

Creel, S. and Christianson, D. 2008. Relationships between direct predation and risk effects. - Trends Ecol. Evol. 23: 194–201.

Cromsigt, J. P. G. M. and Olff, H. 2008. Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. - Oikos 117: 1444–1452.

Cunningham, C. X. et al. 2019. Trophic rewilding establishes a landscape of fear: Tasmanian devil introduction increases risk-sensitive foraging in a key prey species. - Ecography 42: 2053–2059.

Cusack, J. J. et al. 2019. Weak spatiotemporal response of prey to predation risk in a freely interacting system. - J. Anim. Ecol. 89: 120–131.

Danell, K. et al. 2002. Effect of muskox carcasses on nitrogen concentration in tundra vegetation. - Arctic 55: 389–392.

Davies, A. B. et al. 2021. Spatial heterogeneity facilitates carnivore coexistence. - Ecology 102: e03319.

Day, T. A. and Detling, J. K. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. - Ecology 71: 180–188.

Donadio, E. and Buskirk, S. W. 2016. Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. - J. Mammal. 97: 966–977.

Doughty, C. E. et al. 2013. The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. - Nat. Geosci. 6: 761–764.

Doughty, C. E. et al. 2016a. Global nutrient transport in a world of giants. - Proc. Natl Acad. Sci. 113: 868–873.

Doughty, C. E. et al. 2016b. Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. - Ecography 39: 194–203.

Dröge, E. et al. 2017. Risky times and risky places interact to affect prey behaviour. - Nat. Ecol. Evol. 1: 1123–1128.

Edwards, M. S. and Konar, B. 2020. Trophic downgrading reduces spatial variability on rocky reefs. - Sci. Rep. 10: 18079.

Ellis-Soto, D. et al. 2021. A methodological roadmap to quantify animal-vectored spatial ecosystem subsidies. - Journal of Animal Ecology in press.

Estes, J. A. et al. 2011. Trophic downgrading of planet Earth. - Science 333: 301–306.

Fedriani, J. M. et al. 2015. Subtle gardeners: inland predators enrich local topsoils and enhance plant growth. - PLoS ONE 10: e0138273.

Fleming, P. A. et al. 2013. Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? - Mammal Rev. 44: 94–108.

Forbes, E. S. et al. 2019. Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. - Funct. Ecol. 33: 1597–1610.

Ford, A. T. et al. 2014. Large carnivores make savanna tree communities less thorny. - Science 346: 346–349.

Fortin, D. et al. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. - Ecology 86: 1320–1330.

Fryxell, J. M. et al. 1988. Why are migratory ungulates so abundant? - Am. Nat. 131: 781–798.

Gaynor, K. M. et al. 2019. Landscapes of fear: spatial patterns of risk perception and response. - Trends Ecol. Evol. 34: 355–368.

Gervasi, V. et al. 2013. Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. - Ecol. Appl. 23: 1722–1734.

Gharajehdaghipour, T. and Roth, J. D. 2018. Predators attract prey through ecosystem engineering in the Arctic. - Ecosphere 9: e02077.

Gharajehdaghipour, T. et al. 2016. Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. - Sci. Rep. 6: 24020.

Gill, J. L. et al. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. - Science 326: 1100–1103.

Goheen, J. R. et al. 2018. Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU, and GLADE experiments. - Ann. N.Y. Acad. Sci. 1429: 31–49.

Harvey, R. J. et al. 2016. Determining position, velocity and acceleration of free-ranging animals with a low-cost unmanned aerial system. - J. Exp. Biol. 219: 2687–2692.

Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. - Theor. Popul. Biol. 12: 37–48.

Haswell, P. M. et al. 2017. Large carnivore impacts are context-dependent. - Food Webs 12: 3–13.

Hawlena, D. and Schmitz, O. J. 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. - Proc. Natl Acad. Sci. 107: 15503–15507.

Hawlena, D. et al. 2012. Fear of predation slows plant-litter decomposition. - Science 336: 1434–1438.

Hay, C. T. et al. 2008. Trade-offs of predation and foraging explain sexual segregation in African buffalo. - J. Anim. Ecol. 77: 850–858.

Helfield, J. M. and Naiman, R. J. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. - Ecology 82: 2403–2409.

Helfield, J. M. and Naiman, R. J. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. - Ecosystems 9: 167–180.

Hernández, L. and Laundré, J. W. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk (Cervus elaphus) and bison (Bison bison). - Wildlife Biol. 11: 215–220.

Hilderbrand, G. V. et al. 1999. Role of brown bears (Ursus arctos) in the flow of marine nitrogen into a terrestrial ecosystem. - Oecologia 121: 546–550.

Hocking, M. D. and Reynolds, J. D. 2011. Impacts of salmon on riparian plant diversity. - Science 331: 1609–1612.

Hocking, M. D. and Reynolds, J. D. 2012. Nitrogen uptake by plants subsidized by Pacific salmon carcasses: a hierarchical experiment. - Can. J. For. Res. 42: 908–917.

Holtgrieve, G. W. et al. 2009. Large predators and biogeochemical hotspots: brown bear (Ursus arctos) predation on salmon alters nitrogen cycling in riparian soils. - Ecol. Res. 24: 1125–1135.

Hopcraft, J. G. C. et al. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. - J. Anim. Ecol. 74: 559–566.

Hopcraft, J. G. C. et al. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. - Trends Ecol. Evol. 25: 119–128.

Hopcraft, J. G. C. et al. 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. - J. Anim. Ecol. 81: 201–213.

Hunter, M. D. and Price, P. W. 1992. Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities. - Ecology 73: 724–732.

Huntly, N. and Inouye, R. 1988. Pocket gophers in ecosystems: patterns and mechanisms. - BioScience 38: 786–793.

2000. The Ecological Consequences of Environmental Heterogeneity (MJ Hutchings, LA John, and AJA Stewart, Eds.). - Cambridge University Press.

Kane, D. et al. 2019. Quick Carbon: A Rapid, Landscape-Scale Soil Carbon Assessment Tool. - AGU Fall Meeting Abstracts 31: B31E-02.

Kauffman, M. J. et al. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. - Ecol. Lett. 10: 690–700.

Kauffman, M. J. et al. 2010. Are wolves saving Yellowstone’s aspen? A landscape-level test of a behaviorally mediated trophic cascade. - Ecology 91: 2742–2755.

Kays, R. et al. 2015. Terrestrial animal tracking as an eye on life and planet. - Science 348: aaa2478.

Keenan, S. W. et al. 2018. Mortality hotspots: nitrogen cycling in forest soils during vertebrate decomposition. - Soil Biol. Biochem. 121: 165–176.

Kitchell, J. F. et al. 1999. Nutrient cycling at the landscape scale: the role of diel foraging migrations by geese at the Bosque del Apache National Wildlife Refuge, New Mexico. - Limnol. Oceanogr. 44: 828–836.

Kohl, M. T. et al. 2018. Diel predator activity drives a dynamic landscape of fear. - Ecol. Monogr. 88: 638–652.

Laundré, J. W. et al. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. - Can. J. Zool. 79: 1401–1409.

le Roux, E. et al. 2018. Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. - Curr. Biol. 28: 2493–2499.

le Roux, E. et al. 2020. Animal body size distribution influences the ratios of nutrients supplied to plants. - Proc. Natl Acad. Sci. 117: 22256–22263.

Leempoel, K. et al. 2019. Return of an apex predator to a suburban preserve triggers a rapid trophic cascade. - bioRxiv in press.

Leroux, S. J. and Loreau, M. 2015. Theoretical perspectives on bottom-up and top-down interactions across ecosystems. - In: Hanley, T. C. and La Pierre, K. J. (eds), Trophic Ecology: Bottom-Up and Top-Down Interactions across Aquatic and Terrestrial Systems. Ecological Reviews. Cambridge University Press, pp. 3–28.

Leroux, S. J. and Schmitz, O. J. 2015. Predator-driven elemental cycling: the impact of predation and risk effects on ecosystem stoichiometry. - Ecol. Evol. 5: 4976–4988.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. - Can. J. Zool. 68: 619–640.

2005. Ecosystem Function in Heterogeneous Landscapes (GM Lovett, C Jones, MG Turner, and KC Weathers, Eds.). - Springer.

Luttbeg, B. et al. 2020. Predator hunting modes and predator–prey space games. - Ethology 126: 476–485.

Macdonald, B. C. T. et al. 2014. Carrion decomposition causes large and lasting effects on soil amino acid and peptide flux. - Soil Biol. Biochem. 69: 132–140.

Macek, P. et al. 2009. Biological activities as patchiness driving forces in wetlands of northern Belize. - Oikos 118: 1687–1694.

Mackay, J. et al. 2021. Animals connect plant species and resources in a meta-ecosystem. - Landsc. Ecol. 36: 1621–1629.

Makin, D. F. et al. 2018. Changes in feeding behavior and patch use by herbivores in response to the introduction of a new predator. - J. Mammal. 99: 341–350.

McInturf, A. G. et al. 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? - Biol. Rev. 94: 1761–1773.

McNamara, J. M. and Houston, A. I. 1990. The value of fat reserves and the tradeoff between starvation and predation. - Acta Biotheor. 38: 37–61.

McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. - Am. Nat. 113: 691–703.

McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. - Ecol. Monogr. 53: 291–320.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. - Ecol. Monogr. 55: 260–294.

McNaughton, S. J. et al. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. - Nature 341: 142–144.

McNaughton, S. J. et al. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. - Science 278: 1798–1800.

Merkle, J. A. et al. 2016. Large herbivores surf waves of green-up during spring. - Proc. R. Soc. B 283: 20160456.

Middleton, A. D. et al. 2013a. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. - Ecology 94: 1245–1256.

Middleton, A. D. et al. 2013b. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. - Ecol. Lett. 16: 1023–1030.

Miller, J. R. B. et al. 2014. Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. - J. Anim. Ecol. 83: 214–222.

Moll, R. J. et al. 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. - J. Anim. Ecol. 86: 749–765.

Montgomery, R. A. et al. 2014. Where wolves kill moose: the influence of prey life history dynamics on the landscape ecology of predation. - PLoS ONE 9: e91414.

Moore, J. C. et al. 2004. Detritus, trophic dynamics and biodiversity. - Ecol. Lett. 7: 584–600.

Morris, T. and Letnic, M. 2017. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. - Proc. R. Soc. B 284: 20170111.

Oates, B. A. et al. 2019. Antipredator response diminishes during periods of resource deficit for a large herbivore. - Ecology 100: e02618.

Owen-Smith, N. 1988. Megaherbivores: The Influence of Very Large Body Size on Ecology. - Cambridge University Press.

Owen-Smith, N. 2015. Mechanisms of coexistence in diverse herbivore–carnivore assemblages: demographic, temporal and spatial heterogeneities affecting prey vulnerability. - Oikos 124: 1417–1426.

Owen-Smith, N. 2019. Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. - Biol. Conserv. 232: 51–58.

Parmenter, R. R. and MacMahon, J. A. 2009. Carrion decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem. - Ecol. Monogr. 79: 637–661.

Pastor, J. 2005. Thoughts on the generation and importance of spatial heterogeneity in ecosystems and landscapes. - In: Lovett, G. M. et al. (eds), Ecosystem Function in Heterogeneous Landscapes. Springer, pp. 49–66.

Pastor, J. et al. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. - Ecology 74: 467–480.

Pausas, J. G. and Bond, W. J. 2019. Humboldt and the reinvention of nature. - J. Ecol. 107: 1031–1037.

Pausas, J. G. and Bond, W. J. 2020. On the three major recycling pathways in terrestrial ecosystems. - Trends in Ecology & Evolution 35: 767–775.

Peers, M. J. L. et al. 2018. Quantifying fear effects on prey demography in nature. - Ecology 99: 1716–1723.

Pellegrini, A. F. A. et al. 2016. Woody plant biomass and carbon exchange depend on elephant-fire interactions across a productivity gradient in African savanna. - J. Ecol. 105: 111–121.

Riginos, C. 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. - Ecology 90: 335–340.

Riginos, C. 2015. Climate and the landscape of fear in an African savanna. - J. Anim. Ecol. 84: 124–133.

Riginos, C. and Grace, J. B. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. - Ecology 89: 2228–2238.

Ripple, W. J. and Beschta, R. L. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? - BioScience 54: 755–766.

Ripple, W. J. et al. 2014. Status and ecological effects of the world’s largest carnivores. - Science 343: 1241484.

Risch, A. C. et al. 2020. Effects of elk and bison carcasses on soil microbial communities and ecosystem functions in Yellowstone, USA. - Funct. Ecol. 34: 1933–1944.

Rivrud, I. M. et al. 2018. Reindeer green-wave surfing constrained by predators. - Ecosphere 9: e02210.

Say-Sallaz, E. et al. 2019. Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. - Biol. Conserv. 235: 36–52.

Schmidt, K. and Kuijper, D. P. J. 2015. A “death trap” in the landscape of fear. - Mammal Res. 60: 275–284.

Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. - Science 319: 952–954.

Schmitz, O. J. et al. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. - Ecology 78: 1388–1399.

Schmitz, O. J. et al. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. - Ecol. Lett. 7: 153–163.

Schmitz, O. J. et al. 2010. Predator control of ecosystem nutrient dynamics. - Ecol. Lett. 13: 1199–1209.

Schmitz, O. J. et al. 2017a. Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. - Ecology 98: 2281–2292.

Schmitz, O. J. et al. 2017b. Predator community composition is linked to soil carbon retention across a human land use gradient. - Ecology 98: 1256–1265.

Schmitz, O. J. et al. 2018. Animals and the zoogeochemistry of the carbon cycle. - Science 362: eaar3213.

Seagle, S. W. 2003. Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets? - Oikos 103: 230–234.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? - Science 210: 1041–1043.

Sih, A. 2005. Predator-prey space use as an emergent outcome of a behavioral response race. - In: Barbosa, P. and Castellanos, I. (eds), Ecology of Predator-Prey Interactions. Oxford University Press, in press.

Sinclair, A. R. E. and Arcese, P. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. - Ecology 76: 882–891.

Sinclair, A. R. E. and Byrom, A. E. 2006. Understanding ecosystem dynamics for conservation of biota. - J. Anim. Ecol. 75: 64–79.

Sinclair, A. R. E. et al. 2003. Patterns of predation in a diverse predator–prey system. - Nature 425: 288–290.

Smith, J. A. et al. 2019a. Habitat complexity mediates the predator–prey space race. - Ecology 100: e02724.

Smith, J. A. et al. 2019b. Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. - Oecologia 189: 883–890.

Smith, J. A. et al. 2021. Where and when to hunt? Decomposing predation success of an ambush carnivore. - Ecology 101: e03172.

Staver, A. C. and Bond, W. J. 2014. Is there a ‘browse trap’? Dynamics of herbivore impacts on trees and grasses in an African savanna. - J. Ecol. 102: 595–602.

Staver, A. C. et al. 2009. Browsing and fire interact to suppress tree density in an African savanna. - Ecol. Appl. 19: 1909–1919.

Staver, A. C. et al. 2011. The global extent and determinants of savanna and forest as alternative biome states. - Science 334: 230–232.

Staver, A. C. et al. 2019. Grazer movements exacerbate grass declines during drought in an African savanna. - J. Ecol. 107: 1482–1491.

Steenweg, R. et al. 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. - Front. Ecol. Environ. 15: 26–34.

Strickland, M. S. et al. 2013. Trophic cascade alters ecosystem carbon exchange. - Proc. Natl Acad. Sci. 110: 11035–11038.

Subalusky, A. L. and Post, D. M. 2018. Context dependency of animal resource subsidies. - Biol. Rev. 94: 517–538.

Subalusky, A. L. et al. 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. - Proc. Natl Acad. Sci. 114: 7647–7652.

Thaker, M. et al. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. - Ecology 92: 398–407.

Towne, E. G. 2000. Prairie vegetation and soil nutrient responses to ungulate carcasses. - Oecologia 122: 232–239.

Turner, M. G. and Chapin, F. S. 2005. Causes and consequences of spatial heterogeneity in ecosystem function. - In: Lovett, G. M. et al. (eds), Ecosystem Function in Heterogeneous Landscapes. Springer, pp. 9–30.

Turner, M. G. and Gardner, R. H. 2015. Ecosystem Processes in Heterogeneous Landscapes. - In: Turner, M. G. and Gardner, R. H. (eds), Landscape Ecology in Theory and Practice. Springer, New York, NY, pp. 287–332.

Valeix, M. et al. 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? - Behav. Ecol. Sociobiol. 63: 1483–1494.

van der Graaf, A. et al. 2006. Surfing on a green wave–how plant growth drives spring migration in the Barnacle Goose Branta leucopsis. - Ardea 94: 567–577.

van der Waal, C. et al. 2011. Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. - Oecologia 165: 1095–1107.

van Nes, E. H. and Scheffer, M. 2005. Implications of Spatial Heterogeneity for Catastrophic Regime Shifts in Ecosystems. - Ecology 86: 1797–1807.

Vanak, A. T. et al. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. - Ecology 94: 2619–2631.

Veldhuis, M. P. et al. 2014. A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant-soil water balance (S Schwinning, Ed.). - J. Ecol. 102: 1506–1517.

Waldram, M. S. et al. 2008. Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. - Ecosystems 11: 101–112.

Wang, L. et al. 2009. Remote sensing of nitrogen and carbon isotope compositions in terrestrial ecosystems. - In: West, J. B. et al. (eds), Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping. Springer, pp. 51–70.

Wardle, D. A. et al. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. - Funct. Ecol. 16: 585–595.

Wilmers, C. C. et al. 2016. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. - Ecology 96: 1741–1753.

Winnie, J. A. et al. 2008. Habitat quality and heterogeneity influence distribution and behavior in African Buffalo (Syncerus caffer). - Ecology 89: 1457–1468.

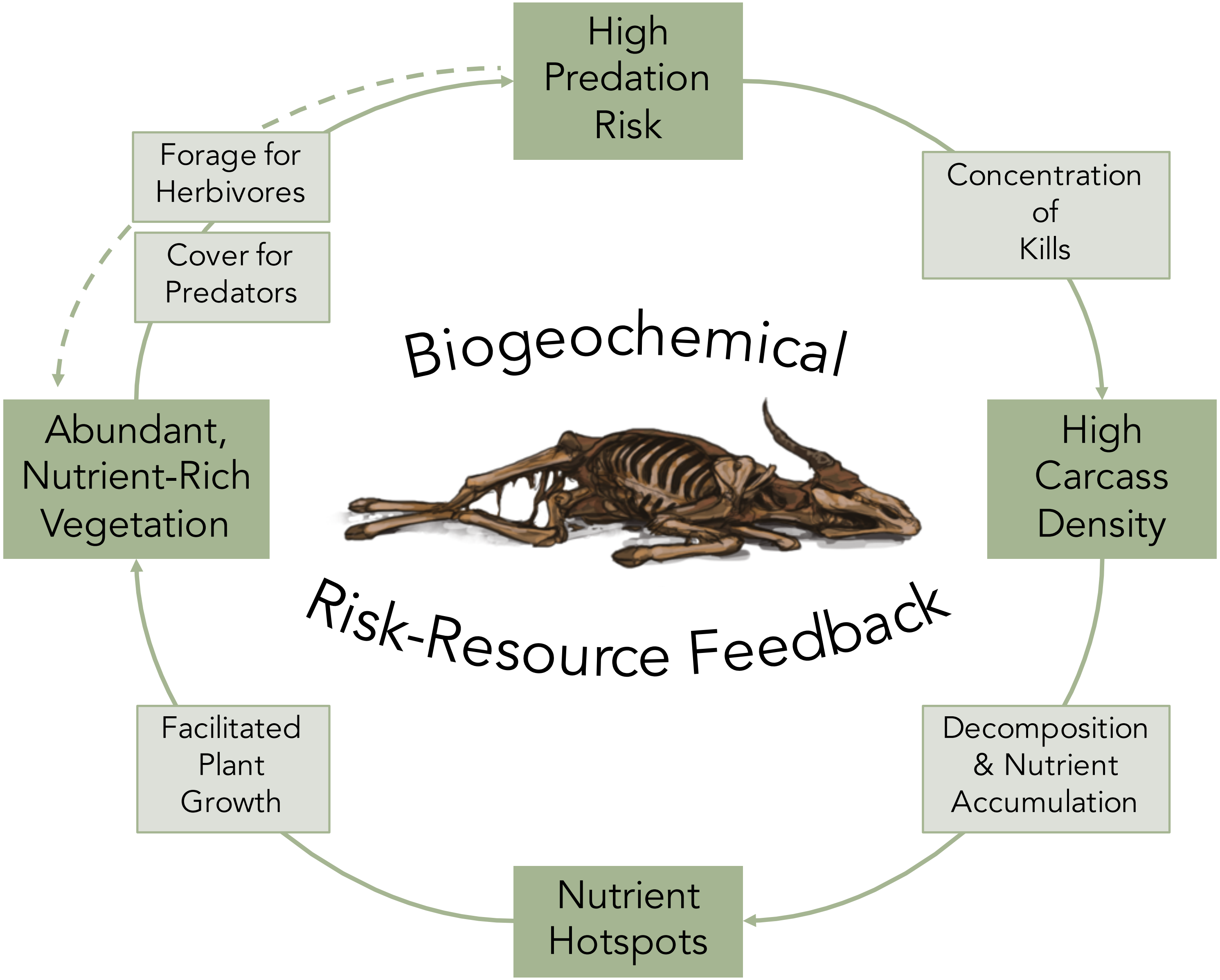
Wirsing, A. J. et al. 2021. The context dependence of non-consumptive predator effects. - Ecol. Lett. 24: 113–129.

Wolf, A. et al. 2013. Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. - PLoS ONE 8: e71352.

Young, T. P. et al. 1995. Long-term glades in acacia bushland and their edge effects in Laikipia, Kenya. - Ecol. Appl. 5: 97–108.

Young, H. S. et al. 2015. Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. - Ecol. Appl. 25: 348–360.

Figure 1. Theorized positive feedback loop between predation risk and nutrient availability in the biogeochemical landscape of fear. Where there is strong spatial variation in predation risk on the landscape, high carcass density in risky habitats where predation success is high may generate nutrient hotspots as carcasses decompose. In turn, nutrient accumulation after decomposition could stimulate plant growth and quality, resulting in abundant, nutrient-rich vegetation in risky habitats. Finally, this increased plant quantity and quality simultaneously provides cover for ambush predators and forage for herbivores, increasing the probability of predator-prey interactions and reinforcing the risky nature of these sites. The dashed line indicates an indirect positive feedback between predation risk and vegetation abundance, mediated by herbivory. While the attraction of herbivores to nutrient-rich forage at nutrient hotspots could potentially initiate a negative feedback if herbivores graze or browse down vegetation (thus denuding risky sites and rendering them less advantageous hiding spots for predators), if the perceived risk of predation is sufficiently high, herbivores with access to other resources may avoid even these high-quality sites or may remain highly vigilant, reducing their foraging rates. If the former, nutrient hotspots may act as an attractant only in times of scarcity or for undernourished individuals. In either case, herbivory remains lower than the quantity and quality of forage would predict, but high enough to sustain a prey base for the predator population at risky sites.



Biogeochemical Risk-Resource Feedback

High Predation Risk

Concentration of Kills

High Carcass Density

Decomposition & Nutrient Accumulation

Nutrient Hotspots

Facilitated Plant Growth

Abundant, Nutrient-Rich Vegetation

Cover for Predators

Forage for Herbivores

Figure 2. A framework for the spatial biogeochemical consequences of antipredator behavior. When prey habitat domain, or the spatial extent of the area used for foraging, extends beyond that of its predator, antipredator behavior often takes the form of a habitat shift away from risky areas to safer areas with low predator activity (Schmitz et al. 2004, 2017). This habitat shift can concentrate foraging and nutrient recycling in safe habitats, generating and maintaining nutrient hotspots, as in grazing lawns in African savannas. When prey habitat domain largely overlaps with that of its predator, providing few spatial refugia from risk, antipredator behaviors generally take the form of time budget shifts (e.g. altered diel activity patterns) or other non-spatial behaviors such as increased vigilance. These behaviors largely do not alter the spatial distribution of nutrients or their rates of cycling on the landscape. However, antipredator strategies often combine these different behavioral approaches. When prey are obligated to enter their predator's habitat domain because it contains some essential resource (such as high-quality forage or water), they may mitigate risk through a combined habitat and time budget shift, traveling between safe and risky habitats while attempting to track periods of low predator activity. This combined habitat and time budget shift can drive nutrient subsidies as prey consume high-quality forage in risky habitats and egest and excrete nutrients in safe habitats as they move across the landscape to avoid predators.

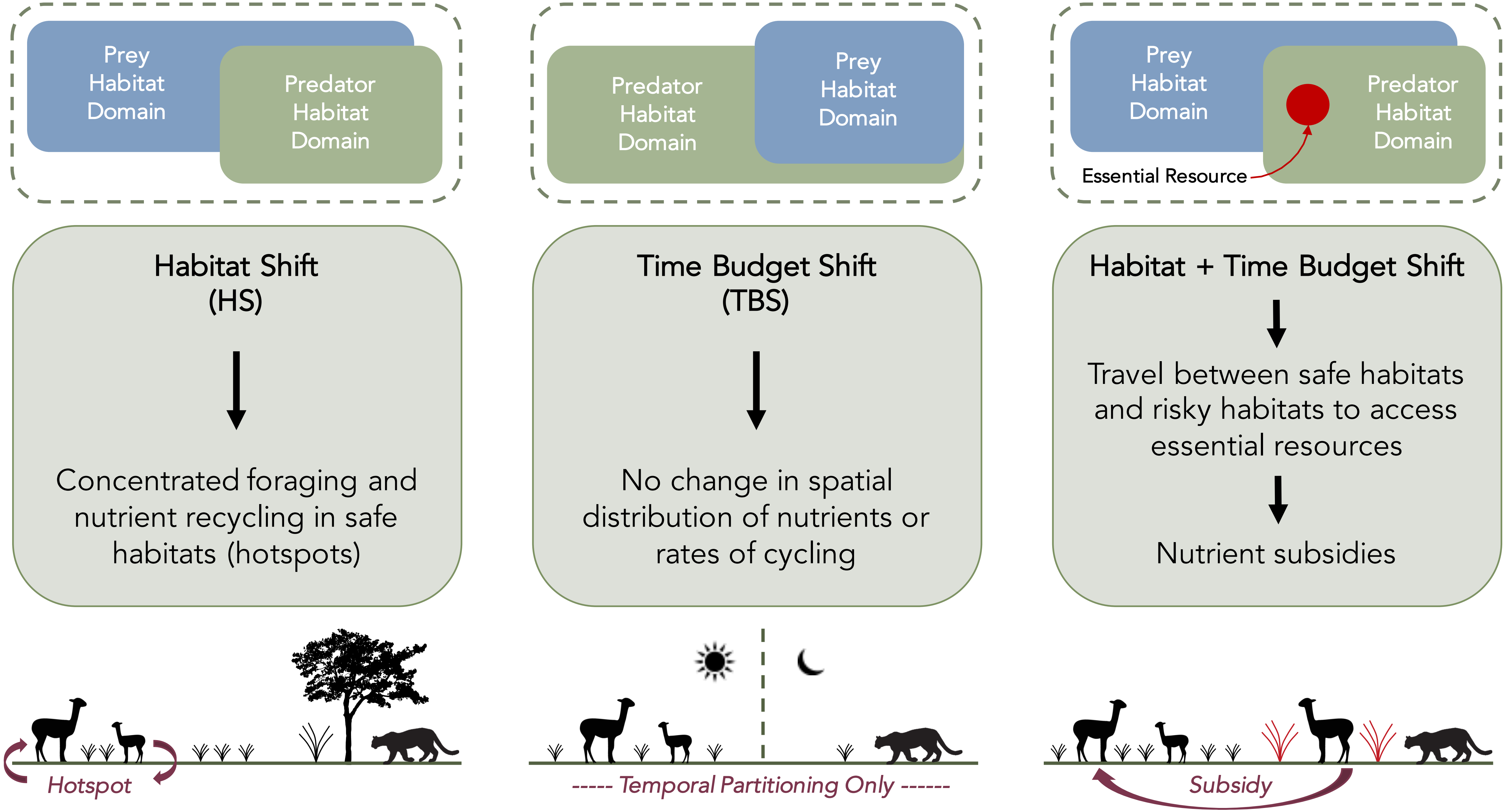

Prey Habitat Domain
Predator Habitat Domain
Habitat Shift (HS)
Concentrated foraging and nutrient recycling in safe habitats (hotspots)
Hotspot
Predator Habitat Domain
Prey Habitat Domain
Time Budget Shift (TBS)
No change in spatial distribution of nutrients or rates of cycling
----- Temporal Partitioning Only ------
Prey Habitat Domain
Predator Habitat Domain
Essential Resource
Habitat + Time Budget Shift
Travel between safe habitats and risky habitats to access essential resources
Nutrient subsidies
Subsidy

Figure 3. Shifting body size structure in animal communities generates heterogeneity cascades in ecosystems. In a world dominated by highly mobile megafauna with low vulnerability to predation (A), these megaherbivores may have homogenized ecosystems by consuming, processing, transporting, and depositing nutrients evenly across their large home ranges (Doughty et al. 2016). In the wake of the Pleistocene extinctions and more modern suppression of remaining megaherbivore species by humans, even the most faunally diverse ecosystems are largely dominated by mesoherbivores – mammalian herbivores large enough to range widely and consume large quantities of forage, but small enough to be highly susceptible to predation by large carnivores. In these contemporary mesoherbivore ecosystems (B), predators reinforce and steepen underling abiotic gradients in resource availability by discouraging herbivory in more nutrient-rich sites with high risk, while occasionally also driving the generation of isolated, productive patches in safe habitats via the creation of grazing lawns and sites with high levels of herbivore-mediated nutrient cycling. In some of these ecosystems, megaherbivores can still transport nutrients across the risk gradient and act as homogenizing forces (see le Roux et al. 2018); nevertheless, the non-consumptive effects of predators on herbivore behavior also reinforces heterogeneity in predator-dominated ecosystems. However, as predators are extirpated from diverse landscapes due to human persecution and habitat fragmentation (C), mesoherbivores will be released from predation risk and may abandon their traditional antipredator behaviors, foraging more uniformly on the landscape and homogenizing ecosystems as their megaherbivore predecessors once did.

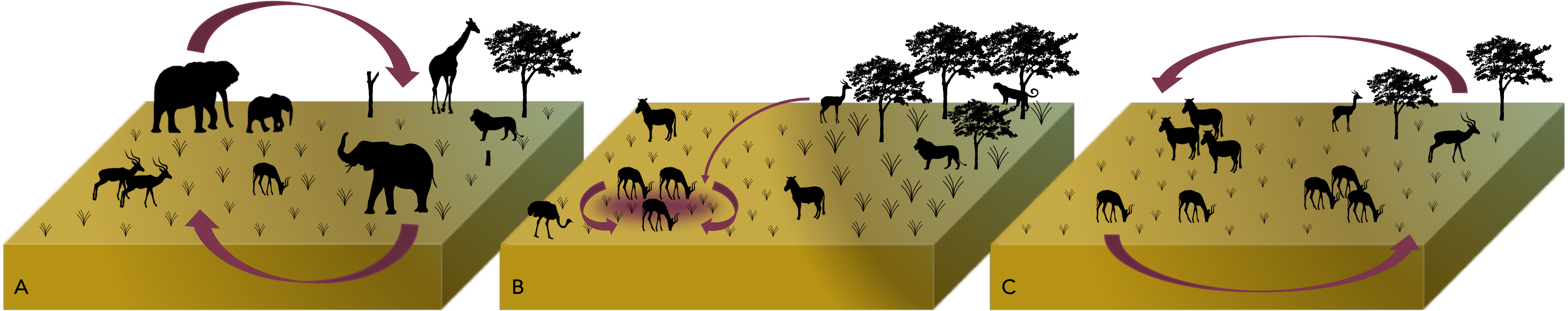

A
B
C

Figure 4. A simple framework for predicting contexts in which predator-prey interactions should act as heterogenizing vs. neutral or homogenizing forces. The synthesized research and novel hypotheses presented in this paper can be summarized into the following broad predictions: predator-prey interactions should **increase landscape heterogeneity** in ecosystems where trophic links are strong and there is high spatial variation in predator consumptive and non-consumptive effects. Strong predator-prey trophic links often occur in simple systems where there is one apex predator specialized on just one or a few large herbivore species. High spatial variation in predator consumptive and non-consumptive effects is most likely in systems dominated by ambush predators, who hide and rapidly attack prey in opportune habitats with sufficient cover – maintaining predictable sites with higher perceived risk on the landscape, where kills are often clustered. In contrast, predator-prey interactions should **decrease landscape heterogeneity** in ecosystems where trophic links are weak (e.g. diverse systems with multiple predators and prey, or systems with large herbivores who are less susceptible to predation) or where there is low spatial variation in top-down predator effects (e.g. systems dominated by actively hunting predators who track prey across the landscape, or when prey mitigate risk by altering their daily activity patterns rather than their space use).

Heterogenizing Force	Homogenizing Force
Strong Predator-Prey Trophic Links • Simple systems (one predator, one herbivore) • Specialized predators	**Weak Predator-Prey Trophic Links** • Diverse systems (multi-predator, multi-herbivore) • Low prey susceptibility (e.g. large body size)
High Spatial Variation in Predator Consumptive and Non-Consumptive Effects • Ambush predator • Predictable sites with high perceived risk • Clustered kills & carcass deposition	**Low Spatial Variation in Predator Consumptive and Non-Consumptive Effects** • Actively hunting predator • Antipredator response is temporal rather than spatial