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TROPHIC CASCADES AS A BASIS FOR REWILDING

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Introduction

Rewilding is a conservation strategy that is becoming increasingly popular throughout the world. Although the term has multiple meanings, rewilding usually indicates a long-term conservation goal of maintaining or increasing biodiversity, while reducing the impact of present and past human interventions through reintroduction of extirpated species and ecological restoration. Because one of the most important taxonomic groups to have suffered human-caused extirpation are large carnivores (Ripple et al., 2014), they have often become the focus of rewilding strategies. One additional justification for large carnivore rewilding is that they will cause trophic cascades, via trickle-down effects of top predators on plants and other species in an ecosystem. Here, we review the evidence for trophic cascades and the utility of using this strategy to support rewilding of large carnivores.

Most conservationists are familiar with trophic cascades as a basis for rewilding from Yellowstone National Park (YNP) where wolves were reintroduced in 1995. This concept has been popularised by a video called ‘How Wolves Change Rivers’, which combines footage of Yellowstone with narration by journalist George Monbiot (Sustainable Human, 2014). This video has been viewed > 43 million times, been adopted in school curriculums globally, and has contributed to popularising/mainstreaming the concept that rewilding wolves has caused trophic cascades in Yellowstone. In the video, Monbiot explains that when wolves were reintroduced to the park, they ‘radically changed the behavior of the deer [sic]’ to avoid areas where they were most vulnerable to predation, and ‘bare valley sides quickly became forests of aspen and willow and cottonwood’ due to decreased herbivory by deer. The video also states that trophic cascades from wolves helped change the behaviour of rivers and decreased soil erosion in the park. Therefore, ‘the wolves ... transform not just the ecosystem of the Yellowstone National Park ... but also its physical geography’. Although the video is provocative and the idea of trophic cascades by wolves in Yellowstone is highly cited, there is no scientific consensus that these effects have occurred, which we review below. Despite this ambiguity, wolf-induced trophic cascades in Yellowstone are the paradigm of the benefits of large carnivore reintroduction.

In this chapter, we aim to provide some clarity for those who are interested in rewilding to create trophic cascades as a conservation tool. The chapter is in four sections: an introduction

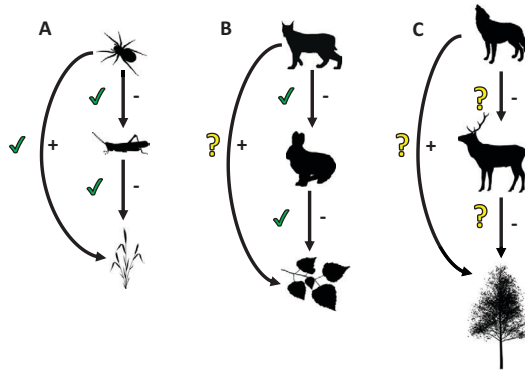


Figure 6.1 Evidence for trophic cascades across ecosystems (**A**), in large carnivores (**B**), and in Yellowstone (**C**). Although **A** and **B** show Connecticut grassland and boreal forest food webs respectively, we intend these silhouettes to be more general and represent trophic cascades across ecosystems and in large carnivores, respectively. Straight lines from predator to herbivore represent the direct effect of predation, which is negative on the herbivore. Straight lines from herbivore to primary producer represent the direct effect of herbivory, which is negative on the primary producer. Curved lines from predator to primary producer represent the indirect effect, which is positive on the primary producer. Checkmarks show that there is substantial positive evidence for the direct or indirect effect, although there may be a few exceptions. Question marks show that there is mixed evidence/a lack of scientific consensus for the effect. We did not find any effects which had a total lack of evidence. (**A**) shows the classic spider-grasshopper-grass/forb trophic cascade (e.g., Schmitz 2008), which here represents evidence for trophic cascades across all ecosystems. (**B**) shows a lynx-snowshoe hare-deciduous shrub trophic cascade, where although direct effects occurred, an indirect effect was not found (Sinclair et al., 2000). This represents evidence for trophic cascades in large carnivore systems. (**C**) shows a wolf-elk-aspen trophic cascade in Yellowstone, where there is mixed evidence for trophic cascades (Peterson et al., 2014, 2020; MacNulty et al., 2020).

and history of trophic cascades, evidence for large carnivore trophic cascades, evidence for trophic cascades in Yellowstone, and whether we should justify rewilding on the basis of trophic cascades. Throughout, we will refer to Figure 6.1, which summarises the best available evidence on trophic cascades in the first three chapter sections. One thing to expect in the scientific literature is a lack of consensus—where this is the case, we will categorise an interaction as ‘maybe’. If we categorise an interaction as ‘yes’ or ‘no’, this means that there is majority evidence to suggest that this interaction does or does not occur, but there might be counterexamples one can find in the literature. We will provide evidence for and answer questions surrounding trophic cascades and whether the addition or removal of carnivores will have cascading consequences for ecosystem functions.

Basics of trophic cascades

What is a trophic cascade? A *trophic cascade* is caused by reduced herbivory of plants in response to carnivores’ numerical reduction of herbivorous prey, leading to increases in plants’ growth, biomass, cover, reproduction, or survival. Therefore, a trophic cascade requires evidence of three interactions: 1) reduction of herbivores by carnivores; 2) reduction of plants by herbivores; and 3) the indirect increase in plants by carnivores via suppression of herbivory (Ford & Goheen, 2015). Three-species cascades are the simplest and most familiar cases (e.g., Yellowstone’s wolf-elk-vegetation). The archetypal form of trophic cascades has been generalised and blurred due

to the popularisation of the idea to include many other indirect food web interactions (e.g., Ripple et al., 2016). However, we will focus on the trophic cascade that is invoked in rewilding campaigns. Carnivores demographically (consumptive—eating/killing) or behaviourally (non-consumptive—scaring) suppress herbivorous prey, leading to plants' enhanced growth, biomass, reproduction, survival, etc.

Trophic cascades have been known about since at least Darwin's time (Ripple et al., 2016). Many of the early examples illustrate what happens when top predators are eliminated from ecosystems. Aldo Leopold (1949) wrote about the destruction of habitat by deer in the US following wolf extirpation in his *Thinking Like a Mountain*. To quote: 'I have watched the face of many a newly wolfless mountain, and...seen every edible bush and seedling browsed, first to anemic desuetude, and then to death'. Leopold is presaging that the losses of top predators in an ecosystem can abruptly change vegetation and move ecosystems into different states. Later, Hairston, Smith, and Slobodkin (1960) introduced this idea into scientific discourse as the *green world hypothesis*, that is, predators allow plants to flourish by reducing the numbers of herbivores.

One notable example of trophic cascades is in Pacific kelp forests, where sea otters were hunted to near extinction during the maritime fur trade in the 18th–19th centuries. Sea otters preyed on herbivorous sea urchins, so the eradication of sea otters cascaded to defoliate kelp forests throughout the Pacific (Estes and Palmisano, 1974). As sea otter populations recover and decline, ecosystems shifted between the states of the kelp-dominated (otters) and urchin-dominated (no otters). Another example of trophic cascades occurred in Venezuela where hydroelectric dams flooded an area in the tropics creating small islands free of predators. This led to 10–100 times greater numbers of rodents, howler monkeys, iguanas, and leaf-cutter ants on these predator-free islands than the mainland, cascading to severely reduce seedlings and saplings of canopy trees (Terborgh et al., 2001).

Trophic cascades occur through two nonexclusive mechanisms—density mediation or behavioural mediation (Ripple et al., 2016). *Density-mediated trophic cascades* occur through a numerical reduction of herbivores by predation, which then lead to increase biomass of primary producers. *Behaviourally-mediated trophic cascades* involve nonlethal, antipredator responses of herbivores to the risk of predation. For example, seagrass productivity increased in response to declined foraging by dugongs and sea turtles in the presence of tiger sharks (Burkholder et al., 2013). There are also *knock-on effects*, where changes in plants via trophic cascades can trigger further changes back up the food chain (Ripple et al., 2016). One controversial example is the trophic cascade of wolves to elk to berry-producing shrubs in Yellowstone, which has been hypothesised to have a knock-on effect to berry-consuming grizzly bears (Barber-Meyer, 2015). For the rest of this chapter, we will primarily focus on trophic cascades, not broader indirect or knock-on effects.

Behaviourally-mediated trophic cascades can be driven by fear of predation, which generate what is known as the *landscape of fear*. This is a mental map that describes the continuous change in predation risk that an animal perceives as it navigates its physical landscape (see Figure 4 in Kohl et al., 2018). The landscape effects of fear can cascade from individuals to ecosystems, including changes in prey physiology, demography, plant growth, and nutrient cycling (Laundré et al., 2001; Laundré et al., 2010; Kohl et al., 2018). However, predator hunting mode and prey antipredator behaviour can modulate the strength of the landscape of fear. For example, active-search hunting predators are expected to have weak/nonexistent fear-mediated effects, whereas sit-and-wait ambush predators should have the strongest effects (Schmitz, 2008). Antipredator vigilance and avoidance of risky places can be negligent in food-limited prey that can easily escape predators without vigilance (Brown, 1999). These behaviours, in addition to predation risk being unevenly distributed across space and time due to highly mobile predators and prey,

can lead to highly dynamic landscapes of fear (Kohl et al., 2018). We will revisit these ideas later when we discuss trophic cascades in Yellowstone.

Many of the earliest and best evidence for trophic cascades comes from aquatic ecosystems. This is because whole lakes with contrasting fish communities can be more readily experimented on to generate trophic cascades with the addition or removal of top fish predators. In North American lakes, piscivorous fish (like bass, pike, or salmon) can reduce populations of zooplanktivorous fish (like minnows), which can affect zooplankton communities, which in turn can change phytoplankton levels (Carpenter et al., 1985). Removal of piscivorous fish can therefore change water from clear to green by allowing phytoplankton to flourish. In the Eel River in northern California, steelhead and roach consume fish larvae and predatory insects. These smaller predators prey on midge larvae, which feed on algae. Experimental manipulations of these food webs by removing steelhead and roach led to large increases in algal biomass (Power, 1990). Despite these classic examples, trophic cascades in lake ecosystems are certainly not ubiquitous, with one review finding only 7 of 17 studies of piscivores on algae supporting trophic cascades (Drenner & Hambright, 2002).

Lake ecosystems have had a wide range of experiments and are quite robust, but experiments are a lot harder to do in marine and terrestrial ecosystems. Shurin et al. (2002) ran a meta-analysis of 102 trophic cascade experiments across different ecosystem types and found that the effect of predator removals on plant biomass were stronger in aquatic ecosystems than terrestrial ecosystems. These differences may relate to food web complexity (aquatic webs are simpler and thus cascades are stronger), metabolic rates (large herbivores in terrestrial systems have higher metabolic rates and are less efficient consumers relative to aquatic herbivores), and lack of plant defenses in aquatic systems (reduces strength of herbivory in terrestrial systems), which may lead to weak or nonexistent trophic cascades in terrestrial food webs (Shurin et al., 2002). Yet, many terrestrial predators such as spiders, beetles, lizards, guilds of birds, weasels, ants, and many others have been found to have cascading effects on plants (Terborgh & Estes, 2010).

Trophic cascades in large carnivores

Trophic cascades are difficult to experimentally study in large carnivores, especially due to their wide-ranging behaviour. Because of this, very few trophic cascades have been robustly experimentally studied (Ford & Goheen, 2015). Many studies rely on positive correlations between carnivore and plant abundance, which are not rigorous tests of trophic cascades because they are without experimental control, replications, and multiple competing hypotheses (see Box 1.1; Ford & Goheen, 2015). Because of this, much of the evidence for trophic cascades relies on historical observations of large increases in herbivores accompanied with intensive browsing on plants following large carnivore eradication (see Ripple et al., 2010).

Deer populations exploded throughout North America by the early 1900s following the extirpation of large predators like wolves, cougars, grizzly and black bears. For example, deer biomass was a fifth in areas with wolves than where wolves were absent or rare (Crête & Daigle, 1999). There is also evidence that large carnivores can reduce ungulate populations (see Figure 3A in Ripple & Beschta, 2012 and Figure 2 in Peterson et al., 2014), where each additional predator species results in a stepwise reduction in ungulate abundance. However, in some cases, functional redundancy and interspecific competition may drive compensatory mortality in ungulates. For example, Tallian et al. (2016) found that theft of wolf-killed ungulates by grizzly or brown bears slowed down wolf predation in Yellowstone and Scandinavia, respectively. In sum, there is convincing evidence that predation by large carnivores can have an important top-down influence and reduce ungulate abundance (Figure 6.1), however, counterexamples exist

and the role of interspecific competition between predators and human harvest on predator regulation of prey needs to be explored further (Vucetich et al., 2005).

When deer populations exploded throughout North America, many plant communities were reshaped (Ripple et al., 2010). On the Allegheny Plateau in northwestern Pennsylvania, USA, following the extirpation of wolves and mountain lions in the late 1800s, overabundant deer eliminated most northern hardwood saplings like eastern hemlock and deciduous shrubs. A long-term, replicated experiment found that deer reduced sapling density and growth rates, while also favouring browse-tolerant species (Horsley et al., 2003). Deer may be moving the northwest Pennsylvania forests into an alternative state characterised by dense grasses and ferns that inhibit establishment of tree seedlings (Ripple et al., 2010). In sum, intense herbivory by overabundant deer is occurring throughout North America and there is widespread evidence that ungulates impact the structure of ecosystems through herbivory (Côté et al., 2004). But can large carnivore rewilding reverse these continental scale patterns in plant recruitment?

We will now discuss the evidence that large carnivores can cause trophic cascades by discussing one of the most robust natural experiments with wolves in Banff National Park, Canada (Hebblewhite et al., 2005). Wolves naturally recolonised Banff through dispersal in the early 1980s. High human activity surrounding the town of Banff displaced wolves from the region, creating a natural experiment to study the effects of wolves in areas of high human activity ('low wolves') and low human activity ('high wolves'). Elk were a magnitude more numerous, survival and recruitment were higher, and predation rates were lower in the low wolf area. Predation of wolves on elk cascaded to plants, where willow production was 7x greater in high wolf areas due to reduced browsing. High wolf areas also had decreased aspen browsing and increased recruitment (Hebblewhite et al., 2005). The effects on plants led to cascading indirect or knock-on effects for birds and beavers. Songbird diversity and abundance doubled in high-wolf areas due to denser, tall willows available for habitat for nesting and reproduction. The number of active beaver lodges increased due to reduced elk densities and thus, greater abundance of willow via wolf predation (Hebblewhite & Smith, 2010). In sum, the natural experiment in Banff provides compelling evidence that large carnivores like wolves can create trophic cascades that reshape ecosystems.

There are many other examples of purported large carnivore trophic cascades in the literature (Terborgh & Estes, 2010; Estes et al., 2011)—including dingoes in Australia, jaguars on islands in South America, and most notably, wolves in Yellowstone. However, one weakness of many of these studies (which is common in ecology due to difficulties in doing well-controlled experiments), is that they are uncontrolled, unreplicated, and rely on correlations between plant and carnivore abundance (see Box 1.1 and Ford & Goheen, 2015). For example, most of the trophic cascade studies in Yellowstone (e.g., Painter et al., 2015) compare age or size class distributions of plants in areas with and without wolves present, but without a contemporaneous control to ensure such changes were not because of other factors, like weather. The trophic cascade hypothesis predicts that a range of plant age or size classes will be missing when carnivores were extirpated, due to intense elk herbivory. However, this approach rests on the assumptions that: 1) the loss of wolves can account for increases in elk; 2) increased elk led to loss of age/size classes; and 3) that other factors (e.g., weather, disease, other predators) had comparable effects over time on plant and elk abundance, across areas with wolves present and absent (Ford & Goheen, 2015). Unfortunately, these assumptions are rarely tested in the well-known literature in Yellowstone, with many alternative drivers left unconsidered.

In fact, Ford & Goheen (2015) found only two large carnivore experiments out of six where the length of food chains was manipulated (e.g., added/removed predators, herbivores, etc.) and trophic cascades occurred. For example, in the famous Kluane experiment, Sinclair et al.

(2000) found that lynx suppressed hares, and hares suppressed woody plants, but the abundance of woody plants was indistinguishable regardless of whether lynx were present. Similarly, Ford et al. (2015) found that the recovery of African wild dogs in the Laikipia Plateau in central Kenya reduced their primary prey, dik-dik, and dik-dik browsing suppressed tree abundance, but a trophic cascade did not occur. These negative results in the trophic cascade literature point to the complicated nature of the indirect effect of carnivores on plants. Many herbivores are not vulnerable to predation, and many species of herbivores do not suppress plants. Additionally, many plants have high defenses against herbivory. Moreover, food web reticulation, predator hunting strategies and antipredator defences, environmental heterogeneity, and many other factors are known to weaken or eliminate trophic cascades. We suggest that future research should focus on identifying the factors that drive large carnivore trophic cascades, especially with such mixed evidence, instead of just identifying cascades in systems.

Trophic cascades in Yellowstone

Restoration of wolves to Yellowstone was in fact motivated by the intention to restore natural regulation of elk by large carnivores due to overbrowsing in the Yellowstone northern range (Varley & Brewster, 1992). The introduction of wolves into Yellowstone correlated with a precipitous decline in elk populations. Subsequently, many studies inferred that the change in elk numbers or fear of predation decreased herbivory on deciduous shrubs like aspen, willow, and cottonwood. Thus, wolves in Yellowstone could have indirect effects on plants, which could possibly cascade via knock-on or indirect effects to other species, such as beavers. Here, we will review the most current evidence in Yellowstone for trophic cascades, starting with the first logical step of establishing whether wolves indeed caused elk abundance to decline.

There is no scientific consensus on whether wolves were the primary cause of the recent Yellowstone elk population decline. Wolves certainly contributed to the decline in elk, but what is in question is how much of the decline is due to wolves. For example, from 1995 to 2001, wolf populations were small, predation rates were low (3.7%), and they had only a small effect on elk abundance (Peterson et al., 2014; Metz, 2021). Later (2005–2010), elk predation rates increased to around 14% (see Figure 1b in Peterson et al., 2014). However, wolves are low success hunters of a wide range of prey that are typically small, old, in poor health, or rendered vulnerable by landscape features. Predation success rates hardly succeed 20% and are less than 10% in elk. Half of elk killed are calves, and 85% of female adult elk are more than ten years old, indicating that wolves could be primarily compensatory sources of mortality on elk (MacNulty et al., 2020).

There are also a host of alternative hypotheses that drove the decline in elk in Yellowstone (Peterson et al., 2014; MacNulty et al., 2020). The density of grizzly bears in Yellowstone may have tripled between the early 1980s and late 1990s, which correlated with an increase in elk calf mortality. Barber-Meyer et al. (2008) found that bears were the leading cause of elk calf mortality, and that mortality by grizzly and black bears increased from ~23% in 1987–1990 to ~60% in 2003–2005. Similarly, the average number of cougars in northern Yellowstone increased 76% from 1987–1993 to 1998–2004, which could be another predation pressure exerted on elk. Another factor affecting elk abundance is superadditive harvest of female elk by human hunters (Vucetich et al., 2005). Human harvest of female elk, in combination with multiple predation pressures and dwindling numbers, may become a factor reducing elk populations. Bison populations in the park have also been increasing since wolf reintroduction, and dramatically shifted to the northern range where they overlap with elk more. Although early studies indicated that competition between elk and bison was insignificant, these factors may have

changed in the present (MacNulty et al., 2020). Other climatic factors such as drought can also modulate the effects of large carnivores and harvest, which is projected to increase in the future with climate warming (Peterson et al., 2014; MacNulty et al., 2020). In summary, the declining number of elk in Yellowstone could still cause a trophic cascade, but not solely due to the reintroduction of wolves into the park.

Despite the lack of consensus on the numerical effects of wolves on elk, many researchers proposed that the landscape of fear was established soon after wolves were reintroduced, causing elk to avoid risky places where wolves could kill them (Peterson et al., 2014). The landscape of fear was inferred from increased vigilance behaviour, shifts in habitat use from nutritious, high-risk open areas to poor-nutrition, low-risk closed forests, decreased diet quality and body fat, and reduced pregnancy rates (see Introduction of Kohl et al., 2018). But other studies have found that elk selected for open areas, maintained body condition and pregnancy rates, and did not change their migratory patterns or winter home ranges in the presence of wolves. Kohl et al. (2018) used extensive GPS data from elk and wolves in Yellowstone to find that the landscape of fear is highly dynamic. Wolves hunted at dawn and dusk, and so elk avoided riskier places when wolves were most active, but safely accessed those places during lulls in wolf activity. Similarly, Kohl et al. (2019) found that in response to predation pressure from both cougars and wolves, elk avoided risky areas in places where both were active, using forested rugged areas during daylight (when cougars are least active) and grassy, open areas at night (when wolves are least active). Lastly, Cusack et al. (2020) found that elk did not change their home ranges in response to wolves. In fact, elk encountered wolves every 7 to 11 days, and frequently survived those encounters. This indicates that changes in temporal use of habitat along with antipredator behaviour during encounters with wolves (e.g., grouping, fighting back, running) help decrease chronic fear-induced effects (MacNulty et al., 2020). In fact, scientific consensus is leaning towards the hypothesis that if any trophic cascade from wolves to plants in Yellowstone is occurring, it is likely a result of a density-mediated, not behaviourally-mediated trophic cascades (Kauffman et al., 2010; Painter et al., 2015; Kohl et al., 2018).

Next, we examine the second causal step in establishing whether wolves caused a trophic cascade, whether there were increased productivity of plants. There is some scientific agreement that reduced densities of elk are driving increased productivity in deciduous plants in Yellowstone, however these changes in growth may be due to multiple factors other than or in interaction with wolf predation, and changes in growth are spatially heterogeneous (Peterson et al., 2020). Aspen, willow, and cottonwood have not grown taller than a height of 1m for decades in northern Yellowstone, and by 2006, aspen saplings have grown to ~1.5m (Peterson et al., 2014). There are large gaps in recruitment of aspen and cottonwood after the 1920s when wolves and other large carnivores were mostly absent (Painter et al., 2015; see Figure 15.1 in Peterson et al., 2020). Other plants had high levels of herbivory from elk, including alder, berry-producing shrubs, and relatively unpalatable conifers (Peterson et al., 2020). However, there are a host of competing hypotheses which could cause the growth of plants like aspen, including temperature, moisture, snow pack, bison herbivory, and competition with conifers.

Plant responses for other woody species are more complex. For example, increased height in willow have occurred with decreased elk herbivory, but the response appears patchy and related to the surrounding water table, beaver flooding, and other factors. Willow was only able to grow tall when protected from elk herbivory in places where the water table was experimentally raised and beavers were restored (Marshall et al., 2013). To emphasise the challenge that interpreting complex trophic cascades cause with uncontrolled, non-experimental observations, consider the beaver. As wolf reintroduction to Yellowstone has been strongly popularised, few are aware that beavers—the ultimate ecosystem engineer (Rosell et al., 2005)—were reintroduced just

outside the park from 1986 to 1999 by the US Forest Service (Smith & Tyers, 2012). Thus, combined with Marshall's innovative beaver dam experiments, it is equally as likely that the reintroduction of beavers has been the main trigger of willow responses in Yellowstone. The spatial variability in beaver recovery is also strongly consistent with the spatial variation in willow recovery.

Some point out that the discussion of trophic cascades in Yellowstone has only focused on communities (aspen, willow, and cottonwood) that represent 4% of its total area, and that although these communities are important and biodiverse, many other ecosystem processes occur in the 75% of the area that is comprised by grasslands and coniferous forest which have been unexplored (Peterson et al., 2014). We are only familiar with one study that examined the effects of trophic cascades on grasslands in Yellowstone, which found that reductions in elk decreased grazing intensity and changed biochemical cycling (Frank, 2008). However, this study was carried out during times with relatively insignificant levels of wolf predation (1995–2000), leading some to question these findings (Peterson et al., 2014). Moreover, bison are known to be strong ecosystem engineers of Yellowstone's grasslands (Geremia et al., 2019). However, bison are much harder for wolves to kill than elk, leading wolves in Yellowstone to scavenge bison more often, which implies a lack of direct numerical response of wolves on bison (Tallian et al., 2017; Metz, 2021), and therefore, little likelihood of a trophic cascade.

So in conclusion, we are challenged to answer whether trophic cascades are occurring from wolves to elk to plants in Yellowstone. Much of the evidence for trophic cascades examined age/stage distributions of plants with assumptions that missing age/stage class distributions are due to heightened elk herbivory from missing wolves (Painter et al., 2015; Peterson et al., 2020). As mentioned previously, this method is not experimentally robust and makes some assumptions to arrive at the conclusion of trophic cascades (Ford & Goheen, 2015). Furthermore, these studies, particularly for aspen, are plagued by poor sampling designs and biased field measurements (Brice et al., 2021). Evidence from others (Kauffman et al., 2010; Painter et al., 2015; Kohl et al., 2018) suggests that any indirect effect of wolves on plants is mainly the result of density-mediated trophic cascades. For example, in an experimental test of the behaviourally-mediated trophic cascade hypothesis, Kauffman et al. (2010) found that elk herbivory on aspen demography did not change in areas where elk are at higher risk of predation by wolves. These results lead us to conclude that the evidence for trophic cascades in Yellowstone is mixed. To summarise the most current thinking of effects of elk herbivory on plants (see Peterson et al., 2020): plants have grown taller in some areas, but this is spatially and temporally variable for many reasons including browsing intensity and groundwater availability, and in some areas bison grazing is counteracting reductions in elk herbivory. There is some evidence of knock-on effects of willow growth to songbirds (Baril et al., 2011), but little evidence to show knock-on effects to beavers (Marshall et al., 2013), grizzly bears (Barber-Meyer 2015), or other species. More robust experiments are needed that explore all trophic levels in the system (wolves, elk, plants), instead of just plants, to move beyond this uncertainty (*sensu* Ford & Goheen, 2015).

Should we rewild large carnivores to produce trophic cascades?

Three important questions to ask when evaluating the potential for rewilding large carnivores to produce trophic cascades are: 1) what do we expect from a trophic cascade; 2) how relevant are general trophic cascades to the specific system in question; and 3) what are other reasons to reintroduce large carnivores? First, introducing a large carnivore to an ecosystem is certainly going to have consequences for an ecological community but predicting the flow

and magnitude of the cascade could be exceedingly difficult. As we have shown (Figure 6.1), trophic cascades are not ubiquitous in systems with large carnivores. In some cases, the effects of trophic cascades may be different from what one expects. For example, Schmitz (2006) found that spider predators had no indirect effect on the biomass of a plant community, but they affected plant community composition that increased nitrogen cycling and light penetration. Similarly, although reduced elk herbivory may have increased the growth of aspen sapling height in Yellowstone (Painter et al., 2015; Peterson et al., 2020), sapling growth may be a relatively unimportant factor of aspen demography in clone maintenance (Peterson et al., 2014). This is all to say that reintroducing large carnivores may induce trophic cascades, but whether they matter and whether they can reshape ecosystems will be extremely context specific, depending on the ecological history, complexity of the community to which the large carnivores are restored, primary productivity of the system, and ultimately, the human impacts.

Secondly, many of the places where large carnivore trophic cascades are being reported are in relatively intact areas with small human footprints—like National Parks in the US. However, most ecosystems on Earth are dominated by humans, with huge legacies of destructive land use and harvest. Trophic cascades may be relatively minimal or nonexistent in human-modified landscapes where the effects of humans overshadow any direct or indirect effects of carnivores. For example, the recolonisation of wolves in Sweden led to a change in how humans hunted moose, which reduced numerical effects of wolves on moose (Wikenros et al., 2015). Muhly et al. (2013) found that outside protected areas in Alberta, humans affected vegetation through agriculture and forest modification, which weakened top-down trophic cascades from wolves to elk. To quote the famous wolf biologist David Mech (2012): ‘How significant a beneficial effect can wolves have on songbirds compared with the negative effects of logging, grazing, clearing, or farming? How important would wolf effects on trout be where trout are stocked and harvested, streams are polluted, and river banks grazed?’ We recommend deeply considering the extensive impacts from human land-use and high human densities which are considerable, prior to reintroducing large carnivores to putatively create trophic cascades.

Lastly, as conservation biologists, it can seem that often the justification for conserving or reintroducing large carnivores is so that trophic cascades can be created (Peterson et al., 2014). As we have shown, the potential for restoring trophic cascades with reintroduced large carnivores needs further research, but could still be an important tool in restoring ecosystems. But why not also argue for carnivore reintroduction on other moral, ethical, or cultural grounds—such as the value of biodiversity or the importance of carnivores to Indigenous Peoples (e.g., Shelley et al., 2011)? We think these considerations could be more productive for planning and prioritising large carnivore reintroduction. To quote Aldo Leopold (1949) again, ‘A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise.’

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