Trophic Cascades in a Multicausal World: Isle Royale and Yellowstone

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Abstract

Questions of whether trophic cascades occur in Isle Royale National Park (IRNP) or Yellowstone National Park's northern range (NR) cannot lead to simple, precise, or definitive answers. Such answers are limited especially by multicausality in the NR and by complex temporal variation in IRNP. Spatial heterogeneity, contingency, and nonequilibrium dynamics also work against simple answers in IRNP and NR. The existence of a trophic cascade in IRNP and NR also depends greatly on how it is defined. For example, some conceive of trophic cascades as entailing essentially any indirect effect of predation. This may be fine, but the primary intellectual value of such a conception may be to assess an important view in community ecology that most species are connected to most other species in a food web through a network of complicated, albeit weak, indirect effects. These circumstances that work against simple answers likely apply to many ecosystems. Despite the challenges of assessing the existence of trophic cascades in IRNP and NR, such assessments result in considerable insights about a more fundamental question: What causes population abundance to fluctuate?

1. INTRODUCTION

Much that is known about trophic cascades is based on field experiments involving the manipulation of small subsets of an ecosystem, comprised of just a few species living in small areas (e.g., Schmitz et al. 2000). Understanding how that knowledge applies to large, complicated, and uncontrolled ecosystems is analogous to recreating conditions of the Universe's Big Bang in a laboratory (e.g., Hung et al. 2013). That analogy highlights the value of studying trophic cascades in large, complicated ecosystems, such as Isle Royale National Park (IRNP) and the northern range (NR) of Yellowstone National Park (YNP). The distinctive contribution of these ecosystems to our understanding of trophic cascades is associated with three challenges to studying trophic cascades in any large, complicated ecosystem: (*a*) quantifying patterns with adequate precision at appropriate spatial and temporal scales, (*b*) accurately inferring causal relationships from complicated sets of correlations, and (*c*) comparing those observations with conceptual notions of what constitutes a trophic cascade.

The third challenge is grossly underappreciated (Polis et al. 2000) and provides context for understanding the other two. The theoretical origins of trophic cascades suggest they are community-wide phenomena involving changes in the biomass of primary producers, in response to changes in herbivore biomass due, in turn, to changes in predator biomass (e.g., Hairston et al. 1960, Oksanen et al. 1981, Fretwell 1987). Trophic cascades are sometimes conceptualized as entailing a food chain embedded within a food web rather than an entire food web (Polis et al. 2000). Others have conceived of trophic cascades in broader terms and in doing so have concluded that trophic cascades are widespread. Polis et al. (2000, p. 473) reflected on this tension: "Pace et al. (1999) suggested that. . .trophic cascades are widespread" but came to that conclusion, in part, by conceiving of "trophic cascades as 'strong interactions within food webs that influence the properties of the system,' thereby including a much wider spectrum of interactions. Thus, 'trophic cascades' of new are no longer 'trophic cascades' of old." In spite of this criticism, broader conceptualizations are persistent and reflected in a recent articulation noting a trophic cascade occurs when "the impact of a predator on its prey's ecology trickles down one more feeding level to affect the density and/or behavior of the prey's prey" (Silliman & Angelini 2012, p. 44). Such conceptualization is tantamount to equating a tropic cascade with nearly any indirect ecological effect of predation.

Without passing judgment on the appropriateness of any particular definition, we find some definitions are far more permissive in their inclusion of a much wider range of phenomena. Conceptualizing a trophic cascade as any indirect ecological effect of a predator is extremely permissive because most species in a food web are thought to be indirectly connected (if only weakly) to most other species of a food web (McCann 2011). By that broad conceptualization, detecting the existence of a trophic cascade would be far less illuminating than characterizing its nature, i.e., the extent and strength of indirect effects. Evaluations of trophic interactions in complicated ecosystems, such as IRNP and NR, yield an important lesson: Whether a trophic cascade has occurred depends on its definition. Nevertheless, to evaluate a trophic cascade involves an assessment of the influence of predation and herbivory on population dynamics of many interacting species.

2. PREDATION

2.1. Yellowstone's Northern Range and the Challenge of Multicausality

The migratory movements of what has historically been the largest elk herd in North America define the NR (1,530 km^2, 45°N, 11°W), which is the habitat of these elk (Lemke et al. 1998). Approximately two-thirds of the NR lies within the northern portion of YNP, and the remainder extends northward. NR elk are preyed on by wolves, grizzly bears, black bears, and cougars. They

have also been hunted by humans outside the boundaries of YNP. Elk represent ~90% of wolves' diet, with the remainder comprised of bison and deer (Metz et al. 2012). Humans have also been an important influence on the abundance of grizzly bears (Schwartz et al. 2010), bison (White et al. 2011), and, more recently, wolves (Smith et al. 2013). The NR of YNP and IRNP represent two extremes in complexity: The former now supports all native large carnivores, whereas the latter contains just one. Making reliable inferences about causality in complex, uncontrolled ecosystems requires considerable care.

The stunningly conspicuous pattern in the NR is due to the precipitous decline of elk following the reintroduction of wolves in 1995 (**Figure 1a**). From that pattern and analyses of other considerations, many have been content to infer that wolves caused the decline (Creel et al. 2007, Ripple et al. 2014; but see Mech 2012, Eisenberg et al. 2013). This inference has been reinforced
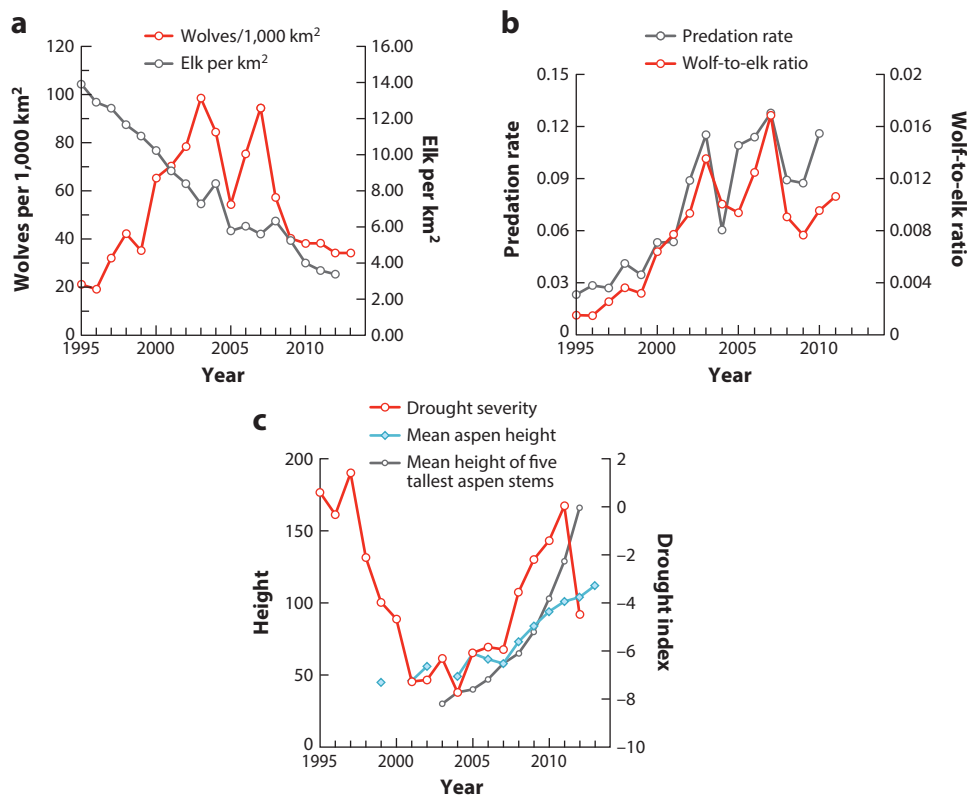

Figure 1

(*a*) Abundance of wolves and elk and (*b*) predation rate and wolf-to-elk ratio for the northern range of Yellowstone National Park (see **Supplemental Table 1**: For all **Supplemental Material**, follow the link from the Annual Reviews home page at **http://www.annualreviews.org**). Predation rate is the estimated proportion of elk killed by wolves each year (for details, see Vucetich et al. 2005). (*c*) Palmer Drought Severity Index for northwestern Wyoming (*red line* shows deviation from long-term average, indicated as zero, so negative numbers reflect drought conditions), the mean height of randomly sampled aspen in each of 113 clones (*blue line*) (E. Larsen, personal communication), and the mean height of the five tallest stems selected in each of 87 plots (*gray line*) (Painter 2013). Methodological differences among investigators generate the peculiar circumstance whereby the mean height is greater than the mean height of the five tallest trees (for years prior to 2007) (**Supplemental Sidebar 1**).

▶ Supplemental Material

by well-publicized predictions that wolves would cause elk to decline (e.g., Boyce & Gaillard 1992, Lime et al. 1993) and a strong, clear narrative presented frequently in public media (e.g., Monbiot 2014). Nevertheless, this inference about wolves' numerical impact on elk is misleadingly simple.

2.1.1. Harvest and drought. In the decade following wolf reintroduction, drought and recreational harvest of elk outside the Park boundaries almost certainly influenced the abundance of NR elk. Those factors also appear capable of explaining the observed decline in elk abundance without invoking the influence of wolf predation (Vucetich et al. 2005; see also Eberhardt et al. 2007). Mean harvest rate had been ~6% before wolf reintroduction. For the first decade following wolf reintroduction, harvest was managed in a manner that led harvest rate to increase to an average of 9% (as high as 17%). The harvest focused on killing female elk when they are pregnant during the late winter (Lemke 2003). As expected and intended, such a harvest appears to have caused elk to decline (Eberhardt et al. 2007). As elk density steadily declined and as managers and the general public became concerned about that decline, state hunting regulations were eventually changed to reduce harvest pressure. In particular, harvest rates were reduced to 1–2% during 2006–2009, and the harvest of antlerless elk was entirely eliminated in 2010.

2.1.2. Bears and cougars. In the NR, the density of grizzly bears rose and may have tripled between the early 1980s and late 1990s (Hamlin et al. 2009), after which their density has remained high. Recent estimates indicate the NR is inhabited by 54–69 grizzly bears per 1,000 km^2 (Barber-Meyer et al. 2008, Hamlin et al. 2009), which is comparable to the average density of wolves in the NR during 2004–2013. Increased bear density was accompanied by a concomitant increase in the mortality of elk calves. Prior to increased bear abundance, the annual rate of calf mortality in the NR had been estimated at 53% (1969–1975) (Houston 1982, p. 241) and 57% (1987–1990) (Singer et al. 1997). By contrast, for a more recent period (2003–2005) during which grizzly bear density was much higher, annual calf mortality was estimated at 78%. Grizzly bears and black bears accounted for 58–60% of these mortalities, and wolves accounted for only 14–17% of them (Barber-Meyer et al. 2008). Increased calf loss to bears is salient because recruitment rates throughout an important period of elk decline from 2001 to 2006 were half of what would be required to balance adult mortality (Hamlin et al. 2009).

Increased bear abundance in the NR (and a concomitant increase in calf mortality) is the result of grizzly bear recovery efforts mandated by the US Endangered Species Act (Schwartz et al. 2006, Interag. Grizzly Bear Study Team 2013). Increased calf predation by grizzly bears may also have been an unexpected and indirect result of another human influence: After the unexpected appearance of lake trout in Yellowstone Lake in the early 1990s, the springtime spawning run of cutthroat trout was reduced as one trout species displaced the other. As grizzly bears were deprived of cutthroat trout, there was a concomitant increase in predation by grizzly bears on elk calves (Middleton et al. 2013b). Grizzly bears have also benefitted from increased opportunities to scavenge carcasses produced by wolves (Wilmers et al. 2003a,b) and, perhaps, from increased berry production that was an indirect effect of reduced elk herbivory (Ripple et al. 2013). The relative importance of each of these influences on elk dynamics is unknown.

Cougar abundance in the NR also increased during the 1990s from 18 to 32 individuals (Ruth et al. 2014). Nevertheless, little is known about the influence of cougar predation on elk dynamics (Ruth & Murphy 2010); it could be minor or it could be significant. The influence of black bears is also poorly understood. However, what is known about their food habits (e.g., tendency to prey on calves) and their abundance in the NR suggests that they could also contribute significantly to the predation pressure exerted by the entire community of predators that reside in the NR. If the

density of predators is a useful indication of predation pressure, the combined impact of predation from cougars, grizzly bears, and black bears very likely rivals or exceeds that of wolves.

2.1.3. Wolves. In the first seven years following wolf reintroduction (1995–2001), wolf predation likely had only a trivial effect on elk abundance. In particular, mean predation rate during this period was 3.7%, and some portion of that predation is likely to have been compensatory, given that wolves tend to prey on elk with low reproductive value (Wright et al. 2006) and given that many elk were in poor condition due to a multiyear drought (Cook et al. 2004).

For the first 13 years following wolf reintroduction (1995–2008), the average predation rate was 6.7%, and most recently (2005–2010), the annual predation rate by wolves was <12% in all but one year (**Figure 1b**). These values are likely overestimates because they are based on the assumption that wolf densities in the NR both outside and inside YNP are equivalent. For further context, predation rates <12% correspond with strong population growth for the IRNP moose population. More specifically, for years of predation rate <12% ($n = 33$), mean growth rate of the IRNP moose population was 0.06 ± 0.02 (SE) and growth was positive in 79% of those years (see Vucetich et al. 2011, figure 4D,E).

Some analyses suggest that the decline of NR elk in the years just following wolf reintroduction is, at least partly, attributable to the nonlethal effects of predation risk, i.e., chronic fear and subsequent nutritional stress resulting in reduced pregnancies (Creel et al. 2007, 2009, 2011, 2013). Nonlethal effects of predation are often capable of affecting population dynamics (Valeix et al. 2009, Willems & Hill 2009, Miller et al. 2013). However, a concern in attributing its influence in this case is that pregnancy rates of NR elk, determined by serum protein (pregnancy-specific protein B), did not decline after wolves were reintroduced (Cook et al. 2004, White et al. 2011). The evidence for and relevance of this observation are discussed by Hamlin et al. (2009) and Middleton et al. (2013a).

2.1.4. Multicausality. The causes of elk decline have shifted from harvest to predation, first by grizzly bears and cougars, then by wolves. This shift has also been corroborated by analyses of the causes of mortality for radio-collared elk (Evans et al. 2006, Hamlin et al. 2009). For the period ending around 2005 (i.e., before the cessation of significant rates of harvest by humans), elk decline would have likely occurred in the absence of wolves. Wolves are also unlikely to have had a significant demographic influence on elk during the decade that followed their reintroduction, given the low rates of wolf predation during that period.

By around 2003, predation rates by wolves had increased considerably (**Figure 1b**). Since then, it is much more likely that wolves have contributed significantly to elk decline. Overall, the decline of NR elk is the result of multiple causes, including harvest, drought, bears, wolves, and, probably, cougars. Future interactions among these factors, as well as an increasing bison population (White & Garrot 2005, Frank 2013) will contribute to a rich and complicated scientific challenge.

2.1.5. The future will be different. Predation rate is the product of the per capita kill rate and predator-to-prey ratio (Vucetich et al. 2011). Prior to 2003, predation rate by NR wolves was low largely because the wolf-to-elk ratio was low. From some time around 2003 to 2011, wolf predation was higher, in large part because the ratio of wolves to elk was higher (**Figure 1b**). The future influence of wolf predation on elk will also depend greatly on changes in the wolf-to-elk ratio, which may be influenced, for example, by density-dependent factors in wolf dynamics (e.g., interference competition, disease) or an increasing preference for bison, which could influence elk abundance by altering exploitive and apparent competition between elk and bison (Ripple et al. 2010). Even factors largely unrelated to wolf-elk dynamics could affect this ratio (e.g., wolf disease,
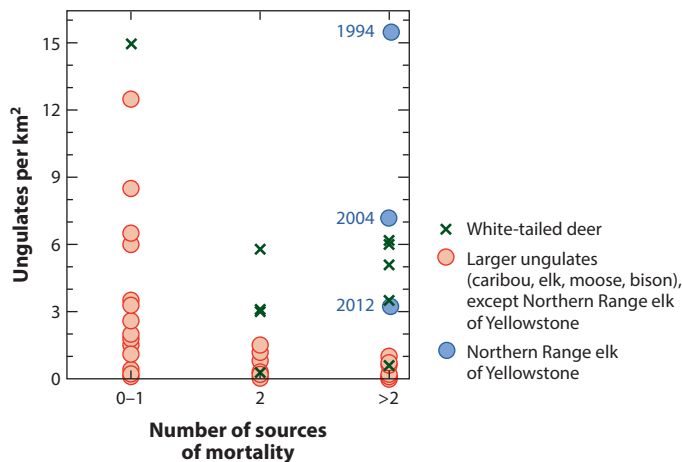
Figure 2

Mean ungulate densities from sites across North America for populations exposed to various numbers of different sources of mortality (adapted from Peterson et al. 2003). Sources of mortality include wolves, bears (two species), human hunters, and cougars: (*exes*) white-tailed deer (*Odocoileus virginianus*); (*circles*) larger species of ungulates (i.e., caribou, elk, moose, and bison). Sinclair et al. (2003) have investigated the relevance of body size.

weather effects on elk, elk migration patterns, and harvest of NR wolves outside the boundary of YNP). There is little basis for making reliable predictions about these changes. Moreover, the IRNP case, presented below, highlights how inherently unpredictable events can trigger major, persistent shifts in ecological dynamics, placing severe limitations on the capacity to make such predictions.

Some insight will be gained by comparing the future density of NR elk to the broad expectation that ungulate density is importantly influenced, not so much by the density of any particular predator, but by the diversity of biotic causes of mortality to which an ungulate population is exposed (**Figure 2**; but compare with **Figure 5a**). When exposed to two or more significant sources of mortality, the density of large ungulates tends to be <2 animals/km². NR elk may maintain higher than expected densities if, for example, seasonal migration outside YNP, where large carnivores are rare, becomes an effective antipredator behavioral strategy (White et al. 2012, Middleton et al. 2013a). Alternatively, if wolves begin to prey on bison more extensively as elk become more rare, then elk could be driven to extremely low densities because of apparent competition. The loss of caribou in many parts of Canada due to apparent competition among caribou, moose, and wolves suggests this possibility (Wittmer et al. 2005).

2.1.6. A long history of human influence. A consideration of the influences humans have had on NR elk throughout the past century provides some context for understanding the recent decline in elk (Houston 1982). In the late nineteenth century, market hunting drove elk abundance to very low levels. After the elimination of market hunting inside YNP and after most large carnivores had been extirpated, elk abundance rose during the early twentieth century. The National Park Service (NPS) began culling elk in the 1930s in response to concerns about overabundant elk. By the 1960s, the NPS was culling as much as 20–30% of the population annually, and elk abundance fell to approximately 4,000. Culling ended in 1967 in response to public outcry. From 1968 to 1976, with negligible harvest and virtually no predation, elk abundance quickly increased to >12,000 (Houston 1982). In 1976, the state of Montana initiated a harvest of NR elk outside the park in

response to renewed concern about competition between elk and livestock (Eberhardt et al. 2007). To limit elk abundance further, the harvest was intensified over time to include pregnant females. This period of intense harvest was, rather strangely, referred to as "natural regulation" (Boyce 1998, Wagner 2006). In spite of that harvest, elk increased to 20,000–25,000 (~15 elk/km^2) by the early 1990s. No ecological principle or phenomena can explain such human influences—they are artifacts of human history and the fickleness of our interests. Even influences that may be attributed to wolves are ultimately attributable to humans. That is, humans are the reason wolves were extirpated and the reason they were restored.

2.2. Isle Royale and the Importance of Temporal Variation

Isle Royale is an island (544 km^2, 48°N, 89°W) located in northwestern Lake Superior, North America. In Isle Royale, wolves are the only predator and primary cause of death for moose, which represent ~90% of wolves' diet (Peterson 1977). Humans do not hunt wolves or moose (for additional background, see Vucetich & Peterson 2004a,b).

Two lines of evidence indicate that wolf predation has been an important influence on moose population dynamics. First, estimates collected during 1971–2014 indicate that wolf predation rate (the proportion of prey killed annually by predation) is a strong predictor of growth rate for the moose population ($R^2 = 0.67$, $p < 10^{-3}$) (Vucetich et al. 2011). The estimated slope of this relationship is −1.8 (±0.21 SE). For context, predation is perfectly compensatory when the slope is zero and perfectly additive when the slope is −1. An estimated slope that is significantly less than −1 could indicate undetected synergy between predation and winter severity or may result from population growth that is influenced by the reduced foraging efficiency of moose during years of high predation risk. The influence of risk-sensitive foraging is another plausible explanation, given that predation risk and winter severity impact moose habitat selection (Montgomery et al. 2012). Finally, other instances in which cause-specific mortality is more than additive have been documented, for example, harvest mortality in NR elk during 1995–2004 (Vucetich et al. 2005; see also Sandercock et al. 2011).

Second, severe winters weaken prey and make them vulnerable to predation. Logically, such interannual fluctuations, rather than top-down processes, might drive predation rates. Nevertheless, predator abundance is a much stronger predictor of predation rate than is any index of winter severity in IRNP (J.A. Vucetich, R.O. Peterson, in preparation).

Temporal variation in predation rate reveals considerable complexity. In particular, predation on IRNP has exhibited three, and perhaps four, distinct phases throughout the past five decades (**Figure 3**). Mean predation rate was high (10.7% ± 0.1%, SE) and had an important influence on moose abundance between 1971 and 1980. In the next two years, the wolf population crashed by 80% owing to the synergistic effects of food stress and disease (canine parvovirus) that humans had inadvertently introduced (Peterson et al. 1998). During this time, the population also likely suffered increasingly from inbreeding depression (Adams et al. 2011). Wolf abundance then remained low for more than a decade, and the mean predation rate dropped (6.2% ± 0.4%) (see also Wilmers et al. 2006). With this reduction in predation, the density of moose increased dramatically from 1.5 to almost 5 moose/km^2 over the period 1981–1995 (**Figure 3**). A concomitant reduced growth of balsam fir during this period, as indicated by tree-ring width, reflects the influence of moose on forest vegetation (McLaren & Peterson 1994).

Two events in the late 1990s triggered another sustained shift. In 1996, a severe winter interacted with food stress, causing the moose population to decline by ~60%. In 1998, genetic rescue by one immigrant wolf bolstered the fitness of the wolf population (Adams et al. 2011). Following these events (1998–2011), mean predation rate increased to 13.8% (±1.6%), moose
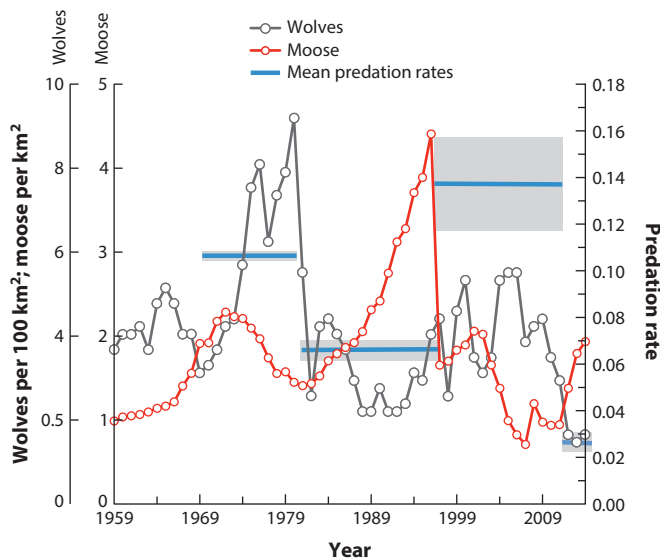
Figure 3

Abundance of wolves (*gray line*) and moose (*red line*) in Isle Royale National Park (Vucetich & Peterson 2014): (*horizontal blue lines*) mean predation rates for four periods; (*gray boxes*) plus and minus one standard error. Methods of estimation are described in Vucetich et al. (2011).

abundance declined to its lowest level (**Figure 3**), and balsam fir responded with increased growth (**Supplemental Sidebar 2**: For all **Supplemental Material**, follow the link from the Annual Reviews home page at **http://www.annualreviews.org**) (see also Vucetich & Peterson 2014). The beneficial effect of genetic rescue ended around 2011 (Hedrick et al. 2014). From 2012 to 2014, predation rate dropped to its lowest observed levels (mean = 2.7% ± 0.3%). In this three-year period, moose abundance doubled (see below). More time is required to understand whether this recent 3-year period will become a persistent condition. The indirect effects of wolf predation on vegetation would likely have gone undetected without those prolonged, alternating periods of high and low predation rates, which appear to be necessary to elicit a response in trees.

3. HERBIVORY ON THE NORTHERN RANGE

3.1. Aspen

Aspen is one of several NR vegetative communities reported to have been involved in a trophic cascade (Ripple et al. 2001, Ripple & Beschta 2007, Ripple et al. 2013). Those reports have been celebrated as well as criticized (e.g., Kauffman et al. 2010, Eisenberg et al. 2013), in particular, for being an artifact of biased sampling (Winnie 2012, Kauffman et al. 2013). This criticism is relevant for understanding which inferences can and cannot be reliably drawn from such observations. However, this criticism is also misplaced for failing to appreciate that no aspen (or willow or cottonwood) had grown beyond a height of ~1 m in the NR for decades, with the exception of aspen that had been inaccessible to elk, such as those growing in exclosures or on steep talus (see references cited in Beschta 2005). Yet, by 2006, some aspen saplings living where elk could browse had grown to ~1.5 m (Ripple & Beschta 2012).

A more complicated concern is whether such observations represent reasonable evidence of a trophic cascade or even an "early view" of a trophic cascade. The answer depends on the definition

of a trophic cascade (see Section 1) and what counts as adequate evidence for meeting that definition. Further complicating the answer, the demography of aspen involves many components (i.e., growth, density, and survival of stems across a range of size classes). Additionally, multiple factors influence each component, one effect of which is to create remarkable spatial heterogeneity.

To appreciate the relevance of spatial heterogeneity, consider the details of an aspen survey for the northwest portion of the NR that lies outside the boundary of YNP plus the adjacent Tom Miner Basin, representing an area of ∼550 km^2 (Kimble et al. 2011). The survey included 315 plots distributed among 24 watersheds, ranging in size from 2 to 10 km^2. On average, the plots exhibited no change between 1991 and 2006 in their density of recruitment stems. Individual watersheds, however, exhibited considerable variation, with 42% showing significant increases, 37% exhibiting significant decreases, and 21% exhibiting no significant change. Because reports of aspen recovery derive from four watersheds that were selected a priori because they had shown growth (Ripple & Beschta 2007), not unlike 42% of the watersheds exhibiting growth just outside the park boundary, a concern is that a species-specific trophic cascade may require an observation of widespread growth. By contrast, a number of these reports may represent only localized growth (Kauffman et al. 2010, Winnie 2012). This concern is bolstered by unpublished analyses suggesting that aspen growth in the NR since 2008 (**Figure 1c**) has been very spatially heterogeneous (E. Larsen, personal communication).

Observing a trophic cascade also requires determining the cause of any growth response. One concern with attributing the growth of NR aspen to reduced herbivory is that elk abundance had previously declined below approximately 5,000 for an 8-year period in the 1960s (Eberhardt et al. 2007). Yet, this period of low abundance was not low enough or long enough to stimulate significant aspen growth. As such, significant aspen growth should not be expected until after elk have declined to approximately 5,000 (i.e., 3.3 elk/km^2 in **Figure 1a**), which was the case only after around 2010.

Localized recovery of aspen in the presence of relatively high elk density might be evidence of a behaviorally mediated trophic cascade (BMTC) (e.g., Beschta & Ripple 2012, 2013). However, spatial heterogeneity in aspen demography may not be, by itself, convincing evidence for a BMTC because aspen demography is spatially heterogeneous even when risk-sensitive foraging by elk is not implicated (e.g., Brown et al. 2006). Moreover, attempts to associate spatial variation in aspen demography to factors that may influence risk-sensitive foraging have failed (Kauffman et al. 2010, Winnie 2012).

Most reports of aspen response in the NR refer to periods when elk had not long been in very low abundance. A concern thus arises that not enough time had passed to observe a response. Fortunately, forthcoming analysis may indicate, notwithstanding significant spatial heterogeneity, that a response had begun by around 2008 (**Figure 1c**) (Painter 2013; E. Larsen, personal communication). Nevertheless, a concern with attributing this growth to reduced aspen herbivory is that it coincided with the alleviation of a multiyear drought, which may have contributed to increased growth (**Figure 1c**). Aspen recruitment also tends to be episodic (Hessl & Graumlich 2002) and the last significant episode in the NR occurred around 1860–1920 (Beschta & Ripple 2013, figure 1B). That episode roughly coincides with the most protracted period of higher than average precipitation (1870–1940) of the past 900 years (Gray et al. 2007) and was also followed by decades of fire suppression.

Twentieth-century declines in aspen may be the combined result of interactions involving water, fire, and herbivory (Yellowstone National Park 1997, Hessl 2002, Natl. Res. Counc. 2002, Beschta 2005). The conspicuous alleviation of one factor, elk herbivory, during the past few years may not be a strong basis for concluding that it is the primary cause of a sea change in aspen demography, as studies have further suggested that aspen do not always respond to experimental

protection from herbivory (Endress et al. 2012). To date, however, there is an absence of research capable of isolating the effect of elk herbivory from other factors that may influence aspen, including temperature (Brown et al. 2006), moisture (Romme et al. 1995), snow pack (Brodie et al. 2012), bovid herbivory (Kimble et al. 2011, Beschta & Ripple 2014), and competition with conifers (Bartos 2001).

Concerns about the cause of growth may be mitigated by observations of the mechanisms that could represent herbivory. For instance, a negative correlation was observed in the same year between browsing intensity and sapling height for plots measured across the NR (e.g., Painter 2013, figure 3a). Mean browsing intensity has also declined over time for plots in which the mean height has also increased (Painter 2013, figure 2.5a). Both patterns could have been the result of a decline in elk preference for aspen as sapling height increased. Other cervids have also exhibited a similar preference (e.g., Hjeljord et al. 1990, Renaud et al. 2003). Thus, observed growth could be attributable to another factor, with reduced herbivory a subsequent consequence and not the ultimate cause of growth. If so, then preference could decline while stem height increased to generate a positive feedback, thereby allowing for additional growth.

The maintenance of an aspen clone requires sufficient growth, survival, and density of stems in several size classes. Although relatively easy to measure (and quite eye-catching), the growth in sapling height over small spatiotemporal scales may be the least important aspect of aspen demography involved in the maintenance of clones (Kulakowski et al. 2004). For example, identifying the five tallest stems in a clone and then retrospectively documenting the past height of those stems (as measured by, e.g., Ripple & Beschta 2007, Painter 2013) may not address the most limiting aspect of aspen demography.

As a result, we return to the question, What constitutes a trophic cascade? If a trophic cascade is any indirect effect of predation, then observing a causal relationship involving any aspect of aspen demography would qualify. If, however, an aspen trophic cascade is an indirect effect of predation on some aspect of aspen demography that limits the maintenance of aspen clones, then some of the evidence indicating an aspen trophic cascade in the NR may be viewed with circumspection. Insofar as aspen demography is manifest on a relatively slow timescale, an evaluation of the indirect effects of wolves on aspen may be impossible for some time. The multicausal nature of aspen demography has also disqualified simple statements about the causes of aspen demography anywhere in western North America (e.g., Sankey 2012, Kulakowski et al. 2013), including the Greater Yellowstone Ecosystem (Hessl 2002, Brown et al. 2006; see also Eisenberg et al. 2013, Seager et al. 2013). There is no reason to think circumstances in the NR will be any simpler.

3.2. Other Vegetation Communities

In many important ways, the response of willow to reduced elk herbivory has been similar to that of aspen. Prior to the extirpation of wolves in the early twentieth century, willow had been common in riparian communities and often grew to 2 m or more in height. By the late twentieth century, decades of intense elk herbivory had caused willow to become rare and short. Within 2 years of wolf reintroduction, remarkable growth in willow tree rings was recorded (Beyer et al. 2007). This response was taken as evidence of a BMTC because elk abundance was still high. Subsequent reports of height increases in willow reinforced this explanation (Ripple & Beschta 2004, Beyer et al. 2007, Beschta & Ripple 2012).

In recent years, a more complicated narrative has begun to emerge for willow in the NR. Whereas elk herbivory has declined, the response in willow appears to have been patchy, occurring in many but not all stands (Marshall et al. 2014). The complicating factor seems to have been the limiting influence of water. That is, willow growth is limited by herbivory and a suite of

factors related to soil-water availability, including beaver flooding, topography, the water table, the presence of grass, and annual precipitation (Wolf et al. 2007, Tercek et al. 2010, Marshall et al. 2013). For example, willow was unable to grow beyond a height of 2 m even when experimentally protected from elk herbivory, unless the water table was also experimentally raised (Marshall et al. 2013). Also, even though willow growth has increased, willow has not been restored, except where beaver were restored. This is not the only case in which the restoration of predation did not bring about the restoration of ecosystem processes (see also Schmitz 2004). The remarkable story of willow is not a restoration narrative as much as a reflection of how willow growth is the complicated result of many factors. The relative significance of these factors will continue to emerge as the impact of overwhelming elk herbivory recedes into the past, unless, however, herbivory by bison continues to increase and reaches high levels (Beschta & Ripple 2014).

Grassland communities represent 40% of the NR. Changes in the productivity and diversity of such communities may constitute an important indirect effect of wolf predation. Nevertheless, only one study has assessed changes in grassland communities since wolves were reintroduced, reporting data only during 1995–2000 when the level of wolf predation was relatively insignificant (Frank 2008). This study suggested that the rate of consumption (but not overall productivity), as well as net nitrogen mineralization, had declined. However, the limited ability of the study's sampling design to account for spatial heterogeneity that is widely appreciated to affect such processes may weaken confidence in its conclusions. More recently, it is becoming clear that increasing bison numbers confound a mechanistic understanding (Frank 2013).

Most generally, discussion of trophic cascades in the NR has focused on communities that represent approximately 4% (aspen, willow, and cottonwood) of its total area. These communities are of special importance to ground flora, birds, and insects with specialized habitat requirements. Nevertheless, most ecosystem processes in the NR occur in the 75% of the NR that is comprised of grasslands and coniferous forest. As objective as science aspires to be, scientific attention seems to have been dominated by an anthropocentric perspective focused on changes easily seen with the naked eye or measured with a ruler.

4. HERBIVORY ON ISLE ROYALE

The terrestrial portion of IRNP is predominantly forest covered. By preferentially consuming deciduous forage and not eating spruce, moose likely accelerated the decline of deciduous trees and the increase in spruce over the past century (e.g., Pastor et al. 1993). The influence of wolf predation on that century-long transition is unclear (but see below). Nevertheless, via their effects on moose, wolves appear responsible for temporal dynamics in the fine-scale spatial patterns of forage growth and consumption, soil nitrogen, and the basal area of conifer trees (DeJager & Pastor 2009). Wolf predation has also influenced spatiotemporal patterns in the distribution of wolf-killed moose carcasses, which creates small-scale spatial heterogeneity in available soil nutrients, with belowground effects on soil microbial communities and aboveground feedbacks that change leaf tissue quality (Bump et al. 2009).

Indirect effects of wolves, specifically BMTCs, are also evident in the foraging patterns of beaver in IRNP. Risk-sensitive foraging by beavers often results in a narrow, well-defined band of conifer trees along shorelines in IRNP (**Figure 4**). The distance beavers will forage from water depends on their preference for specific forage species (they will travel farthest for aspen); slope (Shelton 1962, Jordan et al. 2000); and the presence/absence of predators, which beavers detect by olfaction (Severud et al. 2011).

Wolf predation may also have potentially important indirect effects on the demography of balsam fir. A century ago, fir had been the dominant tree in most of Isle Royale's forests, but it has
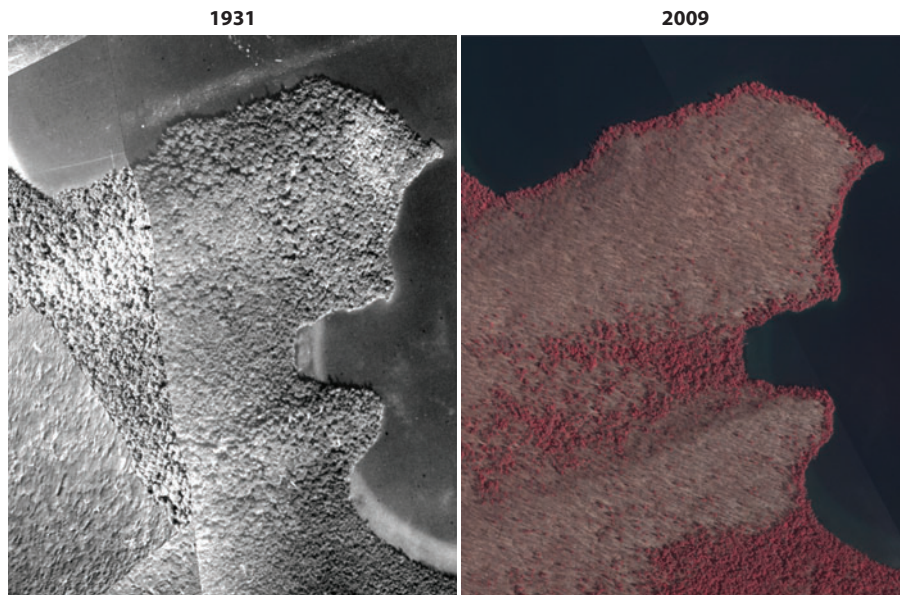
| 1931 | 2009 |

Figure 4

Beavers restrict the distance they forage from shore in response to risk of predation by wolves. That behavior can result in a behaviorally mediated trophic cascade. In this example from Isle Royale National Park, coniferous trees, which are unpalatable to beavers, have replaced deciduous trees that had been removed by beavers. More specifically, the left image was taken in 1931 during the growing season when deciduous trees have leaves, more than a century after beavers had been extirpated. Beavers in Isle Royale recovered sometime in the mid-twentieth century and have been common for the past 60 years. The right image, in color infrared, was taken in 2009 after the growing season, when deciduous trees do not have leaves. Differences in the images indicate that northern white cedar (*Thuja occidentalis*) (*darker red color*) had replaced sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) within ~15 m of the shoreline of Lake Desor (photos courtesy of the National Park Service).

gradually declined since the arrival of moose around 1900 (Janke et al. 1978). The primary winter forage of these moose is balsam fir (Vucetich & Peterson 2005), specifically short fir trees (<3 m) in the forest understory. These trees are common in two areas of Isle Royale, each composing approximately one-quarter of Isle Royale: the eastern portion and most habitats throughout the remainder of Isle Royale that are near (within 1–3 km of) the Lake Superior shoreline (hereafter, the western portion). Moose density is typically three to six times greater in IRNP regions where short fir are common, compared with regions where fir is rare or absent (Montgomery et al. 2014). Wolf density is also approximately two times greater in regions where moose are more abundant (Montgomery et al. 2012, 2014). This tendency for consumers to aggregate in portions of a landscape where resources are most dense would seem to correspond most with a bottom-up process—the antithesis of a trophic cascade (but see **Supplemental Sidebar 3**). An analogous kind of spatial covariance is also apparent at a continental spatial scale and also seems to reflect a bottom-up process (**Figure 5a**). Nevertheless, top-down influences are also reflected in both large-scale spatial variation (**Figure 2**) and fine-scale temporal variation within single study sites (**Figure 5b,c**).

The size structure of balsam fir in IRNP also exhibits striking spatial heterogeneity. In the eastern portion, fir is present in every size class from seedling to canopy tree and browsing pressure is minimal (except during the early 1990s; see below). For the remaining portions of IRNP, fir are common, and either they exist as senescent canopy trees, established a century ago before moose
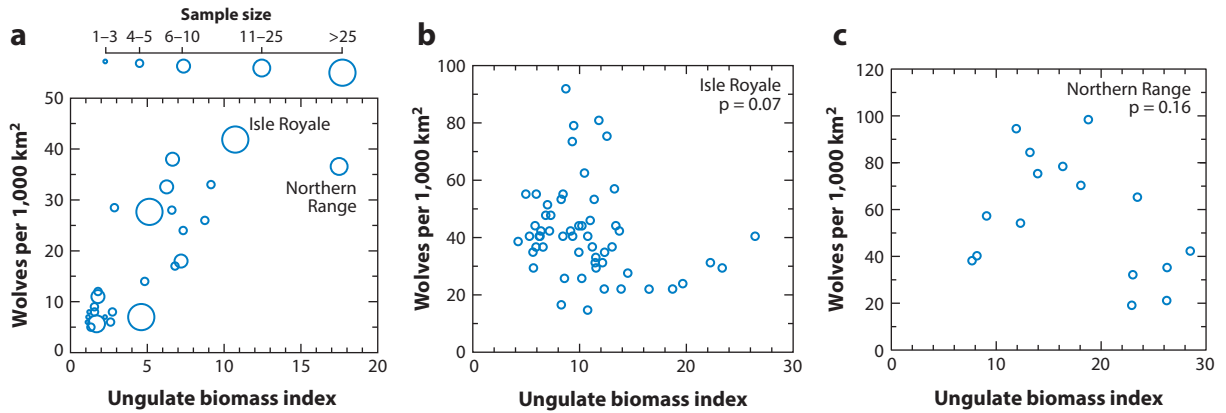
Figure 5

(*a*) Spatial variation in the densities of ungulates and wolves from sites distributed across North America. Data taken from Fuller et al. (2003). (*b*,*c*) Temporal variation in the relationship between the density of ungulates and wolves for Isle Royale and the northern range of Yellowstone National Park. The positive relationship in panel *a* is at least superficially consistent with influential bottom-up processes. By contrast, the lack of positive relationships in panels *b* and *c* suggests the greater influence of top-down processes and is consistent with Lotka-Volterra theory, which is characterized by particularly strong top-down influences. The ungulate biomass index allows the density of ungulate species characterized by different body sizes to be compared directly. The index is described in Fuller et al. (2003) and assumes, for example, that one moose is equal in biomass to two elk.

became abundant, or they are shorter than ~1.5 m (Brandner et al. 1990). In those regions, moose browsing has prevented fir from growing into the canopy for the past century, and many short firs have a morphology reflecting decades of severe browsing (Janke et al. 1978, McLaren 1996).

This spatial heterogeneity in fir morphology at the landscape level is likely an artifact of glacial history. Pleistocene glaciers deposited till that contributed to deep soils in the western portion of Isle Royale but scoured the eastern portion, leaving shallow soils (typically <30 cm) and frequent bedrock exposure (Huber 1973). The richer and warmer soils of the western portion favor deciduous growth (Linn 1957), and the thin soils of the eastern portion result in more frequent wind throws, which create canopy gaps and seedling substrates (rotten logs) that favor the growth of shade-intolerant fir (McLaren & Janke 1996).

Canopy trees are the only source of seeds that regenerate balsam fir. Because of advanced age, canopy trees in the western portion have been dying rapidly and will soon be functionally absent (Frelich et al. 2012). Some short balsam firs in the western portion could have grown into the canopy in the late 1980s and early 1990s, were it not for the dramatic increase in moose abundance that resulted from the loss of wolves caused by a human-introduced disease (**Figure 3**), whose effect was likely exacerbated by inbreeding depression (Peterson et al. 1998). This series of events constitutes the first terrestrial trophic cascade to be documented in a large terrestrial ecosystem (McLaren & Peterson 1994).

The moose population collapsed in 1996 with the most severe winter on record. A year later, a wolf immigrated from the mainland. With the resulting infusion of new genes, inbreeding depression was mitigated for almost two decades. Those events eventually contributed to a protracted period of extremely low moose abundance (2005–2011) (**Figure 3**). Shorter fir trees exhibited increased growth, and by 2013, many were approaching ~3 m, a height at which fir begin to produce seeds and escape moose herbivory by growing into the canopy (**Supplemental Sidebar 2**) (see also Vucetich & Peterson 2014). Potential growth into the canopy has not

▶ Supplemental Material

occurred for more than a century in the western portion, and its occurrence will likely depend on the outcome of an imminent tipping point.

The impairment of predation rate has created this tipping point. During 2012–2014, predation rate dropped to its lowest observed level (<2.7%), moose abundance doubled (**Figure 3**), and the abundance of beaver colonies increased by ~60% to a level where in 2012 approximately half of the >300 sites occupied historically by beavers were again active (Peterson & Romanski 2012; M. Romanski, personal communication). A prolonged period of elevated beaver abundance throughout the extensive wetland habitats at Isle Royale would likely have considerable and long-lasting impacts on forest dynamics (e.g., **Figure 4**) and aquatic plant communities where beaver not only are responsible for creating water impoundments that support aquatic plants, but also, along with moose, are significant consumers of those aquatic plants (Bergman & Bump 2014).

Inbreeding depression among wolves caused the impaired predation, and canine parvovirus, which reappeared in 2007 for the first time in 17 years, may have exacerbated it (see **Supplemental Sidebar 4**). If predation is quickly restored, moose abundance may be suppressed and short fir trees are likely to grow into the canopy. If, however, the functional loss of predation persists for any significant period of time, short firs in the western portion are unlikely to grow into the canopy.

For only the second time in a century, balsam firs have the potential to grow into the canopy in the western portion of IRNP. If enough short firs do not escape by around 2020, the likely result will be the death of virtually every canopy fir tree throughout the western portion. Because fir seeds do not remain viable in the soil for more than ~1 year (McLaren & Janke 1996), the loss of seed-bearing canopy trees would lead to the widespread failure of firs' ability to regenerate themselves (excepting the eastern portion). That failure would have a long-lasting negative impact on community dynamics that would not be readily mitigated by a subsequent restoration of predation. If so, this would not be the first time that a discontinuity in predation shifted ecosystem processes in a manner that was not restored after predation was restored (Schmitz 2004, Marshall et al. 2013).

When or whether predation is restored depends on the impact of inbreeding depression in wolves in upcoming years. The NPS recently announced its decision not to conduct genetic rescue (assisted immigration) in the short term, although doing so would have likely mitigated the effects of inbreeding depression. Concerns that anthropogenic factors, e.g., disease and climate change, had impaired predation suggested, in part, that conducting genetic rescue may be appropriate (Vucetich et al. 2012, 2013a,b; Vucetich & Peterson 2014). Climate warming is implicated because ice bridges form far less frequently and now appear to have been critical for periodic gene flow throughout the history of IRNP wolves (Hedrick et al. 2014).

As in the case of elk management and wolf reintroduction in YNP, this decision by the NPS is based on policy. Even though this decision will have considerable impact on ecosystem health, it could not have been anticipated through consideration of any ecological principle. The direct and indirect influences of humans (e.g., climate change, disease, culling, harvesting, wolf reintroduction, decisions about genetic rescue) suggest that humans, not predators, are the dominant influence on ungulate density, even in protected areas.

5. CONCLUSION

Since wolves colonized IRNP around 1949, they have exhibited multiyear periods of strong top-down influence on moose, interrupted by multiyear periods of weak influence. The indirect effect of wolves on vegetation has varied similarly. Each new period appears to have been triggered by some exogenous random event, including introduced disease, a catastrophically severe winter, and an unlikely immigration event that mitigated inbreeding depression among wolves.

Supplemental Material

When wolves were reintroduced to Yellowstone, NR elk declined dramatically. However, the appropriateness of assigning wolves as the causal agent is limited by the influence of harvest, drought, and predation by other predators—influences that have varied considerably since wolves were first reintroduced. With dramatic declines in elk, important changes in the vegetative communities have been observed. Although herbivory has been a key influence, other factors have also almost certainly been important.

Evaluating trophic cascades in large, complicated ecosystems requires data that are difficult to collect and inferences about causality that are difficult to make reliably. Those circumstances give reason to recall Bayes' theorem: Given the observed data, the probability a trophic cascade (or any event) has occurred is proportional to one's prior belief about the probability that a trophic cascade has occurred. The logic of hypothesis testing (frequentism) is analogous: One's belief in a trophic cascade depends greatly on whether one is willing to believe so until proven otherwise, or unwilling to believe until definitively proven. When data are difficult to gather and interpret, the influence of one's a priori disposition is strong and unavoidable.

Judging where trophic cascades have occurred in a multicausal world, dominated by human influence, also depends greatly on what constitutes a trophic cascade. Ripple et al. (2014, p. 157) asserted that, "Hunting by humans…may itself cause trophic cascades, because humans are also predators with the potential for ecological impacts." By that logic, any process that kills herbivores with ecological impacts counts as predation. Drought would, for example, qualify. Yet, a fundamental difference among predation, harvest, and drought is the potential for feedback. Drought involves, essentially, no feedback; predation and harvest differ profoundly in the nature of their feedback. The importance of this difference is reflected by the fact that predation theory and harvest theory are distinct subdisciplines. Being too permissive about what counts as predation reduces questions about trophic cascades merely to questions about the importance of herbivory. That reduction seems to betray the original fascination with trophic cascades—a remarkable result of feedback that occurs among adjacent trophic levels. Treating harvest and predation as interchangeable is inappropriate because they are not, and doing so would erode motivation to conserve predators.

Asking questions about trophic cascades in a multicausal world raises additional peculiar questions: Has a trophic cascade occurred in the NR, even if elk would have declined in the absence of wolf predation? What portion of the aspen clones in the NR would have to be affected to qualify as a trophic cascade? Did a trophic cascade occur if reduced herbivory led to increased aspen recruitment, but not enough to regenerate most clones? Without satisfying answers to such questions, the standards for assessing trophic cascades will remain elusive.

Yet, such questions are an unavoidable artifact of applying a simple concept to a complicated world. A trophic cascade, especially as the idea is associated with Hairston et al. (1960) and Oksanen et al. (1981), is an intellectual construct born in an imaginary world of simple food chains governed by equilibrium dynamics. By contrast, most ecosystems are uncontrolled and entail complicated, multicausal food webs governed by nonequilibrium dynamics (Botkin 2012). Spatial heterogeneity (McCann 2011) and contingency (Schmitz 2010) further complicate ecosystems. Although a trophic cascade is a coherent concept in such a world, the greatest intellectual contribution of asking "Have trophic cascades occurred in Isle Royale or Yellowstone?" may be to highlight that this question, in many cases, may not have a simple, precise, or definitive answer. This circumstance recalls a remark by Sir D'Arcy Thompson, the father of mathematical biology, from his classic *On Growth and Form* (1942, p. 643): "It is the principle involved, and not its ultimate and very complex results, that we can alone attempt to grapple with." Do not misunderstand. Questions about trophic cascades have led to great insight about a much more fundamental question, "What causes populations to fluctuate?"

Scientific understanding is not the only concern in asking questions about trophic cascades in IRNP and YNP. The answer is also a weapon in the social discourse on the value of conserving top predators. Too often, this discourse seems to imply that the appropriateness of conserving a top predator depends critically on demonstrating that its decline or recovery is the cause of a trophic cascade (however such may be defined). There may be value in understanding how this rationale is affected by what seem to be important limits in understanding the past influence of predators (even in well-studied systems) and greater limits to accurately predicting their future influence. Important as those limits are, however, they do not undermine the conclusion that the direct and indirect effects of top predators are considerable at many times and in many places.

If those circumstances and appeals to the precautionary principle that they inspire represent insufficient motivation to conserve top predators, then additional lines of reasoning may be necessary. Conserving top predators may also require reasoning akin to that expressed by the founder of the wolf-moose project at IRNP, Durward L. Allen (1954, pp. 256–57):

> [I]mpartial sympathy toward all creatures, regardless of their diet, is an attitude of the cultivated mind. It is a measure of a man's civilization. If ever we are to achieve a reasonable concord with the earth on which we live, it will be by our willingness to recognize [and] tolerate. . . the biological forces and relationships. . .in the living things about us.

If the power of such reasoning to dissolve antagonistic attitudes toward nature seems doubtful, then we may run the inescapable risk of continuing to lose predators and perhaps more.

DISCLOSURE STATEMENT

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