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Wolf, elk, and aspen food web relationships: Context and complexity

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ABSTRACT

Like most ecological communities, aspen (*Populus tremuloides*) forests are influenced by a synergy of bottom-up (resources-driven) and top-down (predator-driven) processes. Since the 1920s, ecologists have observed the decline of many aspen communities throughout the Intermountain West. The extent and possible drivers of this decline are topics of much recent scientific study. In addition to bottom-up effects, which include drought, fire suppression, and disease, ungulate herbivory is a contributing factor. Trophic cascades are ecological relationships in which an apex predator produces strong top-down, direct effects on its prey and indirect changes in faunal and floral communities at lower trophic levels. Apex predators, such as the gray wolf (*Canis lupus*), have been linked to aspen vigor and recruitment, via trophic cascades mechanisms. Scientists have hypothesized that returning wolves to the landscape enables aspen to recruit into the forest overstory, via the density-mediated and behaviorally-mediated effects of wolves on their ungulate prey, primarily elk (*Cervus elaphus*). We present a synthesis of scientific findings on this topic, identify trends in the ecological impacts of wolves in aspen communities in a variety of ecosystems, and suggest areas for further investigation. Knowledge gaps include the interaction of top-down (e.g., predators) and bottom-up (e.g., drought, fire, hydrology, logging) effects, and how the ecological context of the interaction affects the outcome. Future horizons involve exploring these food web relationships as a complex of inter-level interactions in a more integrated, empirical manner. We suggest adopting a new standard for the aspen/wolf ecology literature by shifting its emphasis and lexicon from trophic cascades to food web studies. Such an integrated approach can help managers create more resilient aspen communities.

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1. Introduction

Aspen (*Populus tremuloides*), the most widely distributed tree species in North America (DeByle and Winokur, 1985), has been declining in large portions of the Intermountain West since the 1920s (Murie, 1926–1954; Leopold, 1943). The extent and possible drivers of this decline have become topics of much scientific investigation (Romme et al., 1995; White et al., 1998; Kulakowski et al., 2006; Hogg et al., 2008; Worrall et al., 2008). This decline is of conservation concern for many reasons, including the fact that aspen provides important habitat for elk (*Cervus elaphus*), songbirds, and other species (DeByle, 1985; Romme et al., 2001; Hollenbeck and Ripple, 2008; Oaten and Larsen, 2008).

A prominent ecological debate in the past 50 years concerns whether resources have a stronger influence on plant communities than predation (Murdoch, 1966; Sinclair, 2003). Resources, such as

moisture and sunlight, are necessary for plant growth. Predation controls herbivore pressure on plants (Hairston et al., 1960), thereby driving sometimes strong trophic effects throughout communities. Additionally, competition and omnivory create complex trophic linkages among community members (Menge and Sutherland, 1976; Polis and Strong, 1996). In the 1920s, ecologist Charles Elton linked wolf (*Canis lupus*) presence to food web effects that can release plants from ungulate herbivory (Elton, 1926). More recently, these food web relationships have been linked to aspen conservation (Ripple et al., 2001; White et al., 2003). However, resources available to aspen provide the energetic foundation to sustain this species, and so also may be strong regulators of aspen dynamics.

In this paper, we review the food web research that has examined the ecological factors that influence aspen growth and stand dynamics. Factors such as moisture, disturbance, herbivory, and human natural resources use create diverse, multi-causal aspen responses (Eisenberg, 2012). All may be as important drivers of aspen overstory recruitment as wolf presence, depending on context (White et al., 2003). As managers strive to create more ecologically resilient aspen communities, all of these factors have become key elements to consider in aspen forest management.

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2. Trophic cascades theoretical background

2.1. Trophic cascades components and top-down effects

A food web is a theoretical construct that depicts trophic relationships in a community (Elton, 1926). Ecologists have identified the fundamental components of a food web as primary producers (plants), primary consumers (herbivores), and secondary consumers (predators) (Darwin, 1859; Elton, 1926; Hairston et al., 1960). Predators can include apex predators, defined as a carnivore species that dominates its trophic class (Terborgh et al., 2010) and can have strong effects on other food web components (Navarrete and Menge, 1996; Soulé et al., 2005).

Trophic cascades are ecological relationships in which an apex predator produces a strong direct effect on its prey and strong indirect changes in faunal and floral communities at other trophic levels (Paine, 1980; Crooks and Soulé, 1999). Trophic cascades can be stronger at the lower end of the productivity gradient, such as in Arctic or arid ecosystems (Oksanen and Oksanen, 2000). Ecologists have observed that when apex predators such as wolves are removed, the species that was their primary prey increases significantly in number (Hairston et al., 1960; Paine, 1969). This increase is termed an irruption (Leopold et al., 1947). An irruption leads to intensive consumption of food resources and indirectly affects other species dependent on those plant communities (Berger et al., 2001; Bailey and Witham, 2002; Hebblewhite et al., 2005a).

While the density-mediated effects (reduced prey numbers) of predation have long been documented (Lotka, 1907), behaviorally-mediated effects (altered prey feeding behavior) are a more recent discovery. Apex predator presence changes prey feeding behavior (Schmitz et al., 1997; Landré et al., 2001; Fortin et al., 2005), by making prey more vigilant (Lima and Dill, 1990). This top-down mechanism (Polis and Strong, 1996) reduces the time prey spend eating (Brown et al., 1999) and can enable vegetation to regrow (White et al., 1998). For example, in an old-field experiment, Schmitz et al. (1997) found behaviorally-mediated effects of arthropod presence on grasshoppers. However, several experimental studies have attributed reduced prey vigilance in systems with a high predator population to prey differential response to complex cues. Ferrari et al. (2010) causally linked a reduction in anti-predator response by fish to adaptive decision making.

Both density-mediated and behaviorally-mediated mechanisms have the potential to create trophic cascades. Nevertheless, the existence of behaviorally-mediated effects remains a debated topic in the wolf → elk → aspen trophic cascades literature (Ripple and Beschta, 2004; Halofsky and Ripple, 2008; Kauffman et al., 2010). The fact that behaviorally-mediated responses are not simple (Brown and Kotler, 2004) has fueled this debate. For example, Creel et al. (2008) found lower elk vigilance at a site with a higher proportion of time spent at risk (higher number of wolves), and higher vigilance at a site with fewer wolves.

Simple apex predator presence does not ensure that trophic cascades will occur. In low densities, apex predators may not be ecologically effective (Soulé et al., 2003). An ecologically effective population of an apex predator is defined as one sufficient to produce trophic cascades (Soulé et al., 2003; Estes et al., 2010).

2.2. Bottom-up effects and trophic trickles

Bottom-up effects may stimulate or reduce vegetation growth (Borer et al., 2005). Lindeman (1942) described energy passing upward through trophic levels, which he envisioned as distinct and functionally homogeneous sets of green plants, herbivores, and primary carnivores. He referred to this as bottom-up control of ecological communities. Soil moisture influences plant growth

(Bassett, 1963). Nutrient (e.g., nitrogen, phosphorus) availability may increase after fire, also stimulating growth (Belleau et al., 2006). Bottom-up effects include vegetation effects on herbivores, such as food resource availability (Murdoch, 1966). Anthropogenic modifications of plant communities also can cause bottom-up effects. For example, timber harvest creates early-seral forest communities (Swanson et al., 2010).

Hunter and Price (1992) suggested that strong bottom-up effects prevail in all systems. They observed that "... the removal of upper trophic levels leaves lower levels intact, whereas the removal of lower trophic levels leaves no system at all." The bottom-up effects present in all food webs may buffer top-down effects (Power, 1992). Studies in a variety of settings and systems have documented weak top-down effects, termed trophic trickles (Power, 1990; Hunter and Price, 1992; McAnn et al., 1998; Halaj and Wise, 2001; Dawes-Gromadski, 2002; Menge, 2005; Kauffman et al., 2010). A trophic trickle is defined as a situation where an apex predator is present, but has limited indirect effects on vegetation (Strong, 1992). Highly speciose systems can demonstrate trophic trickles (Strong, 1992).

Like most ecological communities, aspen forests are structured by a synergy of bottom-up (resources-driven) and top-down (predator-driven) effects (Schmitz et al., 2006; Eisenberg, 2012). Ecological context (e.g. spatial landscape heterogeneity and climate patterns) influences the relative importance of these effects. Such context may cause woody species recruitment to be more strongly influenced by bottom-up than top-down effects (Marshall, 2012). In a wolf → elk → aspen food web, for trophic cascades to occur, wolves must have a strong effect on elk, and elk must have a strong effect on aspen. If both effects do not occur simultaneously, then the result could be a trophic trickle or a system dominated by bottom-up effects.

3. Aspen conservation status and associated factors

3.1. Aspen conservation status and recruitment

A forest's ability to persist over time depends in part on successful growth of young trees into the canopy (van der Valk, 2009). A variety of environmental factors influence this recruitment, including nutrient and moisture availability, disturbance, and herbivory (Franklin et al., 2002; Horsley et al., 2003; Littell et al., 2008).

In the Intermountain West, from the mid-1920s until recently, researchers have been finding predominately even-aged, single-storied aspen stands. Composed largely of trees >80 years old (Mueggler, 1989), these stands arose after stand-replacing wild-fires (Kulakowski et al., 2004). This even-aged structure is not an historic condition, largely being the result of unsuccessful recruitment over the past 80 years (Romme et al., 1995). In addition to lack of fire and chronic herbivory (Singer, 1996; Baker et al., 1997; Johnston, 2001; Vavra et al., 2005), ecologists have linked low recruitment to predator extirpation (Romme et al., 1995; Naiman and Rogers, 1997; White et al., 1998; Ripple and Larsen, 2000). However, some of this measured aspen decline may simply be the result of normal forest community succession toward conifer dominance in the absence of fire (Shepperd et al., 2001a). Multiple interacting ecological factors influence aspen population dynamics (Brown et al., 2006; Worrall et al., 2008). These factors operate on a sub-continental scale, and sometimes may be related to trophic cascades (Kashian et al., 2007; Kaye, 2011).

3.2. Effects of predator removal and herbivory on aspen recruitment

Ecologists long have observed the relationship between apex predators and recruitment of young trees into the forest canopy.

Many of these observations have been associated with wolf removal. In 1925, in Grand Teton and Yellowstone (YNP) National Parks, Wyoming, Olaus Murie observed intense herbivory, which he attributed to the elk irruptions caused by wolf removal (Murie, 1926–1954). Fifty years later, in Isle Royale National Park, Michigan, McLaren and Peterson (1994) discovered that wolves produced density-mediated effects on moose (*Alces alces*). This released balsam fir (*Abies balsamea*) from moose herbivory and led to recruitment of this previously suppressed tree species. These effects were more pronounced in areas with a higher number of wolves, which suggested trophic cascades (McLaren and Peterson, 1994). Similar effects have been observed in many boreal and temperate forest ecosystems (Beschta and Ripple, 2009; Ripple et al., 2010). Intensive browse by ungulates has been identified as a factor degrading forests worldwide (Oksanen and Oksanen, 2000; Soulé et al., 2003). Tree sprouts in general subjected to repeated browse developed a stunted, shrubby growth form and ultimately fail to recruit into the canopy (Keigley and Frisina, 1998).

Elk, deer (*Odocoileus* spp.), and domestic ungulates can suppress aspen sprouts and keep them from reaching the overstory. Among the suite of herbivores present in Rocky Mountain elk winter range (low-elevation grasslands with patches of aspen), elk have the strongest impacts on aspen (Houston, 1982; Debyle, 1985; Barmore, 2003). Aspen is considered to be high-quality browse and can provide up to 60% of elk diet during winter months (Hobbs et al., 1981; Canon et al., 1987). Outside of elk winter range and beyond the Intermountain West, deer and domestic ungulate impacts on aspen can be significant (Alverson et al., 2003; Tortenson et al., 2006; Seager et al., in press). In systems without elk, deer can suppress aspen (Leopold, 1943; Binkley et al., 2006). Bison (*Bison bison*) impacts on woody species [e.g., willow (*Salix* spp.)] have been documented (Painter and Ripple, 2012), but have not been measured in aspen communities. Moderate browsing can stimulate production of new shoots by releasing apical dominance (Bilyeu et al., 2008; Johnston, 2001).

A variety of factors influence ungulate use of woody species. Resource quality and position on the landscape (e.g., aspect, elevation) (White et al., 2003), time of year, and snowpack influence browse (Brodie et al., 2012). Elk tend to use south-facing slopes in winter, because these retain more heat and are the first to become snow free, which increases plant availability (Chen et al., 2002). Some research suggests that avoidance of wolf predation can also reduce browse (Ripple et al., 2001; White et al., 2003). However, more recent, studies have failed to find such an avoidance effect (Creel et al., 2008; Creel and Christianson, 2009; Kauffman et al., 2010). The need to conserve energy also can influence ungulate use of woody species. In Oregon, Seager (2010) found that wild ungulates avoided utilizing aspen in areas with significant amounts of down wood. Since wolves were not part of this system, he attributed this effect to ungulate energy conservation. In Glacier National Park (GNP), Montana, and Waterton Lakes National Park (WLNP), Alberta, Eisenberg (2012) found elk avoiding the interior of aspen stands, regardless of wolf population size. Elk co-evolved with wolves, so this could be an instinctive energy-conserving behavior (Geist, 2002).

3.3. Additional factors associated with aspen decline

Large-scale, stand-replacing wildfire plays a key role in regenerating and perpetuating aspen stands and enhancing elk habitat (Cook, 2002). A fire of sufficient intensity and severity to kill the aspen forest overstory stimulates abundant suckering. However, some suckers arise after a light fire, or even in its absence (Bartos and Mueggler, 1981). Conifer invasion, a by-product of fire sup-

pression, can reduce aspen stand size. Many aspen stands are seral communities that give way to conifers (Rogers, 2002; Morelli and Carr, 2011). Conifers have longer lifespans than individual aspen ramets and can overtop aspen. Fire eliminates young conifers from the understory, while stimulating aspen sprouting (Smith and Smith, 2005). The longer fire return intervals found at high elevations enable conifers to reach the overstory and replace aspen (Kulakowski et al., 2004).

In the absence of fire and with chronic elk herbivory, aspen stands fail to successfully recruit new stems, leading to senescent, even-aged stands (White et al., 1998). In GNP, Singer (1979) attributed aspen decline to decades of fire suppression combined with elk browse. But, fire alone may be insufficient to restore aspen. Throughout the Intermountain West, research in aspen stands in elk winter range that burned and did not have wolves has found abundant post-fire suckering, heavy elk browse, and lack of aspen recruitment (Romme et al., 1995; Baker et al., 1997; Barnett and Stohlgren, 2001; Kay, 2001; Bailey and Witham, 2002; Hessel and Graumlich, 2002). Aspen sprout density and elk herbivory intensity are positively linked to fire severity (Bailey and Witham, 2002; Smith et al., 2011).

Additional factors associated with aspen decline include disease, insect outbreaks, and drought (Worrall et al., 2008). In the southern Rocky Mountains, drought is the strongest driver of recent aspen decline (Worrall et al., 2010; Hanna and Kulakowski, 2012). Conifer encroachment and ungulate herbivory can exacerbate drought effects (Shepperd et al., 2001b; Lamalfa and Ryel, 2008; Worrall et al., 2008). Conversely, excessive moisture may increase disease occurrence in sprouts, thereby reducing their ability to recruit into the canopy (Jacobi et al., 1998). In a variety of scenarios and landscapes, from Canada to the southern Rocky Mountains, all of the above factors can cause aspen overstory death and failure of the understory to sprout and recruit (Hogg et al., 2008; Worrall et al., this issue). Aspen functional type (e.g., seral, stable) may further influence aspen response to stressors (Rogers et al., in press).

4. Trophic cascades hypotheses involving wolves, elk, and aspen

4.1. Trophic cascades hypotheses

Prior to the 1995 and 1996 YNP wolf reintroduction, ecologists speculated about the potential effects of wolf removal on elk overconsumption of woody browse species (Leopold et al., 1947). In YNP, these species include aspen, cottonwood (*Populus* spp.), and willow (Romme et al., 1995; Naiman and Rogers, 1997). Returning wolves to this system could reduce the number of elk via predation. Fewer elk could release woody browse species from herbivory and stimulate trophic cascades. Such primary effects could have beneficial secondary effects on other taxa, such as songbirds, beavers, and fish (Naiman and Rogers, 1997).

The YNP wolf reintroduction inspired trophic cascades research that has linked wolves to elk to aspen recruitment (Smith et al., 2003; Ripple and Beschta, 2007, 2011). Ecologists have hypothesized that wolves are enabling aspen to recruit above the browse height of elk and that this provides evidence of trophic cascades (White et al., 2003). This notion has gained popularity in the media; documentaries and magazine articles have promoted the idea that wolves are “saving” aspen (Bass, 2005; Robbins, 2004). Yet some consider these claims to be possibly premature or spurious (Kauffman et al., 2010; Mech, 2012). Still others assert that while the wolf is an apex predator that exerts important ecological effects in food webs, it is but one of the many factors that influence aspen ecology at the landscape scale (Kimble et al., 2011; Eisenberg, 2012).

4.2. Trophic cascades conceptual models

Ecologists use conceptual models to characterize food webs and provide a framework to explore interaction directions and strengths. Such simplified models allow examination of bottom-up and top-down effects (Menge and Sutherland, 1976; Carpenter et al., 1985) and can help quantify these effects (Grace, 2006; Reisner, 2010). Conceptual models are used to study the effects of wolves on aspen communities (e.g., White et al., 1998; Ripple and Beschta, 2004; Hebblewhite et al., 2005a; Eisenberg, 2012).

We created a series of conceptual models to depict the functional components of the wolf → elk → aspen food web (Fig. 1). Many more food web components would be possible, if one were to build an interaction web model for this system (Lavigne, 1995). To represent bottom-up forces, we included Environment (e.g., moisture) and Disturbance (e.g., fire, flooding, and insect outbreaks). For the purposes of this review, we focus on fire, as other disturbance factors (e.g., flooding) have not been addressed in aspen trophic cascades studies. We structured each model horizontally, rather than vertically, to emphasize a less hierarchical structure (Hunter and Price, 1992; Polis, 1994; Menge et al., 1994).

The bottom-up model (Fig. 1a) depicts a case where ecological resources and fire are the strongest drivers of aspen recruitment. In this model, wolves are relatively unimportant members of an aspen community. Sunlight, moisture, and disturbances such as fire sustain vigorous aspen recruitment. Aspen provide improved food resources for elk, which support wolves. Regardless of wolf density, this model represents a system driven via bottom-up energy flow.

Conversely, the top-down model (Fig. 1b) depicts a case where wolf predation is the strongest driver of aspen recruitment. In this model, wolves suppress elk, which releases aspen from herbivory,

and consequently improves food resources for elk. This indirectly creates food resources for wolves, via a positive feedback loop. Both density-mediated and behaviorally-mediated mechanisms result in top-down indirect effects on aspen.

The trophic trickles model (Fig. 1c) illustrates a case where in the absence of bottom-up effects (e.g., disturbance), even at a high density, wolves are unable to indirectly stimulate aspen recruitment. In this model, elk intensely browse aspen. Lack of fire additionally reduces aspen vigor. This combination of factors creates a negative feedback loop in which elk have degraded food resources, and in turn provide diminished food resources for wolves. Thus, wolves are present, but not ecologically effective in driving top-down trophic cascades via density-mediated and/or behaviorally-mediated mechanisms.

5. Synthesis of food web relationships in aspen science

5.1. Early conceptual studies

Landscape-scale trophic cascade studies in general, and wolf → elk → aspen food web studies specifically, represent a fairly new field. Three early studies conceptually examined factors that could be influencing aspen recruitment and discussed the potential role of wolves (Romme et al., 1995; White et al., 1998; Ripple and Larsen, 2000).

In the aftermath of the 1988 YNP fire, Romme et al. (1995) measured aspen regeneration and recruitment, and identified elk as the dominant herbivore impacting the aspen in the park. This study provided a comprehensive summary of the linkages evaluated in YNP (e.g., fire, weather, elk market hunting) and found to be

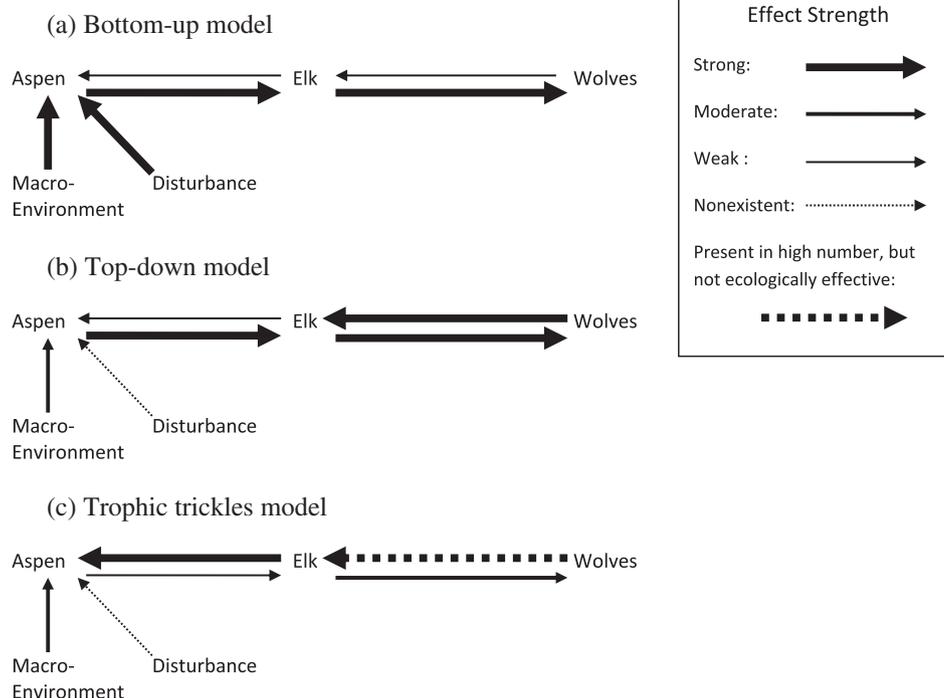


Fig. 1. Conceptual models of top-down and bottom-up effects in a wolf → elk → aspen food web. In these conceptual models, Wolves represent predation; Elk represent herbivory; Aspen represent recruitment into the canopy. The models below portray three different cases of the tri-level food web model proposed by Elton (1926) and others, in which the relative strength of the main components varies (legend). The models have been designed to depict various levels of herbivory (elk impacts on aspen), predation (wolf impacts on elk), aspen recruitment, and disturbance. Arrows pointing up or right represent bottom-up effects. Arrows pointing left represent top-down effects. Effect strength of food web components can be conceptually quantified as follows: Wolves = wolf density; Elk = elk density; Aspen = aspen stem density (relative abundance) in the >2.5 cm ht < 5 cm DBH size class (e.g. recruiting aspen); Environment = ecosystem resources (e.g., moisture, sunlight); Disturbance = fire. Many other cases of these models are possible, the figures below represent classic cases most often identified in the food web literature (e.g., Hairston et al., 1960; Hunter and Price, 1992; Polis and Strong, 1992).

important to aspen recruitment. In the discussion of their findings, the authors speculated about wolf absence as a factor that had allowed the elk population to grow. However, the focus and main conclusions of this study did not link wolves to aspen recruitment. Most notably, the authors concluded that “a single-factor approach to managing and understanding aspen dynamics in YNP is insufficient.” While they did not test this conclusion experimentally, this early observation has been confirmed by later studies.

White et al. (1998) conducted a literature review, focusing on six Rocky Mountain National Parks in Canada and the US. They linked aspen decline to predator extirpation, a top-down, density-mediated effect. The authors further found that fire was failing to stimulate aspen recruitment, which they attributed to intense elk herbivory in the absence of wolves. White et al. (1998) proposed a four-level trophic model that included humans as the apex predator.

Ripple and Larsen (2000) conducted an analysis of aspen overstory recruitment on the YNP northern range. They concluded that successful aspen recruitment occurred from the mid-1700s until the 1920s and then ceased. They hypothesized that the main factor associated with this decline was wolf extirpation. They speculated that wolves may influence aspen recruitment via trophic cascades mechanisms, including the behaviorally-mediated effects of predation risk.

5.2. Wolf → elk → aspen studies

In the past twelve years, approximately eleven wolf → elk → aspen studies have occurred (Table 1), inspired by Romme et al. (1995), White et al. (1998), and Ripple and Larsen (2000). Study findings range from strong top-down effects linked to wolves, to strong bottom-up effects prevailing, to a combination of top-down and bottom-up effects driving aspen recruitment, with potential trophic trickles. Taken as a body, these studies furnish evidence that, as in other systems (e.g., aquatic), it is difficult to cast aspen food web ecology as simple top-down or bottom-up scenarios.

Ripple et al. (2001) conducted some of the earliest correlational research on trophic cascades in aspen on the YNP Northern Range. This important study investigated the effects of wolves on elk behavior. The authors wanted to determine whether reintroduced wolves were influencing elk browse patterns and aspen regeneration via trophic cascades mechanisms. They used elk pellet groups, aspen sucker heights, and the percentage of browsed suckers to measure differences in aspen stands in high and low wolf-use areas. They used wolf telemetry data (VHF radio-collars) to determine high and low wolf-use areas. High-use areas included territories occupied by wolf packs (Ripple et al., 2001). The authors found that wolves had apparently altered elk foraging behavior, with fewer elk pellets in riparian sites that may have had greater predation risk by wolves. Aspen suckers in riparian high wolf-use areas were taller than in other areas measured. They found no significant effect of fire on aspen density or height. This early observational study supports the top-down model (Fig. 1b). It was among the earliest studies to evaluate the behavioral effect of wolves on elk (e.g., Laundré et al., 2001). It did not fully examine bottom-up effects (e.g., moisture, snow pack), which may have been important, too. More recent research has attempted to address bottom-up effects.

Several subsequent observational studies examined the effect of wolf presence/absence on Rocky Mountain aspen communities. All hypothesized that behaviorally-mediated effects would be linked to aspen recruitment. The methods used in these studies differed, but all found top-down effects (Larsen and Ripple, 2003; White et al., 2003; Beschta and Ripple, 2007; Ripple and Beschta, 2007; Halofsky and Ripple, 2008), indicated by aspen recruitment above browse height (Table 1). The top-down model (Fig. 1b) depicts the

food web dynamics identified by these researchers, where wolf presence was the strongest driver of aspen recruitment. These studies all considered top-down and bottom-up factors and their interaction. For example, Larsen and Ripple (2003) found no aspen recruitment after a 1988 fire in the Sunlight Basin, Wyoming, during a period when there were no wolves. They also found no relationship between moisture (e.g., xeric or mesic aspen stand types) and recruitment. In YNP, Halofsky and Ripple (2008) linked the combined effects of fire, changes in elk density and predation risk, and decreased herbivory after wolf reintroduction to facilitated growth of young aspen. However, these studies did not empirically quantify bottom-up effects on aspen regeneration and growth so cannot conclude that bottom-up processes are unimportant. They defined predation risk via an unvalidated model (e.g., more hypothesized impediments to predator detection and escape result in less elk use of site, an indirect measure of risk), rather than directly (e.g., measurement of wolf locations with telemetry data). Therefore, the indirect, unvalidated model for predation risk may be wrong (Kauffman et al., 2010).

Hebblewhite et al. (2005a) investigated the effects of wolf recolonization in Banff National Park, Alberta. In this observational study, the authors hypothesized that variations in wolf presence, would correlate positively to the strength of top-down effects. They measured variations in wolf presence using telemetry data (Hebblewhite et al., 2002) and included a site from which wolves had been partially excluded (the Banff townsite). Additionally, Hebblewhite et al. (2005a) tested for density-mediated and behaviorally-mediated effects of wolves on elk and evaluated trophic cascades in aspen and willow communities. The authors found no significant effects of wolf presence on aspen, as measured by recruitment of young trees into the forest canopy. Aspen sapling densities and recruitment were higher in sites that had been disturbed recently (<25 years) by fire. Willow sites showed a release from elk herbivory correlated positively to wolf presence. The density-mediated effects of wolves on elk were more important than behaviorally-mediated effects. The authors concluded that in an aspen system, bottom-up effects (e.g., disturbance) and other contextual factors interact with and influence top-down (e.g., wolf predation) effects (Hebblewhite et al., 2005a). In this study, the trophic trickles model (Fig. 1c) characterizes aspen findings, and the top-down model (Fig. 1b) represents willow findings.

Binkley et al. (2006) evaluated the density-mediated effects of wolves on deer on the Kaibab Plateau. This study occurred in a system without elk, in which white-tailed deer (*O. virginianus*) are the primary herbivore. The authors revisited a classic case study first presented by Elton (1926), subsequently chronicled in greater depth by Leopold (1943, 1949), and critiqued by Caughley (1970). The Kaibab Plateau lies within both the Kaibab National Forest and Grand Canyon National Park (GCNP), which have different resource management strategies (resource extraction vs. resource protection). Wolves and other predators were removed by the 1920s; deer subsequently irrupted.

This study found lack of aspen recruitment after predator removal. Climate, a bottom-up effect, did not influence aspen recruitment. However, the authors also found complex effects driven by factors such as logging (Binkley et al., 2006). Logging creates early-seral communities (Swanson et al., 2010), an effect that in this study may have attenuated the top-down signature of predation. Early seral-communities offer enhanced food sources for deer via the conifer removal and soil disturbance associated with logging, which release aspen (Shepperd et al., 2001b; Jones et al., 2005). In the absence of wolves on the Kaibab National Forest, during a 30-year period beginning in 1963, Binkley et al. (2006) observed recruiting aspen numbers more than one order of magnitude above the long-term trend. However, this response was not observed within GCNP, which was not logged. Natural resources

Table 1
Wolf–elk–aspen trophic cascades studies.

Author(s)	Study site	Hypothesis	Results	Landscape-scale	Experiment	Consideration of behaviorally-mediated or density-mediated effects	Consideration of bottom-up effects
Ripple et al. (2001)	YNP	Wolves are driving a trophic cascade by modifying elk behavior. Aspen taller in higher predation risk areas such as riparian areas	Elk are avoiding high wolf-use areas, and aspen are taller in these areas	No	No	Behaviorally-mediated	Yes, fire
Larsen and Ripple (2003)	YNP	Predation risk driven by wolves is influencing aspen recruitment and stand dynamics	Changes in ungulate browsing patterns due to differences in predation risk best explain the spatial and temporal pattern in aspen recruitment	Yes	No	Behaviorally-mediated	Yes, fire, moisture
White et al. (2003)	Six Rocky Mountain National Parks in Canada and the US	Elk behavioral patterns created by predation risk, which includes fire, could influence aspen herbivory	Less recruitment where elk density is higher and where there has been no fire. Anthropogenic influences drive aspen dynamics	Yes	No, but used some enclosures	Behaviorally-mediated	Yes, fire
Hebblewhite et al. (2005)	Banff NP	Wolf presence correlates positively with strength of top-down effects	In aspen sites, no correlation between wolf presence and top-down effects; strong correlation between bottom-up effects and recruitment	Yes	No	Behaviorally-mediated and density-mediated	Yes, fire
Binkley et al. (2006)	Kaibab Plateau	Cessation of aspen recruitment on the Kaibab Plateau is linked to deer irruption in the 1920s subsequent to wolf extirpation	Lack of aspen recruitment for the period when deer irrupted in the 1920s	No	No	Density-mediated	Yes, timber harvest, climate
Ripple and Beschta (2007)	YNP	Wolves are driving a trophic cascade by modifying elk behavior. Aspen taller in higher predation risk areas such as riparian areas	Aspen are recruiting in high predation risk areas, such as riparian areas	No	No	Behaviorally-mediated	Yes, moisture
Beschta and Ripple (2007)	Jasper National Park	Wolf presence has been a pivotal factor affecting trophic cascades involving wolves–elk–aspen; herbivory by elk may limit the capability of fire to improve aspen recruitment	Aspen recruitment ceased in the 1900s when wolves were removed, but resumed in the 1960s when wolves returned. Recruitment has not occurred at low predation risk sites, regardless of fire	No	No	Behaviorally-mediated	Yes, fire and climate
Halofsky and Ripple (2008)	YNP	Aspen recruitment is linked to wolves and fire via predation risk	The combined effect of fire and a subsequent decrease in herbivory following wolf reintroduction facilitated aspen growth	No	No	Behaviorally-mediated	No, do not consider fire's influence on aspen growth, only predation risk relationship with fire
Kauffman et al. (2010)	YNP	Landscape-scale differences in aspen recruitment are related to spatial variation in the risk of wolf predation on elk	Aspen are not recruiting, and wolves are not driving a behaviorally-mediated trophic cascade	Yes	Yes	Behaviorally-mediated	Yes, climate
Kimble et al. (2011)	GYE	To determine if aspen recruitment and overstory stem densities in the study area changed from 1991 to 2006; to find associated factors	Aspen are not recruiting and wolf presence is not driving aspen recruitment	Yes	No	Behaviorally-mediated and density-mediated	Yes, climate
Eisenberg (2012)	GNP, WLNP	Aspen browse would be lower and recruitment higher where wolf populations are higher; bottom-up (fire) and top-down (wolf population) factors would both influence aspen demography	Low aspen recruitment in unburned aspen stands compared to burned stands demonstrates the importance of bottom-up effects. Further, in all valleys, fire is necessary for aspen to recruit above elk browse height at all levels of wolf population observed	Yes	No	Behaviorally-mediated and density-mediated	Yes, fire, moisture

management factors (e.g., cattle grazing, deer hunting by humans) increased contextual complexity. This study was among the first to document a complex of inter-level interactions in a more integrated manner. The top-down model (Fig. 1b) represents the general study findings. However, the bottom-up model can be used to depict the effects of timber harvest (Fig. 1a).

More recent research has taken a closer look at some of the contextual relationships implicit in trophic responses and has also increased the rigor of such studies. Kauffman et al. (2010) were the first to employ an experimental approach to measure top-down effects in a wolf → elk → aspen food web. This built on an earlier study (Kauffman et al., 2007), in which the authors identified high predation risk sites via telemetry and kill-site data to quantify predation risk directly. Kauffman et al. (2010) investigated behaviorally-mediated trophic cascades. To determine whether landscape-scale differences in aspen recruitment were related to spatial variation in wolf predation risk, the authors randomly placed small ungulate exclosures on the YNP Northern Range in areas of high, moderate, and low predation risk. High predation risk sites included riparian areas. Contrary to what Ripple and Beschta (2007) found, Kauffman et al. (2010) determined that aspen were not recruiting and that wolves were not modifying elk browsing behavior. Kauffman et al. (2010) incorporated the effects of climate into their analysis, but did not examine fire as a factor in aspen recruitment. Because Kauffman et al. (2010) did not focus on bottom-up effects, the bottom-up model does not strictly represent their findings (Fig. 1a). Using an experimental approach, they tested for a behaviorally-mediated wolf effect on elk and did not find one. Therefore, the trophic trickles model, which suggests that wolves may not be the only or primary drivers of aspen recruitment in a tri-trophic system, represents their findings (Fig. 1c).

Kimble et al. (2011) conducted research in the Northern Range, in the Gallatin National Forest just north of the YNP border. Resource extraction in the form of hunting by humans and timber harvest occurs in this mixed-use landscape. The authors wanted to find evidence of wolf-driven trophic cascades. They re-measured permanent, long-term study sites within this forest, originally measured in 1991 before wolves were present. This study took place in the same general area studied by Larsen and Ripple (2005). Kimble et al. (2011) evaluated both density-mediated and behaviorally-mediated wolf effects on elk. Despite wolf presence, the authors found a lack of top-down effects in the aspen (e.g., recruitment). They did not find that wolf presence caused elk to avoid high predation risk sites (e.g., riparian areas). The trophic trickles model (Fig. 1c) represents their findings.

Eisenberg (2012) investigated food web relationships between wolf predation, elk herbivory, aspen recruitment, and fire. The study setting, in the central portion of the Crown of the Continent Ecosystem, spans the US/Canada border and encompasses GNP, Montana, and WLNP, Alberta. The observations were stratified across three spatially distinct areas: the North Fork Valley, in the western portion of GNP; the Waterton Valley, in the eastern portion of WLNP; and the Saint Mary Valley, in the eastern portion of GNP. All valleys are elk winter range. The valleys have three different observed wolf population levels (Saint Mary: low; Waterton: moderate; North Fork: high), which represent three corresponding levels of long-term predation risk (the probability of an elk encountering a wolf). Ecological characteristics (e.g., climate, soils, elevation, plant associations) are comparable among valleys. Recent fire has occurred in 90% of the North Fork.

The study objective was to examine the relative influence of bottom-up (fire) and top-down (predation risk) factors and the context-dependence of these relationships. Density-mediated and behaviorally-mediated wolf effects on elk were evaluated. Browse on aspen was lower in the North Fork, where there was a high wolf population, suggesting a top-down effect. However, the low aspen

recruitment in the absence of fire in all valleys indicates a bottom-up effect. In sum, the risk of wolf predation alone did not drive the food web relationships observed in this study. Bottom-up and top-down forces worked together in valleys that contained well-established wolf populations, and to a lesser degree in a valley with a low wolf population. Both density-mediated and behaviorally-mediated wolf effects on elk were found, but these relationships were complex. Eisenberg (2012) used wolf density to represent predation risk, in a broad-scale, qualitative way (e.g., wolf population data). The trophic trickles model (Fig. 1c) best characterizes the Eisenberg (2012) study. However, because this was an observational study, trophic trickles could not be empirically documented.

5.3. Top-down or bottom up: is this a false dichotomy?

The studies reviewed above provide evidence of a wide range of effects that can drive aspen recruitment. Differences in findings are attributable to differences in scale (spatial and temporal), location, consideration of bottom-up effects, research design (e.g., correlational vs. experimental work), and methodologies. For example, some landscape-scale studies have found great variation in aspen indirect responses to wolf presence (Table 1). Additionally, detectability of top-down effects may have been influenced by the plant-response variable measured. In a meta-analysis, Schmitz et al. (2000) found trophic cascades stronger when plant damage was the measured response, versus plant biomass or reproductive output.

Some of the contradictory findings of these studies may be due to the increase in scientific knowledge as researchers have come to better understand wolf → elk → aspen food webs, YNP in particular. For example, three studies now disagree with earlier findings about simple behaviorally-mediated trophic cascades (Creel et al., 2008; Creel and Christianson, 2009; Kauffman et al., 2010). In YNP, early studies took necessary first steps at assessing the impacts of behaviorally-mediated trophic cascades (Ripple et al., 2001). Subsequent work held that hypothesis to more rigorous testing and found some top-down effects (Hebblewhite et al., 2005a). More recently, some studies have found nuanced behavioral responses by elk to predation risk by wolves and context-dependence of top-down effects (Eisenberg, 2012). It bears noting that some of the earliest work that examined wolf effects on forest communities other than aspen (e.g., balsam fir) found that bottom-up effects such as fire could attenuate the top-down effects of wolves (McLaren and Peterson, 1994). Significant breakthroughs in soil and fire ecology also have increased our awareness of the complexity of aspen food web relationships (St. Clair et al., 2010; Smith et al., 2011).

A key difference in findings pertains to how predation risk was measured (e.g., indirectly vs. directly). Ripple and Beschta (2007) used topography to define predation risk. Eisenberg (2012) used wolf density to represent predation risk, in a broad-scale, qualitative way (e.g., wolf population data). Hebblewhite et al. (2005b) and Kauffman et al. (2007) also used wolf density to represent predation risk, but in a more quantitative manner (e.g., wolf telemetry data) than Ripple and Beschta (2007) or Eisenberg (2012). These three different approaches to quantifying predation risk may yield divergent results. Some authors have noted that risk of predation by wolves defies a simple definition, and has yet to be fully defined (Hebblewhite et al., 2005b; Eisenberg, 2010).

A deeper look at some tri-trophic components could have changed the results of the studies we reviewed. Elk population dynamics and distribution are complex (Vucetich et al., 2005), as is also the case with most predator species (Lotka, 1907; Taylor, 1984). When designing research that evaluates wolf impacts on elk, we suggest empirically accounting for elk population dynamics. Decreases in elk abundance, distribution, and group sizes driven by

circumstances beyond wolf predation (e.g., climate, food availability, hunting by humans) could contribute to trophic cascades related to wolves (White et al., 2012) and potentially could make wolves more, or less, ecologically effective. Many of the studies we evaluate have not fully incorporated the effects of snowpack. The amount of snow on the ground, a bottom-up effect, can significantly alter elk behavior and aspen growth. During low snow years, elk have easier access to sprouts for browsing (Brodie et al., 2012).

The diverse findings discussed here vividly illustrate that aspen food web relationships, including trophic cascades, cannot be neatly described as top-down or bottom-up scenarios. Like the models we present, many variations of these relationships are likely, depending on context. Hunter and Price (1992) suggested that the dichotomy between top-down and bottom-up effects may be false. They observed that a more interesting question would be to what extent context can influence the relative strength of top-down and bottom-up forces in a community. Over two decades ago, ecologists argued for a more integrated approach to studying community dynamics (e.g., Menge et al., 1994; Power, 1992). More such research continues to be needed.

6. Knowledge gaps

Trophic cascades science in aspen communities is relatively new. The majority of studies on this topic have been done by a handful of researchers working over a period of less than one and a half decades. Consequently, the knowledge gaps in this area are enormous. For example, we have learned that wolves can sometimes exert strong direct and indirect effects in aspen communities, which cascade down through multiple trophic levels (Ripple and Beschta, 2007). However, we know little about how context can influence these effects.

Looking beyond aspen communities, Estes et al. (2011) documented top-down food web effects driven by apex predators in a variety of ecosystems worldwide. These relationships are ecologically ubiquitous (Schmitz et al., 2000). Experiments have found strong causal links between predators and trophic cascades, primarily in aquatic systems (Borer et al., 2005). We suggest that the context and strengths of these effects remain to be fully explored in terrestrial large mammal communities. Further, these relationships can be influenced by a variety of factors. For example, recent studies of wolves, elk, and willows have documented bottom-up effects and trophic trickles (Creel et al., 2008; Creel and Christianson, 2009; Martin, 2012), while others have found strong top-down effects in the same landscape (Beyer, 2006). Studies conducted in the same location get different results due to differences in scale, methodology, and response variables (Schmitz et al., 2000). Further, communities can display both top-down and bottom-up control, with both dominating at different times, depending on ecological circumstances (Schmitz et al., 2006).

During the 1980s–1990s, dozens of experimental studies investigated trophic cascades in aquatic systems and terrestrial invertebrate systems (Schmitz et al., 2000; Borer et al., 2005). Beyond these experiments, reviews and meta-analyses explored the theory behind trophic cascades, including establishment of alternative stable states and tipping points (Hunter and Price, 1992; Power, 1992). Most of these studies found complex, multi-causal food web relationships. We suggest that perhaps it is time for the scientific community to revisit such topics and their application to aspen communities and other terrestrial systems that contain large mammals. Advances in analysis methods, such as the development of structural equation modeling (Grace, 2006), invite such scientific exploration. Such methods have been applied to experimental work on the effects of ungulate herbivory in willows (Baker

et al., 2005; Johnston et al., 2007). Other possible analysis methods to deepen our understanding of aspen food webs could include hierarchical and landscape modeling.

Lack of direct information about predation risk is a basic weakness of many of the studies discussed in this paper. Researchers used subjective criteria to make assumptions about which habitats were risky and which were safe. Later studies have shown that some of these earlier assumptions about risky habitats were wrong. For example, early studies and some subsequent work assumed that wide open habitats were safe for elk (Ripple and Beschta, 2004; Halofsky and Ripple, 2008; Eisenberg, 2012). Other studies using telemetry data have commonly found that these are the places where elk are more vigilant and more likely to be killed by wolves (Hebblewhite et al., 2005b; Kauffman et al., 2007). Predator-prey dynamics are complex and subject to change via stochastic effects and environmental context (Brown, 1999). Further, little is known about the effects on a food web of the interaction between density-mediated and behaviorally mediated effects (Lima, 1998). Current research is underway in YNP to further clarify these relationships (Smith personal communication).

Several topics have yet to be addressed in wolf → elk → aspen food web studies. Research horizons include plant defense compound effects and genetics, factors that can influence aspen growth and dynamics (Mock et al., 2008; Lindroth and St. Clair, in press). Aspen response to climate variability on a landscape-scale and how this influences food web relationships represents another information gap (Schmitz et al., 2003).

7. Conclusion

Trophic cascades driven by apex predators via top-down effects have been identified in ecosystems worldwide (Estes et al., 2011). Accordingly, ecologists recommend conserving apex predators and including top-down effects in management strategies (Estes et al., 2011).

Generalizations about the ecological importance of apex predators to aspen communities are tempting due to the pressing conservation issues at stake (e.g., wolf removal from the Endangered Species List and subsequent control of this species; addressing Sudden Aspen Decline). However, we suggest caution in broadly ascribing strong top-down trophic effects to wolves, given recent research findings about the context dependence and complexity of these relationships (Binkley et al., 2006). Further, it is likely that cascading effects of wolves in aspen communities may be even more variable outside of places such as YNP or GNP and other national parks, due to the anthropogenic influences on wolves, elk, and forest communities in those multi-use systems (Mech, 2012).

Important goals for future research include understanding how context influences food web relationships in aspen communities. Further research is needed on a landscape scale, as most aspen trophic studies have been done on a localized scale (Table 1). Fertile areas for research include experimental studies on the mechanisms underlying aspen response to disturbance, such as fire, within a wolf-driven trophic cascades model. In moving forward, the effects of climate may become more apparent as the functional and numerical responses of wolves change in response to elk density (White and Garrott, 2005). Such approaches would explore food web relationships as a complex of inter-level interactions in a more integrated, quantitative manner.

We recommend that aspen management strategies incorporate what we are learning about wolf → elk → aspen food webs. Wolves can have powerful effects in food webs. These effects have been linked to aspen recruitment (Table 1). Therefore, applying the precautionary principle to create healthier, more resilient aspen

forests would suggest conserving apex predators, as feasible, where their ranges coincide with aspen (Kreibel et al., 2001). However, use of trophic cascades concepts for aspen management will not be a “one-size-fits-all” prescription, due to the effect of context on food web relationships and the broad spectrum of bottom-up effects, such as fire. Lacking apex predators, it is possible to use management tools that create barriers to ungulates (e.g., coppicing, fencing) to mimic apex predator effects, combined with fire treatments. More science needs to be done in order to make such applications effective.

Finally, we suggest shifting the emphasis and lexicon in future aspen/wolf ecology literature from trophic cascades to food web relationships. This shift would more accurately reflect our emerging scientific awareness that, while they may be important, wolf effects are but one of the suite of physical factors and ecological interactions that can influence aspen growth and dynamics.

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