

The primacy of density-mediated indirect effects in a community of wolves, elk, and aspen

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Abstract

The removal or addition of a predator in an ecosystem can trigger a trophic cascade, whereby the predator indirectly influences plants and/or abiotic processes via direct effects on its herbivore prey. A trophic cascade can operate through a density-mediated indirect effect (DMIE), where the predator reduces herbivore density via predation, and/or through a trait-mediated indirect effect (TMIE), where the predator induces an herbivore trait response that modifies the herbivore's effect on plants. Manipulative experiments suggest that TMIEs are an equivalent or more important driver of trophic cascades than are DMIEs. Whether this applies generally in nature is uncertain because few studies have directly compared the magnitudes of TMIEs and DMIEs on natural unmanipulated field patterns. A TMIE is often invoked to explain the textbook trophic cascade involving wolves (*Canis lupus*), elk (*Cervus canadensis*), and aspen (*Populus tremuloides*) in northern Yellowstone National Park. This hypothesis posits that wolves indirectly increase recruitment of young aspen into the overstory primarily through reduced elk browsing in response to spatial variation in wolf predation risk rather than through reduced elk population density. To test this hypothesis, we compared the effects of spatiotemporal variation in wolf predation risk and temporal variation in elk population density on unmanipulated patterns of browsing and recruitment of young aspen across 113 aspen stands over a 21-year period (1999–2019) in northern Yellowstone National Park. Only 2 of 10 indices of wolf predation risk had statistically meaningful effects on browsing and recruitment of young aspen, and these effects were 8–28 times weaker than the effect of elk density. To the extent that temporal variation in elk density was attributable to wolf predation, our results suggest that the wolf-elk-aspen trophic cascade was primarily density-mediated rather than trait-mediated. This aligns with the alternative hypothesis that wolves and other actively hunting predators with broad habitat domains cause DMIEs to dominate whenever prey, such as elk, also have a broad habitat domain. For at least this type of predator-prey community, our study suggests that risk-induced trait responses can be abstracted or ignored while still achieving an accurate understanding of trophic cascades.

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KEY WORDS

aspen, behaviorally-mediated trophic cascade, density-mediated indirect effect, elk, food chain interactions, food web ecology, predation-risk effect, predator-prey interaction, trait-mediated indirect effect, trophic cascade, wolf, Yellowstone National Park

INTRODUCTION

The removal or addition of a predator in an ecosystem can trigger a trophic cascade, where the predator indirectly affects plants or abiotic processes through its direct effects on herbivore prey. Two mechanisms can drive this cascade: (1) carnivores reduce the density of herbivores by capturing and consuming them (“density-mediated indirect effect,” DMIE), and (2) carnivores induce a trait response in the herbivore that modifies its effect on plants (“trait-mediated indirect effect,” TMIE; Peacor et al., 2020). Both types of trophic cascade have been documented across diverse ecosystems, with various predator species triggering change (Borer et al., 2005; Shurin et al., 2002; Terborgh & Estes, 2013). For example, DMIEs have been attributed to sea otters (Estes & Palmisano, 1974) and sea stars (Paine, 1980) in marine environments, various bass species in lakes (Carpenter et al., 2001), and spiders (Carter & Rypstra, 1995) and lizards (Chase, 1998) in terrestrial ecosystems. Similarly, TMIEs have been attributed to the effects of trout (Peckarsky & McIntosh, 1998), spiders (Beckerman et al., 1997; Gastreich, 1999), and ants (Rudgers et al., 2003) on prey habitat use and/or feeding behavior, culminating in increased plant biomass.

A prevailing narrative in ecology is that TMIEs are a significant driver of trophic cascades, reaching a level of influence that rivals or exceeds that of DMIEs (Peacor & Werner, 2001; Preisser et al., 2005; Schmitz et al., 2004). One influential meta-analysis of published experiments estimated that density-mediated effects attenuated through food chains, resulting in a weak effect on a prey’s resources, whereas trait-mediated effects remained strong, accounting for 85% of the total predator effect (Preisser et al., 2005). However, the broad applicability of this narrative is uncertain due to limited evidence of the primacy of TMIEs in natural unmanipulated communities. A recent review revealed that only 35 (13%) of 275 TMIE studies published in recent decades (1990–2018) measured an unmanipulated field pattern (Peacor et al., 2022), and only four of these 35 studies directly tested the relative magnitudes of TMIEs and DMIEs. In these four studies—three focusing on invertebrates and one on vertebrates—three found that TMIEs were more influential than DMIEs (Kimbrough, 2012; Rosa & DeSouza, 2011; Thomsen & Green, 2016) and one found that TMIEs and DMIEs were equally important (Dalton et al., 2013). This limited

knowledge base is problematic because understanding the general importance of an ecological process like TMIEs ultimately requires evidence of its influence on natural field patterns, determined by observational studies of unmanipulated communities (Peacor et al., 2022; Vellend, 2010, 2016). Moreover, applied ecological disciplines including agriculture, conservation, and management require accurate knowledge about the role predators play in free-living systems, including their influence through TMIEs (Peacor et al., 2022).

Predicting the relative importance of TMIEs and DMIEs in a specific ecosystem is challenging because there is no unified theory-based framework that uses explicitly defined fitness functions to describe how fitness-maximizing prey should modify their traits in response to predators. Instead, prediction has been guided by an empirically-based framework that uses the hunting mode of the predator (sit-and-wait, sit-and-pursue, or active), in relation to its habitat domain and that of its prey (narrow or broad), to predict whether trophic cascades are trait- and/or density-determined (Schmitz, 2005, 2010; Schmitz et al., 2004). Species with a narrow habitat domain select only part of the available habitat, whereas species with a broad habitat domain use the entire range of habitat. Nine of the 10 combinations of hunting mode and habitat domain predict that TMIEs are an equivalent or more important driver of trophic cascades than are DMIEs. DMIEs are predicted to dominate only when active predators have a broad habitat domain and prey have a broad habitat domain. Under these conditions, prey are expected to respond only when predation is imminent because encounters with the predator are too infrequent and/or unpredictable to warrant the fitness cost of a more proactive response, such as a habitat shift.

Case study: Wolves in Yellowstone National Park

Wolf (*Canis lupus*) reintroduction to Yellowstone National Park (YNP) is one of the most commonly cited examples of a TMIE involving a large, terrestrial predator in an unmanipulated system (Allen et al., 2017; Moll et al., 2017; Terborgh & Estes, 2013). Although native to the western United States, wolves were eradicated from YNP by the 1920s during a period of general predator

suppression that also reduced the populations of cougars (*Puma concolor*) and grizzly bears (*Ursus arctos*), a carnivore guild that preys heavily on elk (*Cervus canadensis*) (MacNulty et al., 2020a). The northern Yellowstone elk population has fluctuated greatly over time, alongside concerns of whether there were too few or too many elk (see fig. 14.2 in MacNulty et al., 2020a). With an estimated 10,000–15,000 animals in the early 1920s (Barmore, 2003; Houston, 1982; MacNulty et al., 2020a), concerns that heavy grazing and browsing were causing marked changes in vegetation across the landscape resulted in Park managers removing about 70,000 elk between 1920 and 1968 (Houston, 1982; Wagner, 2006). With the herd reduced to approximately 3000 individuals, concern that the elk population was now too low led to the implementation of a policy called “natural regulation” in 1969, in which managers allowed the population to fluctuate naturally inside the Park, eventually reaching a maximum of ~22,000 in January 1994 (MacNulty et al., 2020a; Smith & MacNulty, 2023; Tallian et al., 2017).

During 1995–1997 (following peak elk density), 41 wolves were reintroduced to YNP (Bangs & Fritts, 1996), and researchers reported subsequent decreases in browsing and increases in the height of woody deciduous plants in some areas of the northern region of the Park, namely willow (*Salix* spp., Ripple & Beschta, 2004a, 2006), cottonwood (*Populus* spp., Ripple & Beschta, 2003), and aspen (*Populus tremuloides*, Ripple & Larsen, 2000; Ripple et al., 2001). Some researchers hypothesized that the observed changes in plants were a result of a wolf-caused trophic cascade mediated by effects on elk density and elk behavior (Ripple et al., 2001; Ripple & Beschta, 2004a, 2004b, 2007) (Figure 1).

In this system, the TMIE hypothesis is that wolves altered elk behavior in a way that resulted in increased recruitment of woody deciduous plants in risky places (Ripple et al., 2001; Ripple & Beschta, 2003, 2004a, 2006; Ripple & Larsen, 2000). However, tests of a TMIE have produced inconsistent results, with conflicting evidence of how elk respond to predation risk, as well as the extent that woody plants have recovered since wolf reintroduction and the mechanism of such change. For example, some findings indicated that elk shift their habitat use from open to forested areas in the presence of wolves (Creel et al., 2005; Fortin et al., 2005; Winnie & Creel, 2007) and increase their vigilance (Halofsky & Ripple, 2008a; Laundré et al., 2001; Liley & Creel, 2008; Winnie & Creel, 2007), while others have found weak and/or inconsistent effects of wolf predation risk on elk space use (Cusack et al., 2020; Kohl et al., 2018, 2019; Mao et al., 2005; Smith et al. 2023; White et al., 2009, 2010) and vigilance (Childress & Lung, 2003; Creel

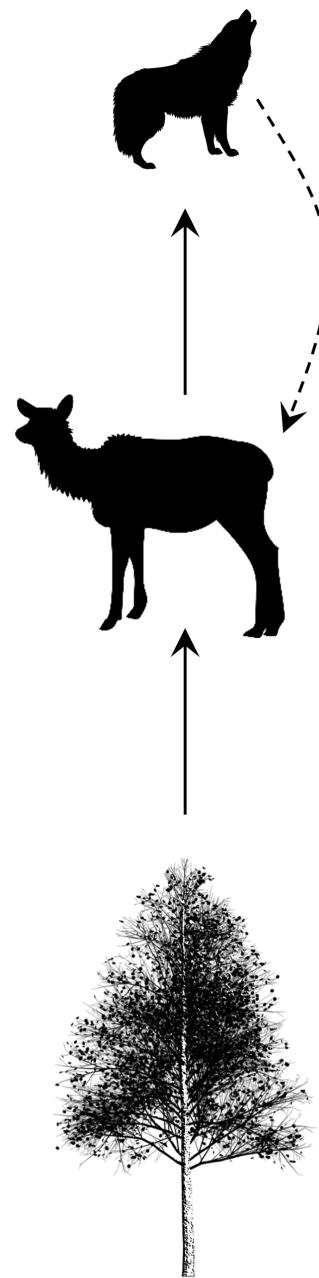


FIGURE 1 Hypothesized mechanisms driving the indirect effects of wolves on aspen in northern Yellowstone National Park. Solid arrows indicate trophic consumptive interactions and energy transfer from resource to consumer (the arrow points toward the consumer). Dashed arrow indicates an effect of wolf predation risk on elk foraging behavior. Wolves may indirectly increase aspen regeneration and height growth by reducing elk consumption of aspen via predation-caused reductions in elk density (density-mediated indirect effect; solid arrows) and/or risk-induced changes in elk foraging behavior (trait-mediated indirect effect; dashed arrow and bottom solid arrow). This figure is adapted from Stahler et al. (2020; fig. 16.1).

et al., 2008; Gower et al., 2009; Liley & Creel, 2008; Lung & Childress, 2007; Middleton et al., 2013; Winnie & Creel, 2007).

While willow (e.g., Ripple & Beschta, 2004a, 2006) and cottonwood (e.g., Ripple & Beschta, 2003) have been part of the TMIE debate, the bulk of studies that have directly tested for a TMIE involving wolves, elk, and woody deciduous plants have focused on aspen. These studies specifically emphasized the height growth of young plants due to interest in the potential for wolves to promote the regeneration of overstory trees. Numerous studies have documented decreased browsing pressure and increased height of young aspen in risky places since wolf reintroduction (Beschta et al., 2016, 2018; Halofsky et al., 2008; Halofsky & Ripple, 2008b; Painter et al., 2014, 2015, 2018; Ripple & Beschta, 2007). However, other studies have documented consistently high browsing pressure and little or no recruitment of young aspen into the overstory (Kauffman et al., 2010; Kimble et al., 2011; Winnie, 2012). For example, Beschta et al. (2018) found that aspen browsing was 14%–15% lower and heights 40–56 cm taller in the presence of risk factors, which they defined as escape and view impediments (e.g., downed logs, local terrain undulations), whereas Winnie (2012) found that browsing increased and the number of young aspen decreased as the number of such risk factors increased. Additionally, Kauffman et al. (2010) found that aspen browsing pressure was unrelated to elk or wolf habitat use and that browsing actually increased with increasing levels of predation risk, contrary to the TMIE hypothesis.

Challenges of quantifying the YNP trophic cascade

Reasons for the muddled evidence of a wolf-elk-aspen TMIE include varying definitions and scales of risk, reliance on qualitative interpretations of time series data, and the use of nonrandomly sampled and nonindependent data (Brice et al., 2022; Fleming, 2019; Kauffman et al., 2010, 2013; Winnie, 2012, 2014; Winnie & Creel, 2017). Furthermore, no study has conducted a direct quantitative comparison of the relative effects of elk density and predation risk on woody plant browsing and recruitment, resulting in uncertainty regarding whether a TMIE or DMIE is dominant in this system.

Many studies documenting evidence for a TMIE for aspen in YNP have defined risk with subjective habitat characteristics that are not derived from predator-based measurements of predation risk (Beschta et al., 2018; Painter et al., 2014; Ripple & Beschta, 2007, 2012). Such habitat characteristics are outlined in table 1 of Ripple and Beschta (2004a), and include terrain features such as rivers, gullies, or cliffs, and biotic factors like downed woody debris or beaver dams that may serve as viewshed

or escape impediments. For example, Ripple and Beschta (2007) classified sites with downed logs >30 cm diameter as “high risk,” and sites without downed logs as “low risk,” assuming elk avoid aspen stands with logs on the ground because these features hinder escape from wolves. While the majority of YNP TMIE studies have used escape and view impediments to categorize risk, the relationship between such impediments and antipredator behavior is unclear (Moll et al., 2017). In their review of carnivore–ungulate predation risk studies, Moll et al. (2017) advised against using subjective habitat characteristics alone to represent risk, as these characteristics are often confounded with other variables and have mixed support in the literature. For example, elk may detect wolves when there is more visibility, but it is also possible such visibility may enhance wolf detection of elk.

Although there are strengths and weaknesses associated with all risk metrics, Moll et al. (2017) recommended using ones derived from predator-based data, which are more likely associated with a biologically meaningful proxy of predation risk. For example, Kauffman et al. (2010) estimated spatial variation in the relative probability of elk kills using a statistical model that included wolf-killed elk sites, a general index of elk density (estimated from an elk resource selection model by Mao et al., 2005), wolf distribution, and several landscape variables (Kauffman et al., 2007). Kauffman et al. (2010) found that browsing and recruitment of young aspen were unrelated to this estimate of spatial variation in wolf predation risk.

A second possible reason for the uncertain conclusions regarding a wolf-driven TMIE is a reliance on inferring patterns from correlational data. Many of the studies that attributed reduced browsing and increased height growth of aspen to a wolf-driven trophic cascade relied on simple qualitative interpretations of time series data rather than on statistical analyses of relationships between the trophic levels (Beschta et al., 2016, 2018; Beschta & Ripple, 2009; Halofsky et al., 2008; Painter et al., 2014, 2015, 2018; Peterson et al., 2014; Ripple & Beschta, 2007, 2012). While decreased browsing and increased plant height since wolf reintroduction are consistent with a trophic cascade, this alone does not indicate causality (Ford & Goheen, 2015; Peterson et al., 2014). Elk preferentially browse plants of a certain height, and stems taller than that height are browsed at a lower rate; as such, stem height is both a cause and an effect of reduced browsing (Brice et al., 2022). Relying on a correlation between time series of browsing and height overlooks this nonlinear relationship.

A final reason for the uncertainty regarding a wolf-driven TMIE is the use of nonrandomly sampled and nonindependent data. Many of the studies on wolf–elk–aspen cascades used nonrandom sampling to assess trends in browsing and height, such as measuring only the three or five tallest plants in a stand (Beschta et al., 2016, 2018; Beschta & Ripple, 2016; Halofsky et al., 2008; Painter et al., 2014, 2015, 2018; Ripple & Beschta, 2007, 2012). Such nonrandom sampling has been shown to estimate faster rates of change in browsing and height compared with stratified random sampling, thereby overestimating the strength of the cascade (Brice et al., 2022; MacNulty et al., 2024). Much of the young aspen data have also been collected using the plant architecture approach, in which researchers use terminal bud scars to reconstruct a year-by-year history of browsing and growth for individual stems (Keigley & Frisina, 1998). Although the developers of the approach emphasized that this method is only valid for the most recent 2–3 years of plant growth (Keigley & Frisina, 1998, pp. 26, 83), many studies in Yellowstone have relied on plant architecture to estimate browsing and height of aspen over periods exceeding 7 years (e.g., Beschta et al., 2018; Halofsky et al., 2008; Ripple & Beschta, 2007, 2012), suggesting such data may not be reliable. For this reason and those outlined above, there is no consensus on the mechanism or strength of a trophic cascade involving wolves, elk, and aspen, despite two decades of research.

Study objectives

The purpose of our study was to quantitatively test the relative magnitudes of DMIEs and TMIEs in an unmanipulated natural community using the YNP wolf–elk–aspen food chain as a case study. Our primary objectives were to (1) determine the extent to which wolf-caused predation risk and elk density drive elk browsing of aspen, and (2) evaluate how changes in browsing due to risk and elk density translate to changes in aspen recruitment. If a TMIE is dominant, as asserted in previous studies (Beschta et al., 2018; Ripple et al., 2001; Ripple & Beschta, 2004b, 2007), we predicted that patterns of browsing and recruitment were explained primarily by spatiotemporal variation in wolf predation risk, with little to no effect of temporal variation in elk population density. On the other hand, if a DMIE is dominant, as expected for a broadly distributed active predator like the wolf and an equally broadly distributed prey like the elk (Schmitz, 2005, 2010; Schmitz et al., 2004), we predicted that patterns of browsing and recruitment would be primarily a function of temporal variation in elk population density, with little to no effect from spatiotemporal variation in wolf predation risk.

To test the relative effects of elk density and predation risk on the wolf–elk–aspen trophic cascade, we built statistical models of aspen browsing and recruitment probability as functions of several spatiotemporal indices of predation risk, alongside temporal estimates of elk population abundance (converted to density). We used aspen data collected in 19 years (1999, 2001–2014, and 2016–2019) at 113 aspen stands across northern YNP, and calculated risk measures from VHF and GPS wolf locations, wolf-killed elk locations, and several habitat characteristics previously shown to index elk predation risk. Simultaneously testing the effects of both elk density and predation risk on aspen in this system clarified the mechanism of Yellowstone's iconic wolf–elk–aspen trophic cascade and provided rare understanding of the relative magnitudes of TMIEs and DMIEs on an unmanipulated field pattern.

METHODS

Study area

Our study centers on northern YNP, specifically the portion of the northern Yellowstone elk winter range that lies within the Park (Figure 2). This 995-km² landscape is characterized by short, cool summers, and long, cold winters (Houston, 1982). The relatively low elevation (1500–2000 m) of the study area creates dry and warm conditions compared with the Park interior, providing important winter habitat to various ungulates, including elk, bison (*Bison bison*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*). Northern YNP also has a guild of large carnivores that includes wolves, cougars, grizzly bears, and black bears (*Ursus americanus*).

Vegetation in northern YNP is dominated by grasslands and sagebrush steppe at lower elevations (mainly big sagebrush [*Artemisia tridentata*], Idaho fescue [*Festuca idahoensis*], and blue-bunch wheatgrass [*Pseudoroegneria spicata*]), and conifer forest at higher elevations (mainly Douglas fir [*Pseudotsuga menziesii*] and lodgepole pine [*Pinus contorta*]). Upland grasslands and wet meadows make up a smaller portion of the landscape, and aspen, willow, and cottonwood are among the few deciduous woody plants in the region (Despain, 1990).

Study species

Aspen

Quaking aspen (hereafter “aspen”) is found across a wide gradient of climatic conditions, but is limited by water

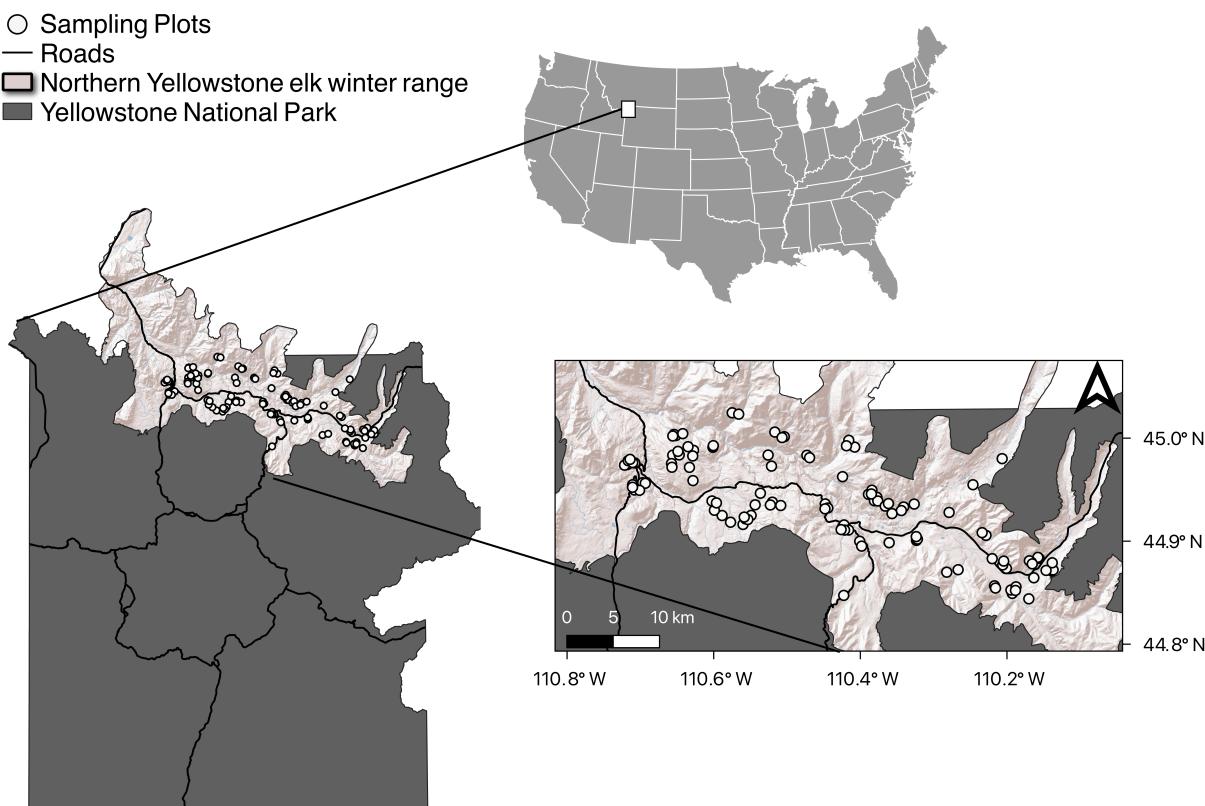


FIGURE 2 Locations of randomly sampled aspen stands in northern Yellowstone National Park. The northern Yellowstone elk winter range is the maximum distribution of the northern Yellowstone elk population during winter when elk often browse young aspen (shaded relief from Esri).

availability in the Intermountain West (Jones & DeByle, 1985). It normally occurs in areas with at least 38 cm of annual precipitation (Jones & DeByle, 1985), and our study area is near this lower limit (Larsen & Ripple, 2003). As aspen growth is primarily limited by the ability of soil moisture to meet high evapotranspirational demands (Mueggler, 1988), drought stress is a common cause of aspen mortality (Hanna & Kulakowski, 2012; Rehfeldt et al., 2009; Worrall et al., 2013). In northern YNP, aspen is scattered in discrete stands on relatively moist mid-elevation benches, near streams, and along conifer forest/shrub steppe ecotones (Houston, 1982).

As a clonal species, aspen often propagates through genetically identical root sprouts, rather than through sexual reproduction (Barnes, 1966). However, fire plays an important role in seedling propagation, helping to increase genetic diversity within stands (Halofsky et al., 2008; Romme et al., 2005; Turner et al., 2003). Prior to fire control policies in the late 1800s, fire recurred every 20–25 years in northern YNP, after which there were no major fires in the area until 1988, when 36% of YNP burned (Despain et al., 1989; Romme et al., 1995). Although the 1988 fires initially stimulated growth, Romme et al. (1995) found that the

difference in aspen seedling density between burned and unburned stands in northern YNP was negligible after just three years. Additionally, there was no difference in height distributions between burned and unburned stands, with seedlings averaging 21–35 cm in height, which Romme et al. (1995) largely attributed to heavy browsing by elk across the study area. They further noted that burned aspen stands subjected to lower browse pressure outside of northern YNP exhibited much faster growth. As such, while fire may be an important mechanism for aspen regeneration when ungulate herbivory is low, extensive browsing caused by high elk densities in northern YNP minimized the importance of the 1988 fires in our study area (Romme et al., 1995).

Historic photographs suggest that aspen only covered 4%–6% of the landscape at Park establishment (Houston, 1982; Meagher & Houston, 1999), and it is considered ecologically important because it supports more species diversity than nearby conifer forests, sagebrush, and grasslands despite covering a relatively small part of the landscape (Chong et al., 2001; DeByle, 1985; Mueggler, 1985). However, aspen experienced a decline in canopy coverage and a lack of recruitment

throughout the 20th century, with only 5% of the existing overstory originating after 1921 (Houston, 1982; Larsen & Ripple, 2005; Ripple & Larsen, 2000).

The dominant opinion as to what caused the failure in aspen recruitment has changed over time. Poor regeneration of overstory aspen in northern YNP was attributed to beaver (*Castor canadensis*) (Warren, 1926) and elk as early as the 1920s (Rush, 1932). As beaver abundance decreased (Smith & Tyers, 2012) and elk abundance remained high (Houston, 1982), some observers emphasized the role of elk in preventing aspen regeneration (Kay, 1990; Klein et al., 2002; Wagner, 2006), while others instead highlighted climate change, fire suppression, conifer succession, and variation in secondary compounds (Barmore, 2003; Bishop et al., 1997; Despain et al., 1986; Houston, 1982; Romme et al., 1995). Following wolf reintroduction, some researchers have returned to the top-down hypothesis, with elk browsing identified as the main driver of historical decrease in aspen recruitment, and climatic factors have largely been regarded as unimportant (Klein et al., 2002; Painter et al., 2014; Ripple & Beschta, 2007; Ripple & Larsen, 2000). However, climate change has already reduced aspen occupancy across the western United States (Rehfeldt et al., 2009; Worrall et al., 2013), and this downward trend is expected to continue, including within our study area (Brice et al., 2022; Pieckle et al., 2015, 2016).

Elk

Elk have been the dominant ungulate in the study area for most of the time since Park establishment in 1872 (Houston, 1982). Across our study period of 1999–2019, winter elk abundance within northern YNP ranged from a high of 13,442 in 1999 to a low of 1986 in 2017 (Figure 3; Smith & MacNulty, 2023; Tallian et al., 2017). These figures represent the number of elk counted in the Park portion of the northern Yellowstone elk winter range. Additional elk from the northern Yellowstone elk population also occur in the non-Park portion of the winter range, north of the YNP boundary (Figure 2; MacNulty et al., 2020a). Wolves, grizzly bears, black bears, cougars, and human hunters have all likely contributed to the elk population decline (MacNulty et al., 2020a). Elk are predominantly grazers, and in winter their diet is approximately two-thirds graminoids and one-third browse (Christianson & Creel, 2007). Aspen is a valuable source of nutrition in winter (Cook, 2002), constituting 5%–7% of elk winter diet (Christianson & Creel, 2007; Singer & Norland, 1994), whereby elk eat the woody stems of young plants that protrude through the

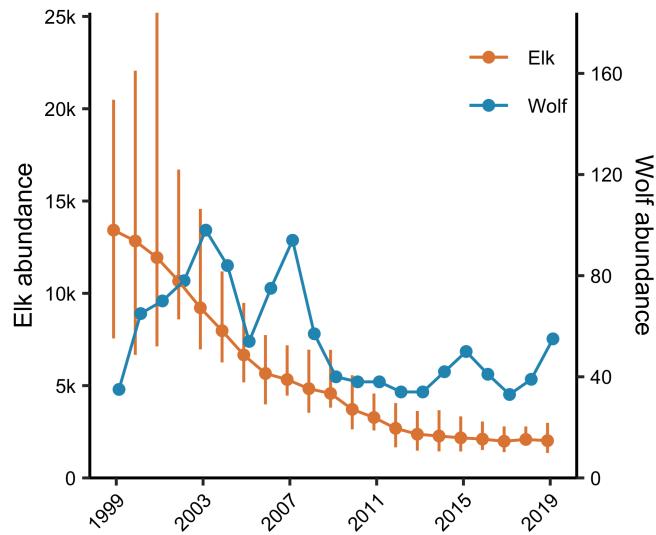


FIGURE 3 Annual abundance of elk (orange) and wolves (blue) within northern Yellowstone National Park. Elk counts are predictions from a state-space model that accounts for the effects of elk group size and forest canopy openness on sightability (Smith & MacNulty, 2023; Tallian et al., 2017). Error bars are 95% CIs derived from this model. Annual wolf abundance was determined through a census conducted at the end of each calendar year. This census involved daily ground and aerial observations of all wolf packs in the study area during a 30-day period from mid-November to mid-December (Cassidy et al., 2022).

snow (Romme et al., 1995). While other ungulates in this system may also browse aspen (e.g., bison, moose, mule deer), camera trap data suggest that elk were the dominant browser during the study, and that the majority of such browsing occurred in winter (see appendix in Brice et al., 2022).

Wolves

Northern YNP hosts the highest density of wolves in the Park (Cassidy et al., 2020). The northern YNP wolf population peaked at 98 individuals in 2003, but has fluctuated around ~40 wolves for the last decade (Figure 3; Smith et al., 2020). Wolves are active predators that chase their prey across open areas, pursuing many more prey than they actually catch (MacNulty et al., 2020a). They have a relatively low hunting success rate, which rarely exceeds 20% (Mech et al., 2001) and is less than 10% when only adult elk are considered (MacNulty et al., 2012). In YNP, elk constituted as much 96% of wolves' winter diet in the first decade following reintroduction, with the majority of kills being calves and older (i.e., 10+ years) adults (MacNulty et al., 2020a, 2020b; Metz et al., 2020a). More recently, bison provided

25% or more of the biomass acquired by wolves in winter, largely through scavenging (Metz et al., 2020a). Wolves are more successful hunting elk when snow depth increases (Huggard, 1993; Mech et al., 2001), and most elk kills occur in flat, open areas close to streams and roads (Kauffman et al., 2007; Kohl et al., 2019).

Data collection

Aspen

Beginning in 1999, we measured young aspen height and browsing at 113 stands selected in a stratified random sample reflecting high and low wolf use areas (see Brice et al., 2022 for details). All stands were selected from aerial photographs taken after the 1988 fires; as such, selected aspen stands were those whose overstory at least partially survived the 1988 fires. Each stand contained a 20×1 m belt transect, and we surveyed all young aspen (≤ 600 cm tall, “stems”) within the transect (“plot”) at the end of the growing season (late July–September) each year. For each stem, we measured height of the leader (i.e., tallest stem), and whether the leader was browsed the previous winter. The number of stands sampled each year varied from 61 to 113 ($\mu = 97.3$, $\sigma = 18.3$), and the number of plots with stems each year varied from 55 to 108 ($\mu = 84.9$, $\sigma = 17.2$). Sampling occurred annually from 1999 to 2019, excluding 2000 and 2015, resulting in 26,012 stem-level observations over 19 years.

Elk

Aerial winter surveys of elk were conducted annually using three to four fixed wing aircraft simultaneously flying nonoverlapping areas between December and March (see Lemke et al., 1998). In years with no survey (i.e., 2006, 2014), elk counts were interpolated with a state-space model that accounts for the effects of elk group size and forest canopy openness on sightability (Smith & MacNulty, 2023; Tallian et al., 2017). We divided annual counts of elk within the Park by the study area (995 km^2) to calculate annual elk density (number of individuals per square kilometer), as required to test for a *density*-mediated effect. The DMIE that we tested refers to effects on aspen caused by the total population density of elk that winters in the study area. We therefore used annual variation in total elk population density rather than spatial elk density as the index for the density-mediated effect of wolves on aspen.

Wolves

Since 1995, the Yellowstone Wolf Project has studied wolves for two 30-day periods each winter: (1) mid-November to mid-December (early winter) and (2) the month of March (late winter). Each winter, 20–30 wolves (~35%–40% of population) were captured and fitted with VHF and GPS collars (Smith et al., 2004). All wolves were captured and handled following protocols in accordance with guidelines from the American Society of Mammalogists (Sikes, 2016) and approved by the National Park Service Institutional Animal Care and Use Committee (IACUC permit IMR_YELL_Smith_wolves_2012). All wolf packs in northern YNP included at least one collared wolf each year. Locations from both VHF and GPS collars were recorded approximately daily during early and late winter periods, and weekly outside of these periods. GPS collars also recorded hourly locations during each 30-day winter study, and at variable times otherwise. During winter study, ground and aerial crews searched for wolf kills by tracking collared wolves and investigating clusters of locations.

Weather variables

Snow water equivalent (SWE) integrates snowpack depth and density and is an important predictor of elk movement and behavior in winter (Proffitt et al., 2011; White et al., 2009). For instance, increasing SWE can act as a physical barrier, reducing elk visits to aspen stands, as well as the amount of aspen height lost to winter browsing (Brodie et al., 2012; Martin & Maron, 2012). SWE may also index site quality, with melting snowpack an important source of water during the growing season (Kretchun et al., 2020). Thus, we obtained data on SWE at each aspen stand from Daymet, which produced daily gridded estimates of weather parameters from meteorological observations at a 1-km^2 resolution (Thornton et al., 2020). We calculated total winter SWE (in tons per square meter) by summing daily estimates from November 1 to April 30 at each stand each year.

As a highly drought-sensitive species, precipitation is an important driver of aspen growth (Jones et al., 1985; Rhodes et al., 2017; Worrall et al., 2013). We thus obtained data on spring precipitation to include in models of aspen recruitment. We estimated spring precipitation as the sum of daily precipitation (in centimeters; sum of all forms converted to water equivalent) from April 1 to July 31, again obtained from Daymet for each stand each year. See Appendix S1 for a description of annual trends in SWE and spring precipitation (Appendix S1: Figure S1a).

Spatiotemporal variation in wolf predation risk

In its simplest form, predation risk can be defined as the probability of prey being killed during some time period (Lima & Dill, 1990). Using this definition, Lima and Dill (1990) decomposed risk into three components based on Holling's 1959 disk equation of the predator functional response: (1) probability of predator–prey encounters (α); (2) the conditional probability of being killed given an encounter (d); and (3) the time prey spend vulnerable to an encounter (T). They further contend that prey should be able to assess predation risk for each of these components, thereby resulting in antipredator behavior at the expense of foraging.

With further inclusion of temporal variability into the definition of risk, Lima and Bednekoff (1999) proposed the *risk allocation hypothesis*, which asserts that antipredator behavior depends on both the immediate and background level of predation risk. Alternatively, the *risky places hypothesis* purports that antipredator behavior varies only in relation to long-term background risk, while the *risky times hypothesis* is that antipredator behavior only varies in relation to pulses of predation risk (Creel et al., 2008). Based on these hypotheses, Moll et al. (2017) categorized metrics of risk for carnivore–ungulate systems into three groups: (1) risky places and (2) risky times based on predator space use or behavior, and (3) habitat characteristics that capture long-term risk or interact with predator space use or behavior to modify risk.

Given the challenge of understanding how prey perceive and respond to predation risk (Cresswell, 2008; Moll et al., 2017), we tested 10 different risk metrics that relate to both the α and d components of predation risk, and each represents a distinct hypothesis about how a TMIE is generated in YNP (Table 1, Figure 1). Broadly, we tested spatial wolf density, spatial density of wolf-killed elk, and landscape openness and topographic smoothness, all of which are measures of absolute risk (i.e., risk unadjusted by local elk density), rather than per capita risk (i.e., absolute risk/local elk density). The choice of whether to use absolute or per capita predation risk depends on the assumptions about how elk perceive risk. Per capita risk assumes that an individual elk is aware of the number of other elk in its neighborhood and adjusts its antipredator response to its individual risk of being killed by wolves. However, per capita risk may not be the appropriate measure of risk in a system like YNP in part because (1) individuals are not uniformly vulnerable to predation (MacNulty et al., 2020a), and (2) local elk abundance is highly variable due to seasonal migration between winter and summer home

ranges, movement within home ranges, emigration, and immigration (Houston, 1982; Smith et al., 2023; White et al., 2010; Zuckerman et al., 2023).

Furthermore, we used absolute rather than per capita risk because numerous studies of the Yellowstone wolf–elk system have demonstrated that elk are (1) responsive to various measures of absolute wolf predation risk (i.e., spatial kill density, spatial wolf density, openness, and roughness; Creel et al., 2005; Forester et al., 2007; Fortin et al., 2005; Gude et al., 2006; Kohl et al., 2018, 2019; Mao et al., 2005; Smith et al., 2023; cf. Cusack et al., 2020), and (2) no more responsive to per capita risk than to absolute risk (Kohl et al., 2018). Additionally, a comparable study of the effect of wolf predation risk on elk–aspen interactions found that an index of per capita risk had no effect on browsing and recruitment of young aspen (Kauffman et al., 2010). Thus, within the context our study system, per capita risk is not necessarily a more appropriate measure of risk than is absolute risk.

Additionally, we tested spatial wolf and kill density on both annual and long-term (i.e., ~20-year average) scales. Testing these two temporal scales allowed us to better understand whether trait-mediated effects of wolves on aspen browsing and recruitment arise from elk reacting to current risk (i.e., this winter), or proactively avoiding areas they remember as risky over many years (Cusack et al., 2020).

Winter wolf spatial density

We first characterized predation risk as the spatial density of wolves in winter (November 1–April 30). We focused on wolf spatial density in winter because this is when northern Yellowstone elk migrate into the study area and browse aspen, and several studies have shown that elk shift their habitat selection in response to wolf density, although this response may vary seasonally (Forester et al., 2007; Fortin et al., 2005; Mao et al., 2005). This metric captures variation in encounter rate (α), based on the assumption that elk are more likely to encounter wolves as wolf density increases (Moll et al., 2017). However, Moll et al. (2017) suggest that predator density will have little to no effect on probability of death given an encounter (d), which is further supported by Kauffman et al. (2007), who found that wolf density was not a strong predictor of kill site occurrence.

We used VHF and GPS locations of wolves in the study area to calculate winter (November 1–April 30) wolf density each year and across years. We restricted the data to wolves with at least 30 days of observations, which proved to be highly correlated with the full 6 months of locations (Pearson's $r = 0.99$). Additionally, we only used wolves with at least 10 locations per winter,

TABLE 1 Covariates used in the analysis of browsing and overstory recruitment of young aspen, the type of indirect effect they represent, and their predicted effects on elk space use, elk browsing, and recruitment of young aspen.

Covariate	Type	Predicted effect on		
		Elk space use	Elk browsing	Aspen recruitment
Height of young aspen			Browsing increases with height up to 120 cm, after which it decreases as height increases	
Snow water equivalent (SWE)	Deep snowpack (indexed by SWE) inhibits elk movement		Browsing decreases with SWE as elk struggle to access stands in deep snow. Aspen buried under snow are protected from elk	Recruitment increases with SWE due to decreased browsing and increased water availability from spring snowmelt
Spring precipitation				Recruitment increases with spring precipitation due to the positive effect of water availability on growth
Elk density	DMIE		Browsing decreases as elk density declines due to direct killing by wolves, i.e., wolf predation	Recruitment increases as browsing decreases, driven by the reduction in elk density due to wolf predation
Spatial density of wolves	TMIE	Elk avoid areas of high wolf density to limit α	Browsing decreases in areas of high wolf density	Recruitment increases in areas of high wolf density due to reduced browsing
Spatial density of wolf-killed elk	TMIE	Elk avoid areas of high wolf kill density to limit α and d	Browsing decreases in areas of high elk kill density	Recruitment increases in areas of high elk kill density due to reduced browsing
Spatial density of wolf-killed male elk	TMIE	Male elk avoid areas of high wolf kill density to limit α and d , but to a lesser extent than female elk	Browsing decreases in areas of high male elk kill density, but the effect is weaker compared to areas with high female elk kill density	Recruitment increases in areas of high male elk kill density due to reduced browsing, but the effect is weaker compared to areas with high female elk kill density
Spatial density of wolf-killed female elk	TMIE	Female elk avoid areas of high wolf kill density to limit α and d , more so than male elk	Browsing decreases in areas of high female elk kill density, but the effect is stronger compared to areas with high male elk kill density	Recruitment increases in areas of high female elk kill density due to reduced browsing, but the effect is stronger compared to areas with high male elk kill density
Landscape openness	TMIE	Elk will avoid open areas due to increased wolf hunting success (limit d)	Browsing decreases as landscape openness increases	Recruitment increases as landscape openness increases due to reduced browsing
Terrain smoothness	TMIE	Elk will avoid flat areas due to increased wolf hunting success (limit d)	Browsing decreases as terrain smoothness increases	Recruitment increases as terrain smoothness increases due to reduced browsing

Note: spatial densities of wolves and wolf-killed elk refer to winter (November 1–April 30) densities.

Abbreviations: α , encounter rate between wolves and elk; d , probability of elk death given an encounter; DMIE, density-mediated indirect effect; SWE, winter (November 1–April 30) snow water equivalent in tons per square meter; TMIE, trait-mediated indirect effect.

the minimum number of locations needed for the models to converge. After restricting the data, there were 142,087 total locations and 777 unique wolf-year combinations (wolf-years) from 1999 to 2019, with wolf-years spanning 30–181 days (median = 152 days) and containing 10–4194 locations (median = 42).

To estimate the spatial densities of wolves, we used the locations to fit individual continuous time movement models (CTMM) to each wolf-year using the ctmm package (Calabrese et al., 2016) in R (V1.2.5019, R Core Team, 2018). We used the Ornstein–Uhlenbeck Foraging (OUF) anisotropic process for each wolf, which

accounts for correlated velocities and restricted space use (Fleming et al., 2014). Once each wolf had its own CTMM, we calculated an autocorrelated kernel density estimate (AKDE) at a 30-m² resolution for each wolf-year. If there were multiple collared wolves within a pack, we averaged their AKDEs and divided by the sum of all values to ensure that the AKDE summed to one and could be interpreted as a probability density.

Once we had a single AKDE for each pack each winter, we weighted each pack-specific AKDE by the corresponding number of wolves in the pack (lone wolves unweighted), and then summed the densities of all packs and lone wolves each winter, resulting in a single wolf AKDE each year (Figure 4a). Finally, we created a long-term average measure of wolf density by taking the mean of all annual AKDEs (Figure 4b). We intersected all spatial layers of risk with the aspen stand locations to derive stand-specific estimates of risk.

Kill spatial density

We next characterized predation risk as the spatial density of wolf-killed elk in winter. As with wolf density, we again tested spatial kill density at both annual and long-term temporal scales. Kill density is expected to be positively related to both encounter rate (α) and the probability of death given an encounter (d) (Moll et al., 2017). Absolute risk based on spatial kill density is a well-established metric of predation risk in wildlife systems (Gervasi et al., 2013; Hopcraft et al., 2005; Lone et al., 2014; Thaker et al., 2011), and two studies have found that absolute kill density affects elk habitat selection (Gude et al., 2006; Kohl et al., 2018; cf. Cusack et al., 2020).

We used positional data of wolf-killed elk to calculate a kernel density estimate (KDE) of elk kills each winter using the `sp.kde` function from the `spatialEco` package in R (Evans et al., 2021). We used a bandwidth of 3 km per the methods of Kohl et al. (2018) and Fortin et al. (2005), and a resolution of 30-m² (Kauffman et al., 2007; Kohl et al., 2018). We also assessed KDEs at 60- and 120-m² resolutions to determine whether elk perceive risk at larger scales. However, all three resolutions were highly correlated ($r > 0.99$ for all), and we therefore used only the 30-m² data in our analyses of aspen browsing and recruitment, following previous studies of wolf predation risk in northern Yellowstone (Kauffman et al., 2007; Kohl et al., 2018).

Previous research about elk response to predation risk has generally overlooked adult males (but see Unsworth et al., 1993), and focused mainly on adult females (Cusack et al., 2020; Fortin et al., 2005; Kohl et al., 2018,

2019; Mao et al., 2005) or all age and sex classes (Kauffman et al., 2007, 2010; Smith et al., 2023). However, Winnie and Creel (2007) measured sex-specific responses of elk to wolf predation risk, and found that adult males were less responsive than adult females to wolf presence despite being more than six times as likely to be killed (Creel et al., 2005). Additionally, Kohl et al. (2018) found that the spatial distribution of adult male elk kills differed from that of adult females and calves (see appendix S1: fig. S1 in Kohl et al., 2018). To test whether the potential behavioral differences between male and female elk cascade to affect aspen, we distinguished kills by sex, creating annual KDEs with all kills ($N = 2448$, annual range = 61–193; Figure 4c), adult male elk and male yearlings ($N = 729$, range = 17–69; Figure 4e), and adult female elk and calves ($N = 1430$, range = 28–125; Figure 4g) for each winter. As with wolf density, we also calculated the long-term averages of kill density using kills across all years for the three categories (Figure 4d,f,h). See Appendix S1 for a description of annual trends in predation risk (Appendix S1: Figure S1b).

Topography and vegetation openness

Finally, we characterized predation risk using two habitat variables that characterize the wolf hunting domain: landscape openness and topographic smoothness. Previous studies have indicated that elk avoid these habitat features because they increase elk vulnerability to predation (Cusack et al., 2020; Kauffman et al., 2007; Kohl et al., 2018, 2019; Smith et al., 2023). Encounter rate (α) is likely unaffected by these variables, as visibility in open, smooth landscapes is increased for both wolves and elk. However, wolves are most successful hunting in such landscapes, thereby increasing elk vulnerability to wolves and the probability of death given an encounter (d) (Cusack et al., 2020; Kauffman et al., 2007; Kohl et al., 2018, 2019).

We extracted land cover type using the Rangeland Analysis Platform (Allred et al., 2021), and calculated openness for each year as the proportion of each 30-m² cell that was not tree cover (Figure 4i). To calculate smoothness, we used a 30-m² digital elevation model (DEM) and the `terrain` function from the `raster` package in R (Hijmans & van Etten, 2014), which produced a map of roughness. Roughness was defined as the difference between the maximum and minimum elevation of a cell and its surrounding eight cells. We converted roughness to smoothness by scaling it from 0 to 1 and subtracting from 1 (Figure 4j). Predation risk from wolves is expected to be greatest in flat (smoothness = 1), open areas (openness = 1) where wolves are most likely to kill elk (Kauffman et al., 2007; Kohl et al., 2019).

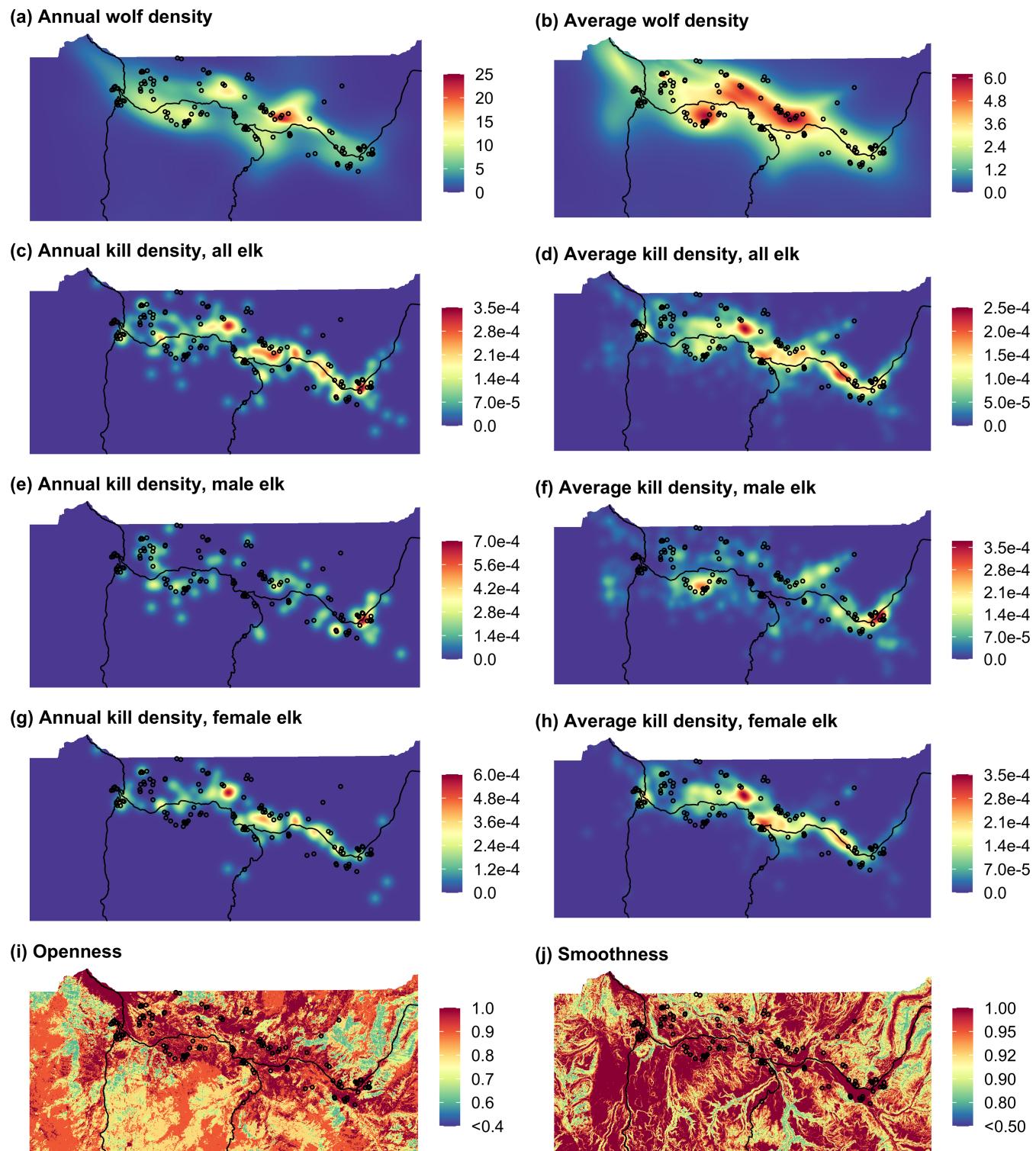


FIGURE 4 Spatial distribution of wolf predation risk in relation to randomly sampled aspen stands (open circles) in northern Yellowstone National Park. (a) Wolf density in 2008 (wolves per square kilometer), (b) average wolf density (wolves per square kilometer), (c) wolf-killed elk density in 2008 (kills per square kilometer), (d) average wolf-killed elk density (kills per square kilometer), (e) wolf-killed male elk density in 2008 (kills per square kilometer), (f) average wolf-killed male elk density (kills per square kilometer), (g) wolf-killed female elk density in 2008 (kills per square kilometer), (h) average wolf-killed female elk density (kills per square kilometer), (i) landscape openness, where 0 is forested and 1 is open, (j) topographic smoothness, where 0 is rough and 1 is flat. Black lines are Park roads. We used 2008 to represent the annual spatial distributions of risk because it was the midpoint of our study period.

Aspen browsing and recruitment

Annual trends

If wolves contributed to a DMIE, we expected annual decreases in browsing and annual increases in height of young aspen to track annual decreases in elk density and increases in wolf density (but note that we cannot infer causation from these patterns alone; Table 1). To examine whether trends in aspen browsing and height across our study were consistent with a DMIE, we fit generalized linear mixed models (GLMMs) of these variables as functions of year with the glmmTMB package in R (Brooks et al., 2017). The browsing model was fit with a Bernoulli error distribution and logit link function, with a binary response for stem-level browsing. Height was fit with a Gamma error distribution and log link function, with continuous stem-level height as the response. Year was a categorical variable in both models, and we specified a random intercept for stand identity to account for repeated measures within stands. To account for temporal autocorrelation, we included a first-order autoregressive covariance structure.

Browsing

To test the relative strength of a DMIE versus TMIE in this system, we modeled browsing as a function of elk density and wolf predation risk. If a TMIE is dominant, as hypothesized in previous studies (Beschta et al., 2018; Ripple et al., 2001; Ripple & Beschta, 2007), predation risk should have a stronger negative influence on browsing compared to elk density. Alternatively, if a DMIE is dominant, as predicted by the active hunting mode of wolves and the broad habitat domains of both wolves and elk (Schmitz et al., 2004), predation risk should have a weaker negative influence on browsing compared to elk density. To model browsing, we fitted GLMMs with the lme4 package in R (Bates et al., 2015) using a Bernoulli error distribution and logit link function. The response was a binary variable for stem-level browsing, and the covariates were stem height, SWE, annual elk density, and predation risk. We included stem height and SWE to control for their potentially confounding effects on browsing (Brice et al., 2022; Brodie et al., 2012).

Rather than creating a single model with all risk variables, some of which were highly correlated, we fitted 10 separate models, each with a different measure of risk that represented a distinct hypothesis about how a TMIE is generated in this system (Table 1). Doing so prevented multicollinearity caused by correlated risk variables, which could otherwise make the interpretation of

coefficients unreliable. As such, all models contained stem height, SWE, and elk density, and varied only by which measure of risk was included. We removed outliers (identified by interquartile range method) of the risk variable in each model, resulting in sample sizes ranging from 23,196 to 26,012 young aspen stems. All covariates were scaled to have a mean of 0 and SD of 1, allowing for direct comparison of the magnitude of model coefficients.

To account for repeated measures across time and space, all models contained crossed random intercepts for stand identity and year. These intercepts signify that all stems within stand i share a common intercept across years, and all stems within year j share an intercept across stands. We also included random coefficients for elk density and annual risk measures (the covariates most central to our hypotheses) that varied by stand because they provided a better fit to the data than intercepts alone (Appendix S1; Brice et al., 2024). Failing to incorporate random coefficients often inflates Type I and Type II errors (Harrison et al., 2018); specifically, including random coefficients yields more accurate estimates of uncertainty, and can increase the power to detect individual variation (Schielzeth & Forstmeier, 2009). We used an unstructured variance–covariance structure to model the correlation between random intercepts and slopes.

Research in northern Yellowstone and elsewhere indicates a nonlinear relationship between browsing and plant height, such that browsing increases with height up to a peak around 100–150 cm, corresponding to elk shoulder height (Brice et al., 2022; Konôpka et al., 2018; Maxwell et al., 2019; Motta, 2003; Renaud et al., 2003; Rounds, 1979). We therefore built models with height represented as a piecewise linear spline and the other covariates as linear. We compared models with a single knot from 100 to 130 cm using corrected Akaike information criterion (AIC_c). Because datasets differed slightly depending on the risk variable (due to outlier removal), we performed model selection separately for each of the 10 risk variables (Appendix S1; Brice et al., 2024). All models contained crossed random intercepts for stand and year, random coefficients for elk density and (where applicable) annual risk that varied by stand.

Additionally, Kohl et al. (2018, 2019) showed that risk can have a nonlinear effect on elk habitat selection, and Painter et al. (2018) suggested a threshold of elk density below which browsing decreases. We thus tested various functional forms of predation risk and elk density (e.g., log transformation, piecewise linear spline), but ultimately determined that the linear effect of both variables was most parsimonious (Appendix S1; Brice et al., 2024).

We assessed model fit by testing the scaled residuals for over/underdispersion, zero-inflation, heteroscedasticity,

and autocorrelation using the DHARMA package in R (Hartig, 2021). We calculated the variance inflation factor (VIF) of each model to check for multicollinearity using the car package in R (Fox & Weisberg, 2019). We estimated R^2 values for fixed and random effects for each model using the partR2 package in R (Stoffel et al., 2021). To interpret and compare effects, we calculated the odds ratios for all covariates by exponentiating the log-odds coefficients. Although our statistical interpretations often refer to the effect of a variable on a response, we emphasize that these relationships are statistical associations rather than known causal relationships.

Recruitment

If a TMIE is dominant in northern YNP, predation risk should have a stronger negative influence on recruitment compared to elk density. Alternatively, if a DMIE is dominant, predation risk should have a weaker negative influence on recruitment compared to elk density. To test whether changes in browsing caused by elk density and risk resulted in these hypothesized changes in recruitment, we built models of aspen recruitment as a function of spring precipitation, SWE, elk density, and risk, again using GLMMs. We classified a stem as ‘recruited’ if it was taller than the maximum preferred browsing height of elk as determined in the browsing analysis (~120 cm, Appendix S1; Brice et al., 2024). We included spring precipitation (i.e., growing season precipitation) in the model to control for the effect of site quality on recruitment, which has a positive influence on growth (Brown et al., 2006; Gustafson et al., 2003; Heineman et al., 2010). Spring precipitation and SWE were not highly correlated ($r = 0.28$), so they could be included in the same model.

We modeled recruitment as a binomial process using logistic regression, where the response was the number of recruited (i.e., successes) versus unrecruited (i.e., failures) stems in each plot ($N_{total} = 1396–1504$). We modeled recruitment at the plot level rather than stem level because all covariates were at this scale (i.e., no stem-level covariates). Again, all covariates were centered and scaled so that effect sizes were comparable. We analyzed separate models for each risk variable, but only included risk variables that had a statistically meaningful influence on browsing. The random effect structure mirrored that of the browsing models, with crossed random intercepts for stand and year, and random coefficients for elk and risk that varied by stand. We again assessed model fit using the DHARMA package and multicollinearity using the car package in R, and calculated R^2 values using the partR2 package.

RESULTS

Temporal trends in aspen

Mean stem height increased from 44.1 cm (95% CI = 39.8, 48.7) in 1999 to 111.8 cm (95% CI = 91.1, 137.1) in 2019, a factor of 2.5 (Figure 5a). However, the SD of stem height increased by a factor of 6.3 ($\sigma_{1999} = 24.1$ cm, $\sigma_{2019} = 151.0$ cm; Figure 5b). Thus, while stem height has increased overall, the response has not been uniform across stems. A probable cause of the overall height increase was the decline in browse probability, which decreased from 0.87 (95% CI = 0.83, 0.91) in 1999 to 0.28 (95% CI = 0.15, 0.46) in 2019 (Figure 5a). This decline began in 2008, with browse probability remaining high ($\mu_{1999–2007} = 0.91$, $\sigma_{1999–2007} = 0.05$) prior to 2008. Similarly, mean height fluctuated around 50 cm ($\sigma = 5.5$ cm) until it started increasing after 2008.

Aspen browsing

In models of browsing, only two measures of predation risk (annual spatial wolf density and annual spatial density of male elk kills) had negative effects consistent with a TMIE, and both had 95% CIs that abutted and/or overlapped zero, indicating a weak effect (Figure 6). The following results refer only to models that included either of these covariates; additional model results are available in Dryad (Brice et al., 2024).

Annual wolf density had a weak negative effect on browse probability ($\beta = -0.10$; 95% CI = -0.21 , 0.007 ; Table 2, Figure 7a), with the odds of browsing decreasing by 9.7% (95% CI = -19.0 , 0.74) for every one SD increase in wolf density (1.8 wolves/km²; 5.3% decrease for every additional wolf/km²). Annual male elk kill density had an even weaker negative effect on browsing ($\beta = -0.086$; 95% CI = -0.17 , 0.003 ; Table 2, Figure 7a), with the odds of browsing decreasing by 8.2% (95% CI = -15.5 , -0.26) for every one SD increase in male elk kill density (5.7E-05 kills/km²). By contrast, elk density had a stronger, positive effect on browse probability (Wolf density model: $\beta = 0.87$; 95% CI = 0.60 , 1.14 ; Male elk kill density model: $\beta = 0.81$; 95% CI = 0.54 , 1.08 ; Table 2, Figure 7b). In the model including annual wolf density, a one SD increase in elk density (3.6 elk/km²) increased the odds of browsing by 139.2% (95% CI = 82.6 , 213.3), or approximately 38.4% for every additional elk/km² on the landscape (Figure 7b).

Browse probability increased with height up to ~120 cm (Wolf density model: $\beta = 0.46$; 95% CI = 0.32 , 0.60 ; Male elk kill density model: $\beta = 0.41$; 95% CI = 0.27 , 0.54), after which point it rapidly declined (Wolf density

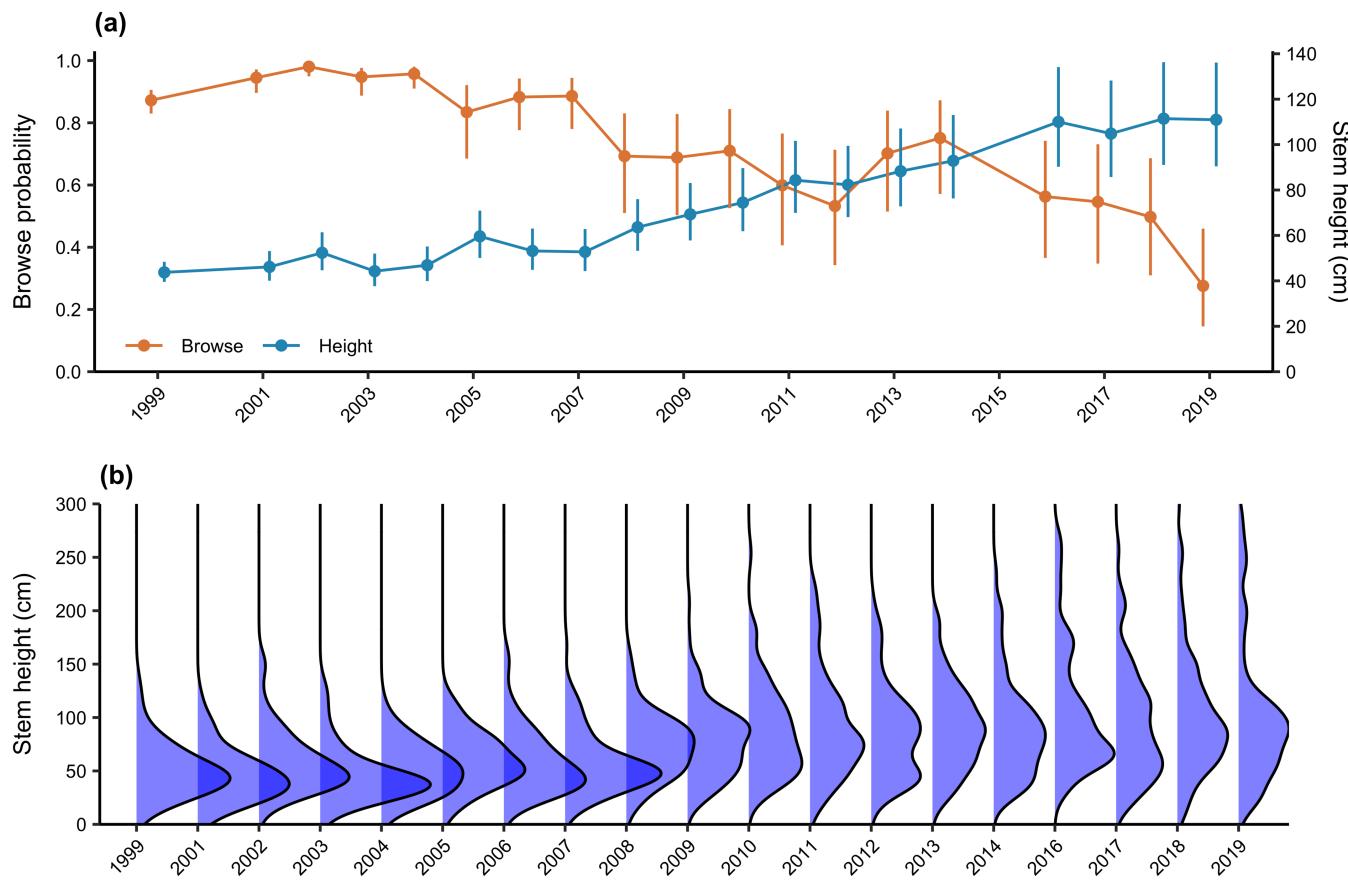


FIGURE 5 Estimated annual trends in browsing and height of young aspen in northern Yellowstone National Park, 1999–2019. (a) Annual mean height of young aspen (blue) and browsing intensity (orange) estimated from generalized linear mixed models with year specified as a fixed categorical variable and stand identity specified as a random intercept. Error bars represent the 95% CI on the annual estimates. (b) Annual frequency distributions of height of young aspen showing increased variance in height over time. No sampling occurred in 2000 and 2015.

model: $\beta = -1.93$; 95% CI = $-2.07, -1.79$; Male elk kill density model: $\beta = -1.87$; 95% CI = $-2.01, -1.73$; Table 2). In the wolf density model, stems shorter than ~120 cm experienced a 6.5% (95% CI = 4.2, 9.2) increase in the odds of browsing with every 10-cm increase in height (Figure 7c). Once stems surpassed the 120-cm threshold, a 10-cm increase in height resulted in a 9.6% (95% CI = 9.3%, 9.8%) decrease in the odds of browsing (Figure 7c).

The effect of SWE on browsing (Wolf density model: $\beta = -0.41$; 95% CI = $-0.54, -0.29$; Male elk kill density model: $\beta = -0.32$; 95% CI = $-0.45, -0.19$; Table 2) was relatively weak compared with the effects of height and elk density. According to the wolf density model, a one SD increase in SWE (5.9 tons/m²) resulted in a 33.9% (95% CI = 25.2, 41.6) decrease in browsing odds, or 5.8% for every additional ton/m² of SWE (Figure 7d).

Wolf predation risk had the weakest effect on browsing compared to the effects of all other covariates, with the relative strength of these effects ranked as: stem height > elk density > SWE > risk. Specifically, short stem height was

4.5× and 4.8× stronger than annual wolf density and annual male elk kill density, respectively. Tall stem height was 19.0× and 21.9× stronger, elk density was 8.6× and 9.5× stronger, and SWE was 4.1× and 3.8× stronger.

The wolf density model explained 51.4% (95% CI = 48.5, 55.0) of the variation in browse probability, with 14.0% of this variation attributed to the random effects of stand identity and year. The male elk kill density model explained 48.9% (95% CI = 47.3, 53.8) of the variation in browse probability, with 13.9% of this variation attributed to the random effects of stand and year. There was more variance between stands (Wolf density model: $\sigma^2 = 0.51$; Male elk kill density model: $\sigma^2 = 0.47$) than across years (Wolf density model: $\sigma^2 = 0.24$; Male elk kill density model: $\sigma^2 = 0.25$).

Aspen recruitment

Annual wolf density ($\beta = 0.11$; 95% CI = $-0.052, 0.28$) and annual male elk kill density ($\beta = 0.16$; 95%

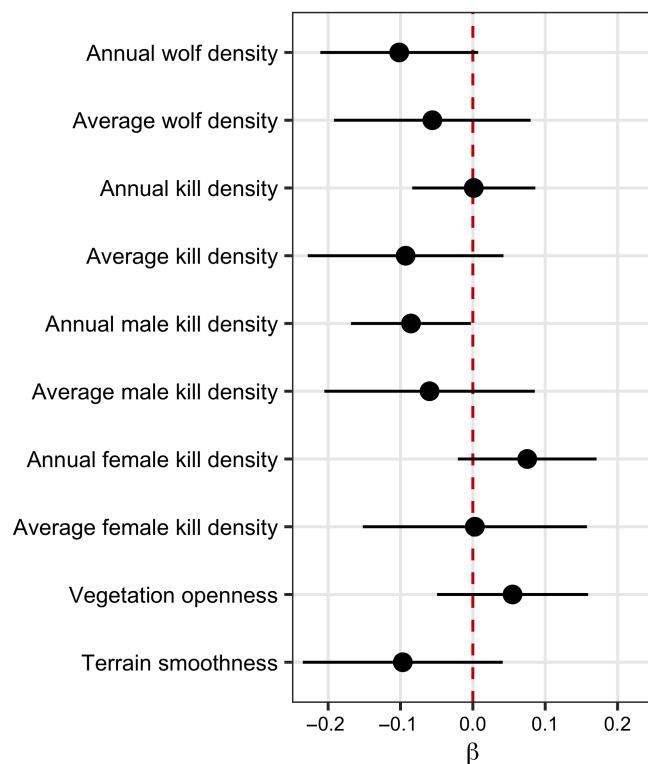


FIGURE 6 Standardized coefficients (log-odds) and associated 95% CIs for risk variables from models of aspen browse probability. Each coefficient is from a different model, each of which includes the same covariates for stem height, snow water equivalent, and elk density together with a different measure of spatiotemporal variation in wolf predation risk. The red dashed line indicates no effect.

CI = 0.040, 0.27) exhibited weak positive effects on aspen recruitment, although the 95% CI for wolf density included zero (Table 3). The odds of recruitment increased by 12.1% (95% CI = -5.1, 32.5) for every one SD increase in wolf density (1.7 wolves/km²), and by 16.9% (95% CI = 4.0, 31.3) for every one SD increase in male elk kill density (5.6E-05 kills/km², Figure 8a). Elk density had the strongest effect on recruitment (Wolf density model: $\beta = -3.17$; 95% CI = -3.89, -2.45; Male elk kill density model: $\beta = -3.18$; 95% CI = -3.93, -2.43; Table 3). In the male elk kill density model, the odds of recruitment decreased by 95.8% (95% CI = 91.2, 98.0) for every one SD (3.6 elk/km²) increase in elk, or about 27.0% for every additional elk/km² (Figure 8b).

Spring precipitation (Wolf density model: $\beta = 0.24$; 95% CI = 0.10, 0.38; Male elk kill density model: $\beta = 0.22$; 95% CI = 0.071, 0.38) and SWE (Wolf density model: $\beta = 0.37$; 95% CI = 0.19, 0.56; Male elk kill density model: $\beta = 0.31$; 95% CI = 0.11, 0.51) both positively affected recruitment (Table 3). In the male elk kill density model, the odds of recruitment increased by 25.1% (95% CI = 7.3, 45.7) for every one SD increase in precipitation (4.0 cm), or approximately 6.3% for every additional cm of precipitation (Figure 8c), and increased by 36.3% (95% CI = 11.4, 66.7) for every one SD increase in SWE (5.7 tons/m²), or approximately 6.4% for every additional ton of SWE/m² (Figure 8d), again as estimated in the model including male elk kill density.

TABLE 2 Coefficient estimates for models of browse probability as a function of stem height, snow water equivalent (SWE), elk density, and two metrics of wolf predation risk (annual spatial densities of wolves and wolf-killed male elk).

Risk metric	Parameter	β	[95% CI]	SE	p
Annual wolf density	Intercept	1.577	[1.305, 1.849]	0.139	<0.001
	Height <120 cm	0.458	[0.318, 0.598]	0.072	<0.001
	Height >120 cm	-1.930	[-2.069, -1.792]	0.071	<0.001
	SWE	-0.414	[-0.538, -0.290]	0.063	<0.001
	Elk density	0.872	[0.602, 1.142]	0.138	<0.001
	Risk	-0.102	[-0.211, 0.007]	0.056	0.068
Annual male elk kill density	Intercept	1.514	[1.240, 1.788]	0.140	<0.001
	Height <123 cm	0.407	[0.272, 0.542]	0.069	<0.001
	Height >123 cm	-1.871	[-2.014, -1.729]	0.073	<0.001
	SWE	-0.322	[-0.451, -0.192]	0.066	<0.001
	Elk density	0.813	[0.543, 1.083]	0.138	<0.001
	Risk	-0.086	[-0.168, -0.003]	0.042	0.043

Note: Coefficient estimates for each parameter are expressed as log-odds. Both models included random slopes for elk density and predation risk that varied by stand identity, and random intercepts for stand and year. Stem height was modeled as a spline, with separate effects for stems less than and greater than 120 cm (wolf density model) or 123 cm (male elk kill density model).

Abbreviations: β , coefficient estimate, p, associated p-value; SWE, winter (November 1–April 30) snow water equivalent in tons per square meter.

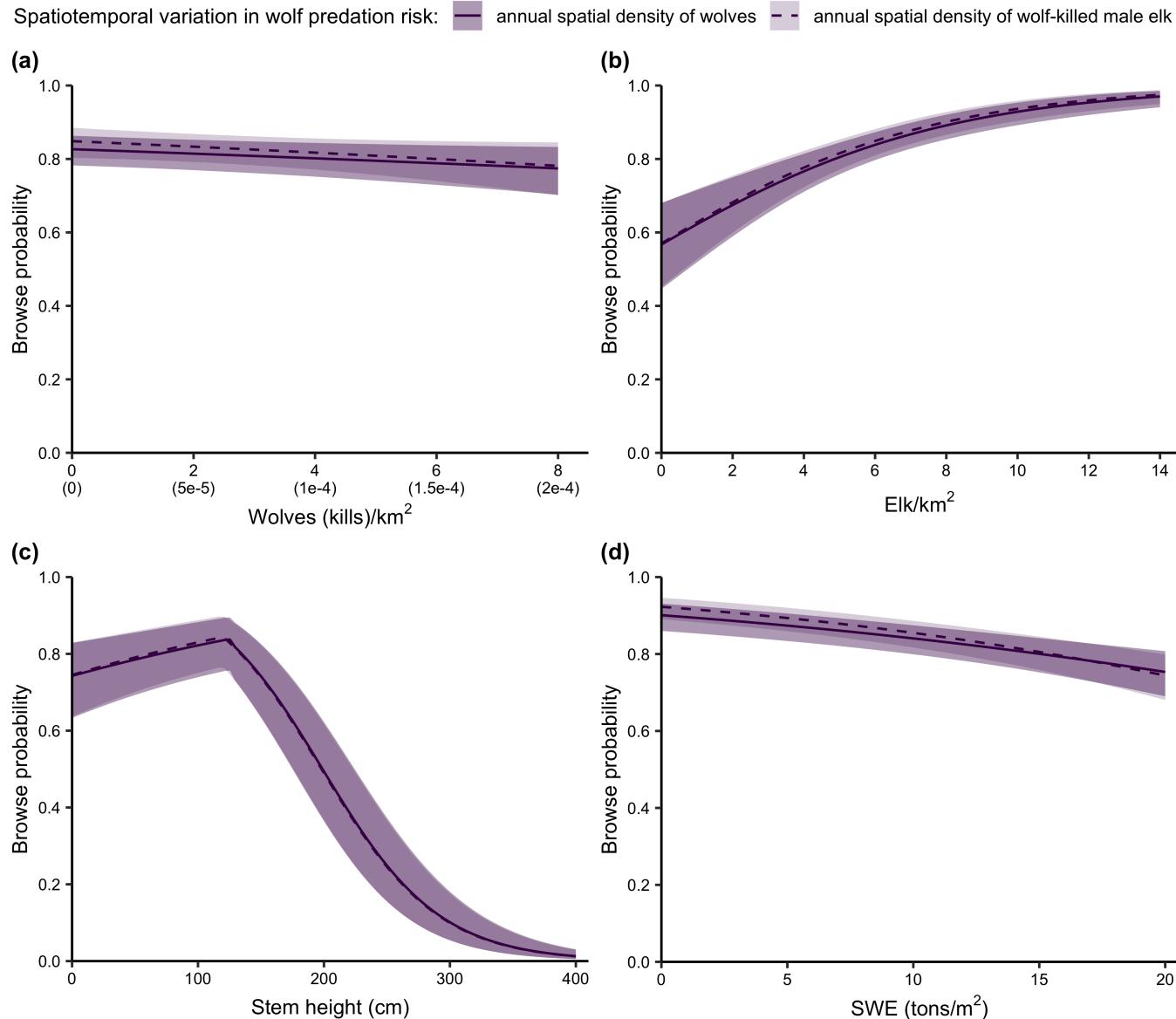


FIGURE 7 Fitted values from models of the probability a young aspen is browsed as a function of spatiotemporal variation in wolf predation risk, annual elk density, stem height, and snow water equivalent (SWE). Solid lines are predictions from the model with annual spatial wolf density as the risk covariate, and dashed lines are predictions from the model with annual male elk kill density as the risk covariate. (a) Effect of risk when other covariates are at mean values. X-axis numbers in parentheses are annual male elk kill densities, X-axis numbers outside parentheses are annual wolf densities. (b) Effect of elk density when other covariates are at mean values. (c) Effect of stem height when other covariates are at mean values. Predictions for heights greater than 120 cm from the model with annual male elk kill density as the risk covariate are obscured by predictions from the model with annual wolf density as the risk covariate. (d) Effect of SWE when other covariates are at mean values. Mean values from annual wolf density model: Stem height = 98.3 cm; SWE = 12.8 tons/m²; annual elk density = 5.4 elk/km², annual spatial wolf density = 2.6 wolves/km². Mean values from annual male elk kill density model: Stem height = 96.5 cm; SWE = 12.8 tons/m²; annual elk density = 5.4 elk/km², annual spatial male elk kill density = 3.3E-05 kills/km².

Wolf predation risk had the weakest effect on recruitment compared to the effects of all other covariates, with the relative strength of these effects as follows: elk density > SWE > spring precipitation > predation risk. The effect of elk density on recruitment was 20–28× stronger than the effect of wolf predation risk (Table 3).

The wolf density model explained 74.6% (95% CI = 66.7, 77.3) of the variation in recruitment probability, with 40.4% of this variation attributed to the random effects of stand identity and year. The male elk kill density model explained 74.5% (95% CI = 66.3, 81.9) of the variation in recruitment probability, with 39.9% of this variation attributed to the random effects of stand

TABLE 3 Coefficient estimates for models of recruitment probability as a function of spring precipitation, snow water equivalent (SWE), elk density, and two metrics of wolf predation risk (annual spatial densities of wolves and wolf-killed male elk).

Risk metric	Parameter	β	[95% CI]	SE	p
Annual wolf density	Intercept	-4.496	[-5.286, -3.706]	0.403	<0.001
	Precipitation	0.244	[0.104, 0.384]	0.072	<0.001
	SWE	0.370	[0.185, 0.555]	0.094	<0.001
	Elk density	-3.171	[-3.892, -2.449]	0.368	<0.001
	Predation risk	0.115	[-0.052, 0.281]	0.085	0.178
Annual male elk kill density	Intercept	-4.862	[-5.705, -4.019]	0.430	<0.001
	Precipitation	0.224	[0.071, 0.377]	0.078	0.004
	SWE	0.309	[0.108, 0.511]	0.103	0.003
	Elk density	-3.179	[-3.932, -2.425]	0.384	<0.001
	Predation risk	0.156	[0.040, 0.272]	0.059	0.009

Note: Coefficient estimates for each parameter are expressed as log-odds. Both models included random slopes for elk density and predation risk that varied by stand identity, and random intercepts for stand and year. Precipitation refers to spring (April 1–July 31) precipitation in cm.

Abbreviations: β , coefficient estimate, p, associated p-value; SWE, winter (November 1–April 30) snow water equivalent in tons per square meter.

identity and year. There was more variance between stands (Wolf density model: $\sigma^2 = 9.10$; Male elk kill density model: $\sigma^2 = 9.39$) than across years (Wolf density model: $\sigma^2 = 0.44$; Male elk kill density model: $\sigma^2 = 0.52$).

DISCUSSION

TMIE and DMIE

A prevailing narrative in ecology is that TMIEs structure communities in a way that rivals or exceeds DMIEs (Peacor et al., 2022; Preisser et al., 2005; Schmitz et al., 2004). However, this narrative is largely based on experimental studies across small spatiotemporal scales that measure risk across a limited range of prey densities, and TMIEs are less commonly tested in large-scale natural systems (Borer et al., 2005; Halaj & Wise, 2001; Pace et al., 1999; Peacor et al., 2022; Schmitz et al., 2000; Shurin et al., 2002; Terborgh & Estes, 2013). Furthermore, direct comparisons of TMIEs and DMIEs on unmanipulated field patterns are rare (Peacor et al., 2022). We addressed this gap by quantifying both TMIEs and DMIEs in an unmanipulated natural community spanning a large spatiotemporal scale.

Despite a wealth of studies arguing for the primacy of TMIEs, both in Yellowstone and elsewhere (Beschta et al., 2018; Preisser et al., 2005; Ripple et al., 2001; Ripple & Beschta, 2004b, 2004a, 2006, 2007; Schmitz et al., 2004), we found little evidence of a TMIE of wolves on aspen. Rather, to the extent that wolves contributed to the decline in elk density (see Vucetich et al., 2005 and discussion below), the indirect effect of wolves on

aspen was density-mediated. This conclusion is supported by the following lines of evidence: (1) only 2 of 10 risk metrics had any meaningful association with browsing; (2) elk density was a stronger driver of browsing than these risk measures by a factor of 8.6–9.5; (3) the weak effects of risk on browsing translated to a meaningful positive effect on recruitment for only one risk metric; and (4) elk density was 20.4× stronger than this risk metric as a driver of recruitment.

The relatively weak TMIE of wolves on aspen that we found is not an unexpected result given the active hunting mode of wolves and the broad habitat domains of both wolves and elk. Prey that have highly active predators, like wolves, are likely to be the least risk averse because the fitness cost of continuous predator avoidance is too great (Schmitz et al., 2004). Furthermore, when both predator and prey have broad, overlapping habitat domains, like wolves and elk in Yellowstone, prey are not expected to exhibit habitat shifts or changes in foraging behavior due to low encounter rates (Schmitz et al., 2004; Wirsing et al., 2021). This hypothesis has been empirically demonstrated by Schmitz et al. (2017), who found that sit-and-wait spiders caused grasshoppers to modify their foraging and habitat use in a way that altered plant biomass, while actively hunting spiders did not. Additionally, this relationship has been demonstrated for the trait response of prey in communities of large carnivores and herbivores by Thaker et al. (2011) and Moll et al. (2016), who both recorded changes in ungulate habitat use and behavior with sit-and-pursue predators (lion and leopard), but not active predators (cheetah, wild dog, hyena).

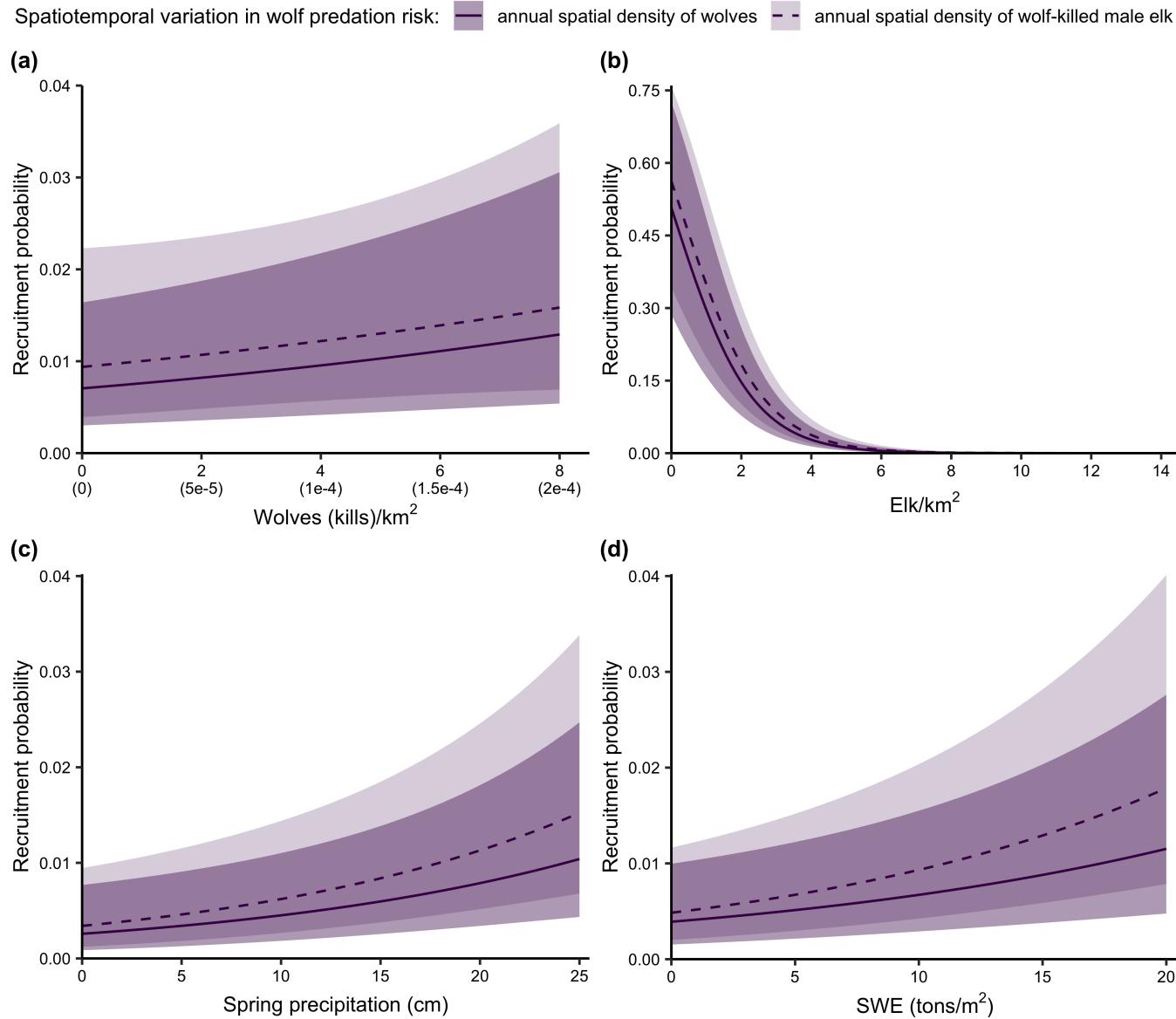


FIGURE 8 Fitted values from the models of the probability a young aspen surpasses ~120 cm of height (i.e., ‘recruits’) as a function of spatiotemporal variation in wolf predation risk, annual elk density, spring precipitation, and snow water equivalent (SWE). Solid lines are predictions from the model with annual spatial wolf density as the risk covariate, and dashed lines are predictions from the model with annual male elk kill density. (a) Effect of risk when other covariates are at mean values. X-axis numbers in parentheses are male elk kill densities, X-axis numbers outside parentheses are annual wolf densities. (b) Effect of elk density when other covariates are at mean values. (c) Effect of spring precipitation when other covariates are at mean values. (d) Effect of snow water equivalent (SWE) when other covariates are at mean values. Note that the Y-axis scale of (b) is different than that of (a), (c), and (d) so the latter effects are visible. Mean values from annual wolf density model: spring precipitation = 19.6 cm; SWE = 12.6 tons/m²; annual elk density = 5.4 elk/km²; annual spatial wolf density = 2.6 wolves/km². Mean values from annual male elk kill density model: spring precipitation = 19.5 cm; SWE = 12.5 tons/m²; annual elk density = 5.5 elk/km²; annual spatial male elk kill density = 3.1e-05 kills/km².

Further support for the weak wolf–elk–aspen TMIE comes from several studies that found little evidence of elk altering their overall foraging or space use in response to wolf predation risk (Cusack et al., 2020; Gude et al., 2006; Kittle et al., 2008; Kohl et al., 2018; White et al., 2010). However, it is worth noting that this does not mean that elk do not respond to acute risk at a

finer temporal scale (Boonstra, 2013). For example, Kohl et al. (2018) found that adult female elk avoided risky places during times of the day when wolves were most active, but used risky places during daily lulls in wolf activity. Similarly, Ganz et al. (2024) found that the diel response of elk to wolves varied seasonally, with elk avoiding wolves most strongly during the day in the

summer, and during the night in the fall. Smith et al. (2019) found a similar response by vicunas to pumas, whereby vicunas reduced their activity at night when pumas were most active and increased activity during the day when pumas were least active. Similarly, Palmer et al. (2021) found that white-tailed deer avoided sites associated with wolf predation risk at dawn and dusk, but used these sites at other times of the day, resulting in no overall difference in visitation rates and foraging activities based on wolf predation risk. The fine temporal scale of deer response to risk ultimately resulted in no overall change to plant biomass. Thus, elk may respond to wolf predation risk at a temporal scale that does not ultimately diminish their use of risky places, thereby resulting in no overall change to browsing and aspen recruitment.

Alternatively, it is possible that predation risk effects only manifest when elk density is low, and elk density may have been too high in earlier studies to detect a risk effect (Creel & Christianson, 2009; Kauffman et al., 2010; Winnie, 2012). To explore this possibility, we tested for an interaction between predation risk and elk density in our browse models, and we found no evidence that the effect of predation risk on browsing was stronger at lower elk densities (Appendix S1; Brice et al., 2024). Our findings contrast with those from experiments demonstrating the primacy of TMIEs, in part because experiments often preclude density effects from operating, such as by employing a “nonlethal” predator (e.g., spider with its jaws glued shut) or by testing for a TMIE across a limited range of herbivore densities (Schmitz, 2005; Werner & Peacor, 2003). As such, our study highlights how an important advantage of observational studies of natural unmanipulated communities is that prey densities are permitted to fluctuate in a way that provides a realistic appraisal of the relative magnitudes of TMIEs and DMIEs in nature. Our results confirm that in systems with a broadly distributed active predator and an equally broadly distributed prey, trait-mediated effects attenuate at the timescale of community dynamics (Schmitz et al., 2004).

Observed risk effects

We detected a weak negative effect of two risk measures (annual spatial densities of wolves and wolf-killed adult male elk) on browsing, suggesting that predation risk cannot be completely ruled out as a mechanism of change. Both of these risk measures were annual, suggesting that elk may respond to a more immediate threat of predation, rather than persistent risk (Kauffman et al., 2010; Schuette et al., 2016). For instance, ungulates have been shown to make short-term shifts away from

immediate wolf presence (Creel et al., 2005; Gude et al., 2006), which could explain the slight decline in browsing with wolf density that we detected (Figure 7a). However, other studies of adult female elk have variously found: no effect of wolf density on elk habitat selection (Cusack et al., 2020; Kohl et al., 2018), that elk do not avoid core wolf use areas (Fortin et al., 2005), and that elk may actually be more abundant in areas of high wolf density (Mao et al., 2005). Importantly, Kauffman et al. (2007) determined that wolf density decoupled from risk in northern YNP after a decade of wolf presence. Furthermore, we found that the effect of wolf density on browsing did not lead to a meaningful change in aspen recruitment. This result suggests that either wolf density alone was insufficient to affect aspen population dynamics, or it was not a functionally important index of wolf predation risk.

The effect of adult male elk kill density on browsing was slightly weaker than wolf density, but it was correlated with increased aspen recruitment. Most previous studies of elk response to wolf predation risk have overlooked adult male elk (but see Unsworth et al., 1993), and focused on adult females (Cusack et al., 2020; Fortin et al., 2005; Kohl et al., 2018, 2019; Mao et al., 2005) or all age and sex classes (Kauffman et al., 2007, 2010). Winnie and Creel (2007) measured sex-specific responses of elk to wolf predation risk, and found that males were less responsive than females to wolf presence despite being more than six times as likely to be killed (Creel et al., 2005). By contrast, Eisenberg et al. (2014) found that males were more vigilant than females in parts of their study area. Both studies, however, centered on elk vigilance, and provided little information on space use. Our results suggest that adult male elk may avoid browsing in risky aspen stands more so than adult female elk. Further exploration of adult male elk space use is needed to support this conclusion.

Drivers of elk density

Although we found elk density to be a strong driver of aspen browsing and recruitment, it is critical to recognize that the decline in elk abundance following wolf reintroduction cannot be attributed to wolves alone. Besides wolves, other important predators that have contributed to the elk population decline include grizzly and black bears, cougars, and human hunters (Figure 9; MacNulty et al., 2020a). The grizzly bear population increased in the Greater Yellowstone Ecosystem between 1982 and 2020 (Corradini et al., 2023; Gould et al., 2024; Kamath et al., 2015), and a recent study found northern YNP to have the highest densities of black bears (20 black

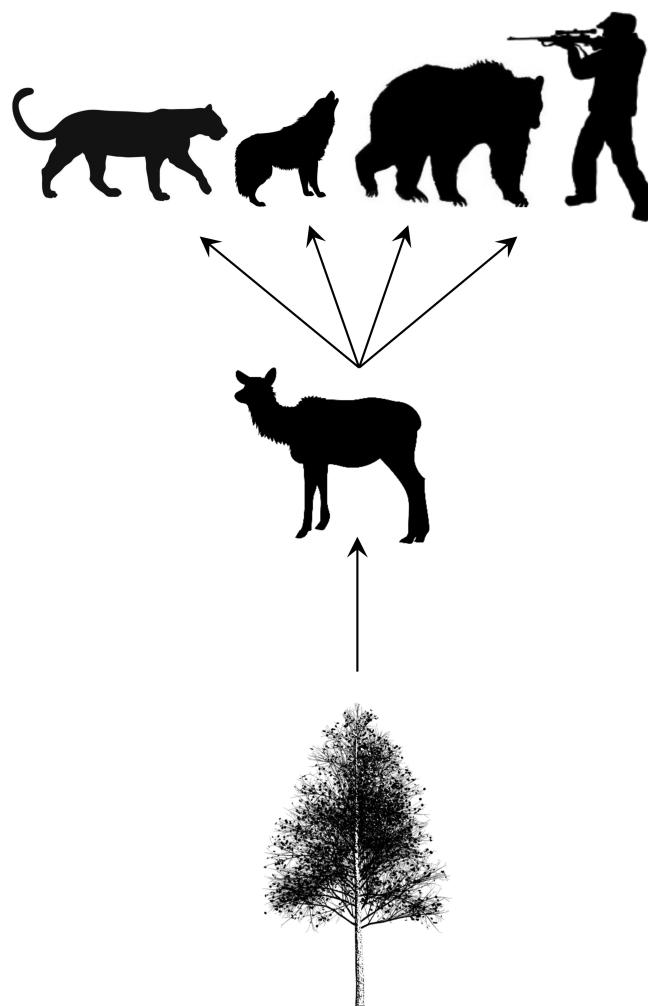


FIGURE 9 Multiple predators of elk likely contribute to a trophic cascade in northern Yellowstone National Park through a density-mediated indirect effect on aspen browsing and recruitment. Besides wolves, the decline in the elk population has been influenced by cougars, grizzly and black bears, and human hunters. All of these predators may indirectly increase aspen regeneration and height growth by reducing elk consumption of aspen via predation-caused reductions in elk density (density-mediated indirect effect; solid arrows). This figure is adapted from Stahler et al. (2020; fig. 16.1).

bears/100 km²) in the northern Rocky Mountains (6–12 black bears/100 km² in other regions; Bowersock et al., 2024). This increase in bears was mirrored by an increase in elk calf mortality, with the proportion of radio-collared calves killed by grizzly and black bears increasing from 23% in 1987–1990 (Singer et al., 1997) to as much as 60% by 2003–2005 (Barber-Meyer et al., 2008). The cougar population has also increased since wolf reintroduction (Ruth et al., 2019), and elk constituted 74.2% of cougar diet in northern YNP from 1998 to 2004 and over 50% in more recent years (i.e., 2016–2019; Stahler et al., 2020), with cougars selecting for calves over

adults (Ruth et al., 2019). Additionally, between 1998 and 2004, cougars killed a larger proportion of the elk population (3.7%–6.7%) than wolves did (2.1%–7.6%) in four of the seven years (Ruth et al., 2019; Metz et al., 2020b)

Hunters contributed to the elk population decline primarily through a limited-permit late-season (December–February) hunt that targeted adult female elk wintering outside YNP's northern boundary (Figure 2; MacNulty et al., 2020a). The state of Montana managed the hunt with the goal of limiting the number of elk wintering outside the park to mitigate overgrazing and agricultural damage on nonpark lands. During each of the eight years following the 1995 wolf reintroduction (1995–2002), late-season hunters, together with general season (October–November) hunters, killed a larger portion of the northern Yellowstone elk population (5.7%–18.7%) than wolves did (1.7%–6.2%) (MacNulty et al., 2020a). Moreover, late-season hunters mainly killed young (2–11 years-old), reproductively valuable females, whereas wolves mainly killed old (12–23 years-old), reproductively senescent females (MacNulty et al., 2020a; Wright et al., 2006). The state of Montana reduced late-hunt permits to <200 in 2005 and suspended the late hunt following the winter of 2009–2010. Several studies suggest that hunter-caused mortality was the dominant driver of elk population decline during the initial years after wolf reintroduction (1995–2004), and that wolf predation was primarily compensatory (Eberhardt et al., 2007; Vucetich et al., 2005; Wright et al., 2006). More recent studies further indicate that wolves were not the sole driver of elk decline after 2004 (Brice, 2022; MacNulty et al., 2020a; Smith, 2021); as such, it is evident that wolves alone did not drive the increase in aspen recruitment that we observed. However, the relative contributions of various elk predators to the density-mediated increase in aspen recruitment (Figure 8b) are still unresolved.

Previous research on the YNP trophic cascade

Our finding that a DMIE is the dominant mechanism of a wolf–elk–aspen trophic cascade in northern YNP supports the hypothesis that elk density was a primary cause of aspen decline in YNP during the 20th century (Kay, 1990; Klein et al., 2002; Wagner, 2006). Although Kauffman et al. (2010) tied elk browse rates to aspen decline, our study is the first to quantitatively demonstrate that browsing and recruitment are tightly correlated with elk density, dispelling the alternative hypothesis that elk density played relatively little, if any, role in aspen decline compared with fire suppression,

climate warming, and conifer succession (Barmore, 2003; Bishop et al., 1997; Despain et al., 1986; Houston, 1982; Romme et al., 1995).

Our results are also consistent with several studies that found little evidence for a wolf-induced TMIE on woody deciduous plants in northern YNP. Kauffman et al. (2010) found that the effects of elk browsing on aspen survival were not diminished by predation risk, while Winnie (2012) also found more browsed stems and lower aspen abundance at risky sites, and Creel and Christianson (2009) documented an increase in willow consumption in the presence of wolves, patterns that are inconsistent with the TMIE hypothesis. Furthermore, although Ripple et al. (2001), the initial study on the Yellowstone TMIE, concluded that predation risk increased aspen regeneration, this claim was based on a significant difference in aspen height between high and low wolf use areas in one habitat type (riparian). They found no difference in heights between high and low wolf use areas in the two other habitat types they examined (xeric upland steppe, mesic upland steppe), nor any difference in browsing between high- and low-risk areas regardless of habitat type. As such, their results align more closely with the weak TMIE observed in our study than with the claim that a TMIE is a key driver of aspen dynamics in YNP.

Our results diverge from several previous studies that found a risk effect in northern YNP (Beschta et al., 2018; Ripple & Beschta, 2003, 2004a, 2006, 2007) for various reasons, chief among them being the way risk was characterized. We built spatially continuous maps of risk, whereas previous studies used categorical habitat characteristics, such as the presence of downed logs, topographic position, and escape or view impediments to define risk (Beschta et al., 2018; Ripple & Beschta, 2003, 2007, 2006; Winnie, 2012). The classification of risk based on such subjective habitat characteristics has limited support in the literature (Kauffman et al., 2010; Moll et al., 2017), largely because it has no demonstrated empirical relationship with data derived from predator-based measurements of predation risk, and can easily lead to spurious correlations.

For example, Ripple and Beschta (2007) initially found less browsing and taller aspen at sites with downed logs, but concluded in a later study that downed logs had no effect (Beschta et al., 2018). Furthermore, Mao et al. (2005) found that, during the summer season, elk shifted to areas with downed trees following wolf reintroduction, possibly to avoid wolves. Thus, using such subjective habitat characteristics to assess risk-driven change to aspen has led to conflicting results. Similarly, Ripple and Beschta (2006) considered upland sites (20 m in elevation above a stream) to be low risk compared with valley-bottom sites,

assuming that the higher elevation of upland sites improved elk detection of wolves by increasing visibility. However, they also noted that many upland sites were confined by adjacent hillslopes that decreased visibility compared with valley bottoms, suggesting that uplands sites were of higher risk. This ambiguity makes it difficult to draw conclusions regarding whether the changes they observed in willow heights at upland versus valley-bottom sites were linked to predation risk, or simply an artifact of some other unmeasured factor.

Our results also likely differ from previous studies that found a TMIE in YNP because of the reliance on nonrandomly sampled data (Brice et al., 2022). Many of these studies base their conclusions on trends in browsing and height of just the three or five tallest young aspen in a stand (see table 1 in Brice et al., 2022). Doing so overestimates aspen recruitment by a factor of 4–7 compared with random sampling, thereby exaggerating the strength of the trophic cascade (Brice et al., 2022).

Some studies have proposed that the reduction in elk density in northern YNP may reflect a risk-induced trait response (Beschta et al., 2018; Painter et al., 2018; Ripple & Beschta, 2012), with fear of wolves pushing elk outside of the Park. While elk emigration is a plausible risk-induced trait response, there is limited evidence that individual elk have modified their migration routes or moved their home ranges from inside to outside the Park because of wolf predation risk (Cusack et al., 2020; Kohl et al., 2018; White et al., 2010). We thus maintain that the annual counts of elk we used represent a density, and not a behavioral, effect.

Slow response of aspen recruitment

Regardless of the indirect effect of wolves on browsing, it is the effect of wolves on recruitment from which we should draw our main conclusions, as plant damage is a short-term measure of impact that may not translate to a change in plant biomass (Halaj & Wise, 2001; Maron & Crone, 2006; Schmitz et al., 2000). We found little evidence that elk response to wolf predation risk has translated to measurable changes in aspen recruitment, with annual adult male elk kill density, the only risk metric to have a nonzero effect on recruitment, predicting a maximum recruitment probability of 1.3% (Figure 8a). This result is in direct contrast to the meta-analysis conducted by Preisser et al. (2005), in which they concluded that density-mediated effects attenuate through the food web while trait-mediated effects remain strong. One explanation for this difference is that our study occurred in an unmanipulated, large-scale system, while the Preisser et al. (2005) meta-analysis only included experimental

studies. While experiments are a powerful way to examine mechanisms, they do not capture the complexity inherent in natural systems: natural patterns are affected by processes over multiple spatial scales, some of which may be larger than can be manipulated in an experiment, and even the most complex experiments can only capture a limited number of interacting variables. It has been further suggested that feedbacks and compensatory mechanisms in natural systems may reduce the contribution of TMIEs found in experiments, resulting in a potential overestimation of the relative magnitude of TMIEs (Peacor et al., 2022; Prugh et al., 2019).

Elk density had a stronger effect on recruitment than did predation risk, but predicted recruitment was still low, reaching a maximum probability of 18.5% at the lowest observed elk density (2017 elk density = 2.0 elk/km², abundance = 1986; Figures 3 and 8b), potentially below the rate necessary to replace the overstory (Mueggler, 1989; Rogers & Mittanck, 2014). This attenuation through the food web has been documented in other systems, such as in Laikipia Plateau in central Kenya, where Ford et al. (2015) found that recolonized wild dogs decreased their prey population by 33%, but this decrease had no effect on plant biomass due to a time lag in indirect effects, variation in rainfall, and foraging by other herbivores (but see Ford et al., 2014). Furthermore, in their review of trophic cascades, Borer et al. (2005) noted that the effects of predation on plant biomass tend to be weak, as plants can often tolerate high levels of herbivory without significant effects on primary production. As a result, carnivore effects are often stronger when measured as plant damage as opposed to biomass or reproduction (Halaj & Wise, 2001; Schmitz et al., 2000), a pattern mirrored by our results (Figures 7 and 8).

While mean aspen height has only increased by a factor of 2.5 since wolf reintroduction, the variation in height has increased by a factor of 6.3. This result indicates that aspen regeneration is patchy across the landscape, with some stands still stuck resolutely in the browse zone while others have largely escaped it. This patchiness is likely due to variation in site productivity (MacNulty et al., 2024), with sites of higher productivity requiring a smaller reduction in range-wide elk browsing to exhibit growth than sites with lower productivity (Kauffman et al., 2010).

Another potential reason for the low recruitment we observed is that browsing only recently declined to levels low enough to permit more widespread height growth. Several studies suggest that little recruitment occurs in stands where more than 20% of stems are browsed (Jones et al., 2005; Rogers & McAvoy, 2018), although this estimate is for spring/autumn browsing, which is potentially more detrimental to growth than is winter browsing (Canham et al., 1994). In our plots, browse probability

remained high despite declining elk abundance, only dropping below 50% around 2018 and reaching a low of 28% in 2019 (Figure 5a). Thus, our results suggest there were only a few years when browsing was potentially low enough to release aspen from its control.

While recruitment may still be low and patchy, our long-term dataset certainly shows a decrease in browsing and increase in mean heights since wolves were reintroduced (Figure 5a). Furthermore, the proportion of stands with an upper quantile of height greater than 120 cm surpassed 50% in 2016; as such, there is an increasing number of stands with a majority of stems surpassing the preferred browse height, allowing them to escape herbivory (Appendix S1: Figure S2). In contrast, several previous studies concluded that there were no landscape-level changes to aspen (Kauffman et al., 2010; Kimble et al., 2011) or willow (Bilyeu et al., 2008) browsing and recruitment in northern YNP. However, these studies all occurred before 2007, while our data indicate that these changes did not begin to occur until 2008 (Figure 5a; Appendix S1: Figure S2), 14 years after wolf reintroduction. This slow rate of change is reflected in a recent study on willow, where Hobbs et al. (2024) found that willow heights averaged 178 cm in 2020, a height well within browse range and below the threshold for restoration. They concluded that, if the observed growth rates persist, it would take an additional 40 years for willow heights to reach the level of those protected from elk browsing. The slow and patchy aspen regeneration we observed highlights the challenge of restoring an ecosystem to its previous state after a disturbance like predator extirpation (Stier et al., 2016).

Other drivers of aspen browsing and recruitment

The nonlinear relationship we observed between stem height and browse probability has been documented in numerous other studies (e.g., Kuijper et al., 2013 [fig. 3]; Maxwell et al., 2019 [fig. 4]; Motta, 2003 [fig. 1]; Rounds, 1979 [table 4]). This relationship demonstrates that browsing limits height until a critical threshold, beyond which height increasingly limits browsing (Brice et al., 2022). As such, height is both a cause and effect of browsing. Relying on a negative correlation between browsing and stem height as critical evidence of a trophic cascade, as previous Yellowstone studies have done (Beschta et al., 2018; Beschta & Ripple, 2016; Beyer et al., 2007), overlooks the importance of this nonlinear relationship.

We also found SWE to be an important driver of both browsing and aspen recruitment, but interpretation of this

effect is complex. First, a positive relationship between SWE and recruitment could be due to deep snowpack, as indexed by SWE, acting as a physical barrier to elk, impeding their movements and protecting aspen where snow is deepest (Brodie et al., 2012; Telfer & Kelsall, 1984). However, wolves are also more successful hunters in deep snow, and predation risk may thus increase with SWE (Huggard, 1993; Kauffman et al., 2007; Mao et al., 2005; Mech et al., 2001). Although SWE was not strongly correlated with any of our measures of predation risk ($|r| = 0.03\text{--}0.41$), it may still represent a form of risk perceived by elk that is independent of our other measures. If so, its apparent effects on browsing (Figure 7d) and recruitment (Figure 8d) could suggest a behavioral effect of risk on aspen. However, this risk effect would still be $\sim 2\text{--}10$ times weaker than the effect of elk density. The positive effect of SWE on aspen recruitment may also reflect enhanced water availability, whereby snowdrifts melt and provide a soil moisture subsidy during the growing season (bottom-up effect; Kretchun et al., 2020; LaMalfa & Ryle, 2008). Brodie et al. (2012) provide evidence for this mechanism, as they documented increased aspen recruitment with increasing SWE inside elk exclosures in northern YNP.

Although we did not test a panoply of weather variables, it is well known that precipitation and temperature affect aspen growth (Brown et al., 2006; DeByle & Winokur, 1985; Gustafson et al., 2003). As such, when predicting the future of aspen in YNP, the recent reduction in browsing pressure must be weighed against the myriad effects of climate change on aspen. In particular, Piekielek et al. (2015) projected that currently suitable aspen habitat in northern YNP will become unsuitable as soon as 2025 due to warming. Additionally, although increasing fire could provide new habitat for aspen (an early successional species; Mueggler, 1985), projections in northeast Nevada suggest that increased fire activity under future climate warming scenarios will result in reduced aspen coverage at elevations similar to our study area (i.e., 1500–2800 m; Yang et al., 2015). Thus, the increased recruitment expected from reduced browsing pressure may be offset by a warmer and drier future.

Limitations

There are several limitations of our study that should be considered. First, we assumed that elk perfectly perceive wolf predation risk, but this is unlikely to be the case (Cresswell, 2008). Although some researchers have found kill density to influence elk habitat selection (e.g., Gude et al., 2006; Kohl et al., 2018), others have not (Cusack et al., 2020). As such, elk either do not respond to this

measure of risk or are not perceiving it accurately. Furthermore, elk may not uniformly perceive risk; rather, age, sex, and body condition could lead to variation in perceived risk that is correlated with elk vulnerability and subsequent habitat selection (Metz et al., 2020a; Smith, 2024). Second, based on kill-recovery models estimated by Smith et al. (2004), we likely missed $\sim 27\%$ of kills, which may have underestimated risk in some places. Additionally, the sample size of annual kills was also relatively small, particularly for adult male elk, which increases the uncertainty in the kill KDEs. Thus, while we attempted to measure predation risk at both short and long timescales, and in a variety of different ways (e.g., predator density, kill occurrence, habitat characteristics), we may have still failed to fully represent what elk perceive as risky places.

Another limitation is the potential for confounding effects from variables not included in the analysis, such as the effects of fire, beaver, and bison on aspen recruitment. Fire is well known to drive many aspects of aspen biology, including seedling germination and suckering (DeByle & Winokur, 1985; Romme et al., 1995; Turner et al., 2003). However, Romme et al. (1995) found no difference in aspen height between burned and unburned stands 2–3 years postfire, and their subsequent study showed that most aspen seedlings grew slowly 12 years postfire, even when protected from herbivory (Romme et al., 2005). Of our 113 aspen stands, 47 were within the boundaries of the 1988 fires (Appendix S1: Figure S3); however, because we selected our stands from aerial photographs taken after the fire, all stands had surviving overstory. Furthermore, as the fires were patchy, stands within the fire boundary did not necessarily burn completely or even at all. Thus, the sampled stands that did burn likely experienced moderate to low fire severity.

Beaver were abundant in YNP in the early 1900s, but declined through the 1950s to 1990s, before increasing in the late 1990s to 2009 (due at least in part to the reintroduction of 138 beavers to streams outside YNP that drain into the study area) (Smith & Tyers, 2012). Beaver cut aspen saplings and mature trees for food and building materials, which can stimulate new growth (McColley et al., 2012; Runyon et al., 2014), and can help maintain aspen through a positive feedback cycle involving beaver pond hydrology (Smith & Tyers, 2012). Similarly, although aspen is not a common component of bison diet, bison can have nonconsumptive physical effects on aspen by rubbing against and snapping saplings and trampling young aspen. Recently, Painter et al. (2023) estimated that 18% of the saplings in their sample had been broken, with evidence to suggest that bison activity was the cause.

While we did not explicitly test the effects of fire, beaver, or bison on aspen browsing or recruitment, we

did include random intercepts for aspen stand identity and year, which account for unmeasured variation across stands and years. Together, they accounted for ~40% of the variation in aspen recruitment that we observed. As such, the unmeasured effects of potentially important drivers excluded from our analysis are at least partially accounted for by the random intercepts for stand identity and year, reducing the likelihood of confounding the effects of the variables included in the model.

Finally, observational studies such as ours cannot fully disentangle DMIEs from TMIEs, which requires some measure of experimental control. However, observational studies of unmanipulated communities are critical for determining whether the TMIEs evident in experiments apply generally to natural field patterns (Peacor et al., 2022; Vellend, 2010, 2016). As such, the lack of experimentation in our study was necessary to pursue the larger goal of understanding the relative importance of TMIEs and DMIEs in free-living systems.

Conclusions

While the prevailing narrative in ecology is that TMIEs rival or exceed DMIEs in strength, examples of TMIEs in unmanipulated, free-living systems are uncommon, regardless of taxa, and studies that quantify the relative importance of TMIEs and DMIEs in such systems are even rarer. Our study helps fill this gap by quantitatively testing the relative effects of DMIEs and TMIEs in an unmanipulated natural community across broad spatio-temporal scales using the YNP wolf–elk–aspen food chain as a case study. We determined that spatial variation in predation risk was a relatively weak driver of aspen browsing and recruitment, and, to the extent that wolves contributed to interannual variation in elk population density, the indirect effect of wolves on aspen was primarily density-mediated. More generally, our findings align with the general expectation that actively hunting predators with broad habitat domains cause DMIEs to dominate whenever prey have a broad habitat domain. For this type of predator–prey community, our study suggests that risk-induced trait responses can be abstracted or ignored while still achieving an accurate understanding of trophic cascades. Finally, the lack of widespread aspen overstory recruitment we observed nearly 30 years after wolf reintroduction in northern YNP highlights the potential limitations of large predator restoration as a tool for promoting rapid vegetation recovery via indirect effects.

AUTHOR CONTRIBUTIONS

Elaine M. Brice, Eric J. Larsen, and Daniel R. MacNulty conceived and designed the study. Eric J. Larsen collected most of the aspen data and Daniel R. Stahler contributed all the long-term wolf and kill density data. Elaine M. Brice and Daniel R. MacNulty analyzed the data and wrote the manuscript, with input from Eric J. Larsen and Daniel R. Stahler.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Brice et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.2bvq83c0d>.

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