ARTICLE

Does restoring apex predators to food webs restore ecosystems? Large carnivores in Yellowstone as a model system

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Abstract

Modification of food webs is a frequent cause of shifts in ecosystem states that resist reversal when the food web is restored to its original condition. We used the restoration of the large carnivore guild including gray wolves (*Canis lupis*), cougars (*Felis concolor*), and grizzly bears (*Ursus arctos horribilis*) to the northern range of Yellowstone National Park as a model system to understand how ecosystems might resist reconfiguration after the restoration of apex predators to the food web. The absence of wolves, cougars, and grizzly bears for nearly a century from the northern range was the primary cause of dramatic changes in riparian plant communities. Willows (*Salix* spp.) were suppressed in height by intense browsing by the dominant herbivore, elk (*Cervus canadensis*). The loss of activity by beavers (*Castor canadensis*) coincided with the loss of tall willows. We hypothesized that intense elk browsing interrupted the mutualism between willow and beavers: ecosystem engineering by beavers was a critical component of willow habitat and tall willows were a critical component of habitat for beavers. This interruption made riparian communities resilient to the disturbance caused by the restoration of apex predators. We hypothesized further that reductions in elk browsing attributable to reductions in elk population size were not sufficient to prevent the suppression of willow growth. To test these hypotheses, we conducted a 20-year, factorial experiment that crossed simulated beaver dams with the exclusion of browsing. We found that willows grew to heights expected for restored communities only in the presence of dams and reduced browsing. Willows experiencing ambient conditions remained well below this expectation. We found no difference in heights or growth rates of willows in experimental controls and willows in 21 randomly chosen sites, confirming that the results of the experiment were representative of range-wide conditions. A reorganized community of large herbivores was implicated in the suppression of willow growth. We conclude that the restoration of large carnivores to the food web failed to restore riparian plant

communities on Yellowstone's northern range, supporting the hypothesis that this ecosystem is in an alternative stable state caused primarily by the extirpation of apex predators during the early 20th century.
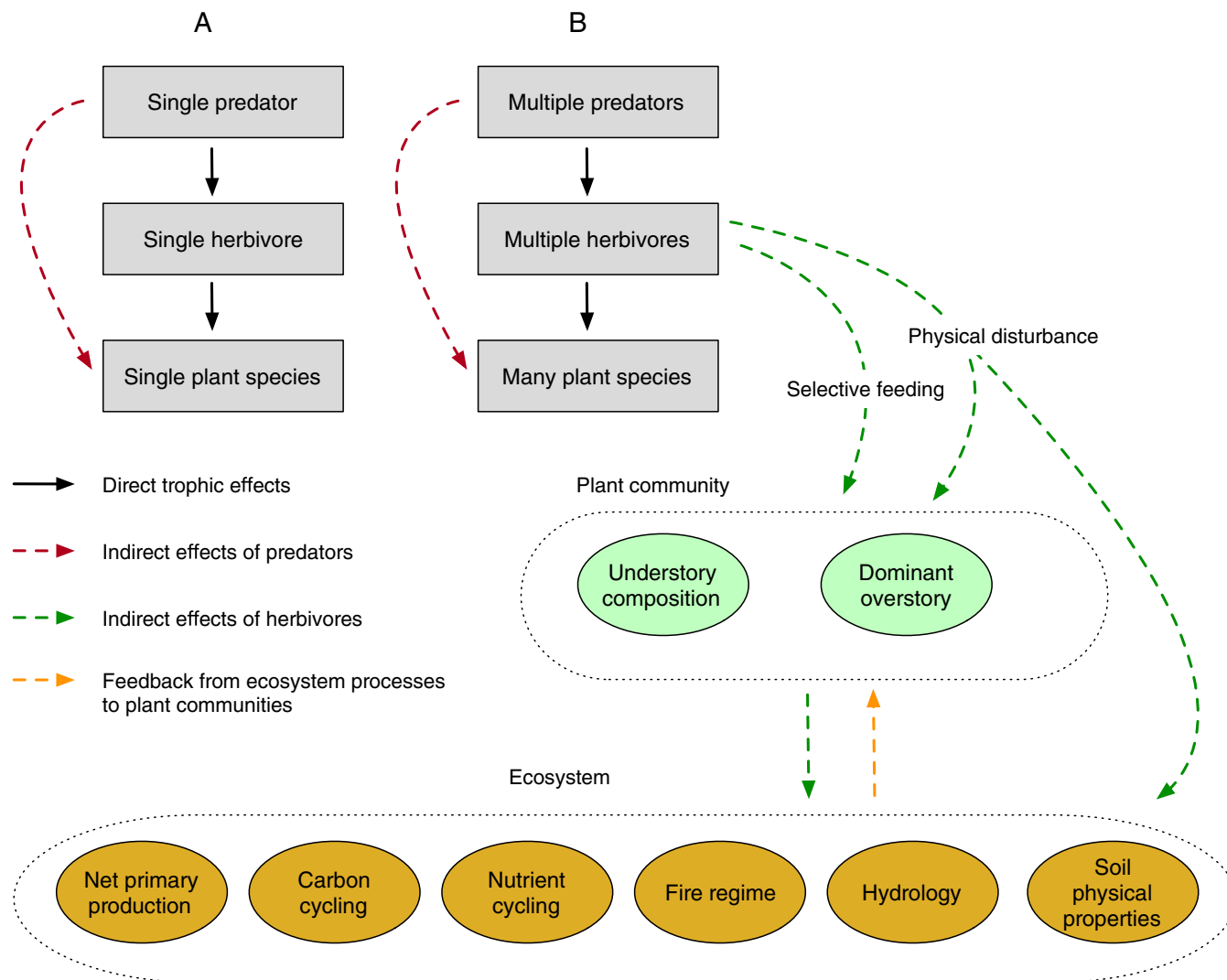
CONCEPTUAL FRAMEWORK

The reintroduction of wolves and the concomitant natural recovery of cougars and grizzly bears to the landscapes of Yellowstone National Park after nearly a century of their absence from the food web created an unusual opportunity to test ecological theory relevant to restoring ecosystems worldwide. Two aspects of the theory are especially subject to evaluation using this model system: ideas predicting the resilience of alternative states to perturbation and ideas about trophic cascades.

Lewontin (1969), and later Holling (1973), theorized that communities and ecosystems can exist in alternative states of biotic and physical organization, states that can shift, one to another, in response to disturbance. State change often results from human-caused environmental stress, creating enduring reorganization of ecosystem structure and function (reviewed by Petraitis, 2013; Scheffer et al., 2001; Scheffer & Carpenter, 2003; Scheffer, 2009). Suding et al. (2004) placed these ideas in the context of restoration management, defining an alternative stable state as one that persists even when the environmental stressors causing the transition to a degraded state are ameliorated by human efforts to restore the system. Empirical evidence from all over the world supports the prediction of the theory that the degradation of ecosystems may not be reversed when initiating stressors are mitigated (reviewed by Folke et al., 2004; Petraitis, 2013; Sinclair & Byrom, 2006; Scheffer, 2009; Scheffer et al., 2001). Resistance to reversal often results when alternative states are induced by changes in the food web, by alteration of the disturbance regime, or by persistent changes in the physical environment (Folke et al., 2004; Petraitis, 2013). Properly designed, long-term experiments are particularly valuable in revealing the stability of alternative states and the forces that stabilize them (Scheffer & Carpenter, 2003; Petraitis, 2013).

The theory of alternative stable states is related to the theory of trophic cascades because modification of trophic relationships is a frequent cause of shifts in ecosystem states that resist reversal when those relationships are restored to their original condition (reviewed by Carpenter, 2001; Folke et al., 2004; Petraitis, 2013; Scheffer & Carpenter, 2003; Scheffer, 2009). Paine (1980)

introduced the term "trophic cascade" to describe changes in food chains caused by experimental manipulations of apex predators, giving rise to the now widely used name for the theory describing top-down effects of predators on herbivores and plants first articulated by Hairston et al. (1960). Trophic cascades occur when apex predators indirectly benefit plants by top-down control of herbivore abundance and/or foraging behavior, thereby causing increases in plant biomass or other relevant indicators of plant performance (Polis et al., 2000; Schmitz et al., 2000). The scale and level of ecological organization at which these benefits must occur to qualify as a trophic cascade remain debatable (Polis & Strong, 1996; Polis et al., 2000; Ripple et al., 2016; Schmitz et al., 2000; Strong, 1992). Nonetheless, the indirect effects of the removal of predators from food webs have now been established by volumes of empirical evidence from freshwater, marine, and terrestrial systems worldwide (reviewed by Persson, 1999; Schmitz et al., 2000; Strong, 1992; but also see Ford et al., 2015; Maron & Pearson, 2011; Meserve et al., 2016 for exceptions).

In contrast, the indirect effects of restoration of predators to food webs after their absence are poorly understood (Allen et al., 2017), and there is no a priori reason to assume that the effects of predator removal should be reversed by their restoration, that is, that the effects of removal and restoration are reciprocal. However, theory does inform what we might reasonably expect. The theory of Hairston et al. (1960) and its manifestation in many empirical examples of trophic cascades operate through the effects of predators on herbivore biomass in linear food chains (Strong, 1992; Persson, 1999). According to classical theory for a three-trophic-level food chain, predators exert indirect effects on plants by changing herbivore abundance or biomass that, in turn, exerts direct effects on plant abundance or biomass (Figure 1A). Schmitz (2008, 2010) put Hairston et al. (1960) in the context of food webs by developing the idea that the indirect effects of predators on plants in complex food webs are accompanied by indirect effects of herbivores on plant communities resulting from selective feeding (Figure 1B). Changes in plant communities, in turn, modify ecosystem properties and processes including net primary production, carbon and nutrient cycling, fire

FIGURE 1 (A). Restoration of a predator to a simple linear food chain is likely to rapidly reverse the effect of its removal because the indirect effects of predators on plants are mediated entirely through biomass and energy flow. (B). Restoration of an apex predator to a complex food web might not reverse the effects of its absence because the indirect effects of unregulated herbivores on plant communities mediated by selective feeding and physical disturbance can alter one or more slowly changing environmental conditions, thereby stabilizing alternative states that emerge after predators are lost from the food web. These changed conditions can make the system resilient to the restoration of predators after a prolonged period of absence. When this is the case, the system shows hysteresis, the failure of an alternative state caused by a perturbation to return to its originating state after the complete reversal of that perturbation. Gray boxes represent the biomass or population size of predators, herbivores, and plants. Ovals represent slowly changing variables and processes. We omitted multiple boxes to represent individual members of species-rich food webs to achieve a simple diagram. To avoid the clutter of multiple arrows, we did not represent feedback among ecosystem properties and processes, which are known to operate. Evidence for the indirect effects (dashed green arrows) shown in (B) is reviewed by McNaughton et al. (1988); Pastor and Naiman (1992); Dublin et al. (1990); Milchunas and Lauenroth (1993); Belnap (1995); Trimble and Mendel (1995); Hobbs (1996); Augustine and McNaughton (1998); Hobbs (2006); Forbes et al. (2019); Smit and Coetsee (2019) and Pringle et al. (2023). This figure is modified from Schmitz (2008; Figure 1).

regimes, hydrology, and the physical properties of soil (Figure 1B).

We can place these ideas in a broader theoretical context informing when restoration of predators would be expected to rapidly reverse the effects of their loss from the food web using the concept of hysteresis. Hysteresis occurs when an alternative state in a community caused by a perturbation fails to return to its originating state after the complete reversal of that perturbation (Beisner et al., 2003; Petraitis, 2013; Scheffer et al., 2001). Restoration of apex predators to a simple, linear food chain with a single predator, single herbivore, and single plant species could be reasonably expected to cause rapid restoration of the food chain to its original state because

the effects of predator removal are mediated through direct trophic effects on biomass and energy flow (Figure 1A). In this case, the system would not show hysteresis, without the opportunity for indirect effects due to selective feeding. In contrast, the effects of predator restoration would not be expected to be reciprocal to the effects of predator removal for complex food webs with multiple predators, multiple herbivores, and species-rich vegetation (Figure 1B; also see Folke et al., 2004, p. 651). Interactions among the many members of the food web occurring when predators were absent, particularly selective feeding of herbivores on a diverse plant community, and the ensuing consequences of these interactions for one or more slowly changing ecosystem properties and processes (Figure 1B) could be reasonably expected to create hysteresis. In this case, it would be unlikely that predator restoration would cause the system to quickly reconfigure to its preremoval state. Accumulating empirical findings suggest that the effects of predator restoration are not reciprocal to the effects of their loss (reviewed by Allen et al., 2017), implying that many systems exhibit hysteresis following the loss of apex predators from food webs.

CORE QUESTIONS

Here, we test predictions of theory on the effects of restoring apex predators to food webs and its relevance for understanding the stability of alternative states using evidence from two decades of experimental and observational studies following the restoration of the large carnivore guild to the northern range of Yellowstone National Park. We address two core questions:

1. Did the restoration of apex predators to the food web reverse the alternative state in the ecosystem that developed after apex predators were extirpated from the system or was that state resilient to the effects of predator restoration?
2. What caused this resilience if it occurred?

HISTORY

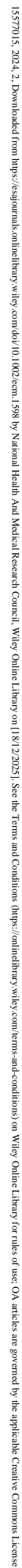### An alternative state on Yellowstone's northern range

The landscapes of Yellowstone's northern range experienced dramatic changes in structure and function over the last century (reviewed by Wagner, 2006). During the early 1900s, communities of willows dominated the riparian zones of the northern range, extending up to 40 m

laterally from stream margins (Peterson et al., 2020). Beaver dams punctuated the stream network, flooded large areas of the landscape, and created hydrologic and soil conditions particularly well suited to the life-history requirements of willows. Engineering by beavers raised water tables and reduced their variability over time, which promoted willow establishment and growth (Larsen et al., 2021). Beaver dams, lodges, pond margins, and runways exposed bare substrate required for germination of willow seeds. We will refer to these conditions as the beaver–willow state (Wolf et al., 2007; Figure 2).

Willows declined in abundance and stature during the mid-20th century (Houston, 1982; Singer et al., 1994; Wagner, 2006) a period when the dominant large herbivore, elk, was abundant (Figure 3A). High-density stands of tall willows were replaced by low-density, short willows in many areas of the range (Figure 2).
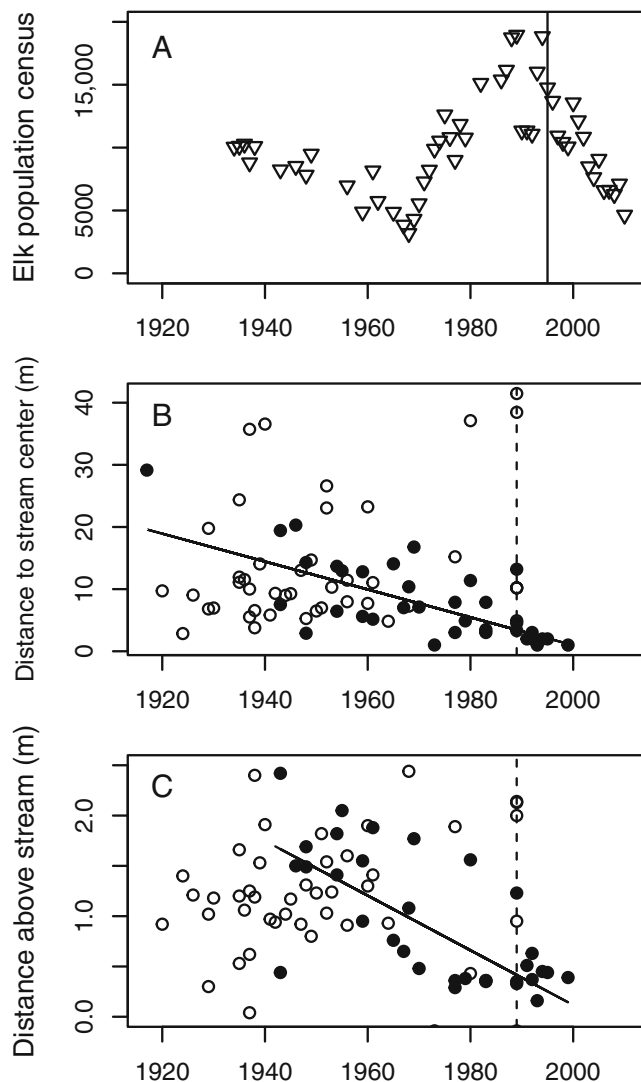
Coincident with the loss of tall willows, beavers abandoned the small streams of the northern range (Jonas, 1955). Warren (1926) found abundant beavers, dams and ponds in the region around Tower Junction in 1921, providing one of the best documented reports of conditions in Yellowstone soon after predator extirpation. However, within 10 years of Warren's reporting, willows were disappearing from areas used by beavers (Bailey, 1930; Figures 2 and 3). R. J. Jonas surveyed the Warren sites in 1953 and found that no beavers were present in any of the 12 sites documented by Warren (Jonas, 1955). Warren estimated that 232 beavers were present in his study sites, but Jonas found no beavers in any of these sites. The persistent absence of engineering by beavers on the northern range was confirmed by repeated surveys of the Warren sites after 1980 (reviewed by Smith & Tyers, 2012).

The loss of engineering by beavers caused enduring changes in the physical environment. Almost one-third of mainstream reaches historically experienced beaver-related aggradation (Persico & Meyer, 2009) and the absence of their engineering transformed expanses of the riparian zone (Figures 2 and 3B,C). Unimpeded by beaver dams, stream flows accelerated, causing locally significant incisions that effectively disconnected channels from their historic flood plains (Wolf et al., 2007; Figure 3C). Radiocarbon dating of woody debris in downcut stream banks revealed that current depths of incisions of streams had not been seen for millennia (Wolf et al., 2007, but also see Persico & Meyer, 2009). The absence of beaver dams lowered water tables adjacent to streams and narrowed the area of exposed substrate and moist soils (Figure 3B,C) required by willows for establishment and growth. Thus, the habitat suitable for willows compressed dramatically, appearing to create a self-reinforcing feedback: willows required disturbance

FIGURE 2 Conceptual model of state change in the small stream network of the northern range of Yellowstone National Park. Rectangles represent stream conditions; ovals represent the condition of willows. The beaver–willow state (green oval and rectangle) was characterized by abundant tall willows and extensive dam building by beavers. Excessive browsing reduced willow height to levels insufficient to support engineering by beaver, causing a transition to the elk–grassland state (tan ovals and rectangles). The tan arrows represent hysteresis; the system is stabilized in the alternative elk–grassland state by changes in the physical environment and the hydrologic regime. The blue arrows indicate the absence of hysteresis; the beaver–willow state is restored after the restoration of apex predators via the same pathway that caused the original transition to the elk–grassland state. This study sought to determine whether the elk–grassland state was stable (exhibited hysteresis) after the perturbation caused by the restoration of apex predators. The figure is modified from Wolf et al. (2007).

by beavers to establish and grow, while beavers required tall willows for food and dam-building materials.

Willow communities were replaced by grasslands in most areas of the northern range by the mid-20th century

(Houston, 1982; Singer et al., 1994; Wagner, 2006). This feedback appeared to stabilize the alternative, short-stature state of willows: the absence of willows removed an important resource for beavers, and the

the alternative state that emerged after the loss of apex predators from the food web as the elk–grassland state (Wolf et al., 2007; Figure 2).

Willow height is an important indicator of the state of riparian zones for several reasons. Sufficiently tall willows are less subject to harm from browsing because some of their stems and catkins are out of reach of many large herbivores. Long willow stems are an essential component of beaver dams, acting as anchors to enhance the structural strength of mud. Finally, height is important to the keystone effects of willows on streams; their upright stems and perennial roots stabilize stream banks, increase deposition of sediment during floods, enhance water quality, contribute coarse woody debris and fine organic matter to streams, and provide habitat for many plants and animals (Larsen et al., 2021; Naiman & Décamps, 1997). Tall willows provide a useful "sentinel" (sensu Petraitis, 2013) for the beaver–willow state; while short willows provide a sentinel for the elk–grassland state.

Causes of change to the alternative state

There were likely multiple causes of the transition from the beaver–willow state to the elk–grassland state. It has been suggested that the shift was caused by changes in climate (Houston, 1982), particularly drying and warming that occurred following the end of the Little Ice Age (Persico & Meyer, 2009, 2013). Fire suppression has also been implicated by Houston (1982) and Despain et al. (1986) because fires create bare substrates needed for willow establishment (e.g., Figure 3B,C). However, although these environmental changes probably contributed to state transition, they could not be the primary cause because a warming and drying climate and suppression of fires affected the entire region, while the dramatic change in the riparian state did not occur outside of Yellowstone, where population densities of elk were kept relatively low by regulated human harvest. Alternatively, a large body of evidence (reviewed by National Research Council Committee on Ungulate Management in Yellowstone National Park, 2002; Wagner, 2006) has argued that the most important cause of state change, if not the sole cause, was excessive browsing by a large elk population:

> "The increase in ungulate browsing over the past century, as evidenced by hedged willows and lost willow stands throughout the lower elevations of the northern range, has caused most of the reduced willow cover and lowered reproduction in this area. (National

FIGURE 3   (A). Elk counts on the northern range in 1930–2010 (Houston, 1982; Taper & Gogan, 2002; Yellowstone National Park, unpublished). The increase in elk numbers after 1970 reflected the elimination of elk culling by park staff. The vertical line indicates when wolves were reintroduced, but populations of other predators, notably cougar and grizzling bears, were restored naturally throughout the 1990s. (B, C). Dendrochronological studies (Wolf et al., 2007) revealed that willows established primarily on alluvium (closed circles) adjacent to streams after 1950. Before that period, plants were established on beaver pond sediments (open circles) that extended up to 40 m from the current stream center. Regressions through points for alluvial establishment show (B) temporal trends in the area of establishment habitat and (C) stream downcutting. Exposed, fine-grained sediment following the fires of 1988 stimulated seedling establishment (dashed vertical lines). Panels (B) and (C) have been redrawn from data in Wolf et al. (2007).

absence of engineering by beavers degraded the habitat for willows by allowing streams to incise and lower the riparian water table (Wolf et al., 2007). We will refer to

Research Council Committee on Ungulate Management in Yellowstone National Park, 2002, p. 79)."

The change in riparian state from tall to short willows (Figure 2) coincided with changes in the terrestrial food web. The northern range historically provided winter habitat for one of the largest migratory elk herds (*Cervus canadensis*) in North America (Houston, 1982). Elk were the primary prey of apex predators in the region, particularly the gray wolf (National Research Council Committee on Ungulate Management in Yellowstone National Park, 2002). However, contemporary analyses indicate that cougars and grizzly bears almost certainly preyed heavily on elk as well (Barber-Meyer et al., 2008; Griffin et al., 2011; Ruth, 2019). Wolves and cougars were extirpated from Yellowstone by the early 1920s. The loss of regulating effects by apex predators on the elk population provides the single best explanation for the high densities of elk observed after 1930 (reviewed by National Research Council Committee on Ungulate Management in Yellowstone National Park, 2002; Wagner, 2006; Figure 3A), although other factors including habitat conversion outside the park (Grimm, 1939), supplemental feeding within the park in the 1920s (Houston, 1982, p. 29), and movement of elk into the park in response to hunting pressure outside its boundaries (Houston, 1982, p. 29 but also see Wagner, 2006, fig. 5) may partially explain these high densities.

Loss of abundant, tall willows and aspen as a result of excessive browsing appears to have been the primary driver of changes in the riparian disturbance regime, the loss of dam building by beavers (Figure 2). Jonas (1955, p. 165) attributed the most important cause of the loss of beavers to the absence of willow and aspen from riparian zones: "The primary factor limiting beaver activity in Yellowstone was lack of the preferred food species of vegetation," which was caused by excessive browsing by elk: "The unfortunate food situation at the time of this survey was a result more from the overpopulation of elk than from any other single cause." (Jonas, 1955, p. 166).

Thus, evidence suggests that abundant elk harmed beavers through interspecific competition for willow and aspen (Flook, 1964). Willow and aspen are obligatory food and building materials for beavers (Baker et al., 2005), but they are alternative foods for elk (Hobbs et al. 1981). Willow and aspen cut by beavers normally resprout (Kindschy, 1989) and provide additional food for beavers. However, once tall aspen and willow are cut, the resprouts are within the reach of browsing elk (Baker et al., 2005). By preventing aspen and willows from growing into large plants, elk can eliminate beaver food, and thus eliminate beavers (Chadde & Kay, 1991).

Effects of the loss of beavers on hydrologic dynamics and riparian water table depths may have been amplified by warmer temperatures and lower stream flows that occurred in the mid to late 1900s compared with the early 1900s (Persico & Meyer, 2009, 2013). However, annual precipitation during the period when beaver activity ceased (1920–1953) was somewhat below average, but not markedly so. There were 10 years of drought conditions from 1927 to 1937 when annual precipitation was below the long-term mean, but in 1915–1953 there were 17 years with above-average precipitation and 20 years with below-average precipitation (Jonas, 1955, fig. 81). It seems unlikely that these conditions were responsible for the loss of beaver activity on the small stream network because beavers are highly successful at damming small streams under low flow and drought conditions, thereby stabilizing water tables in the riparian zone, despite climatic variability (Westbrook et al., 2006).

Up to this point, we have made the case that the primary cause of state change in the riparian zones of the northern range was browsing on willow by abundant elk. This case might seem at odds with the downward trend in elk numbers that seemingly occurred in 1945–1965 (Figure 3A). Elk numbers were reduced by the harvest of elk outside the park in 1940–1955 and culling by park staff in 1950–1968 (Wagner, 2006, fig. 5.1). However uncertainty in population estimates in 1940–1953 (MacNulty et al., 2020, fig. 14.1) suggests that we cannot rule out an increase in the elk population during that period. Moreover, culling by park staff was initiated because of concern about excessive browsing, which the preponderance of evidence suggests had already caused state transition when major herd reduction efforts were started. The dramatic increase in elk numbers after 1968 (Figure 3A) occurred after the elimination of culling as part of the park's change in policy to "natural regulation" (Singer et al., 1998). This spike and the decline in elk numbers in 2010–2022 when the large carnivore guild was restored reinforces the conclusion that the absence of capable apex predators was ultimately responsible for the high densities of elk implicated as causing state transition.
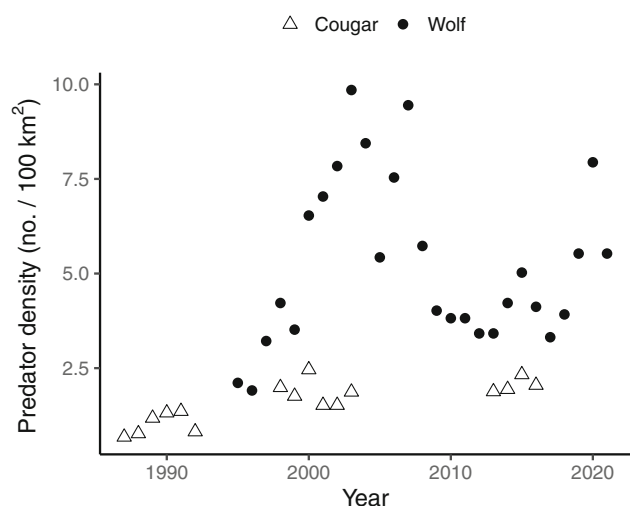
Recap

Here we summarize the approximate chronology of events described above and relate them to ideas about direct and indirect effects of predator restoration developed in the Conceptual Framework. It appears that the direct effects of extirpation of apex predators in the early 1900s allowed the elk population to expand to levels sufficient to cause widespread over-browsing of willows from

1920 to approximately 1935 (Figure 3). These direct, trophic effects occurred relatively rapidly. Indirect trophic effects, the loss of active beaver dams, occurred as a result of browsing-induced losses of plants needed by beavers for food and building materials and required more time to accumulate, occurring in approximately 1920–1955 (Figure 2). Thereafter, abandoned beaver dams breached, allowing accelerated stream velocity and widespread incision of stream beds and banks. Willow establishment effectively compressed to point bars immediately adjacent to streams (Figure 3C), while the established willows occupied terraces meters above the stream (Figure 3B).

Reversal of state change?

The abundance of large carnivores increased dramatically in the northern range from 1990 to 2022. Wolves were restored to the food web in Yellowstone in 1995. The wolf population increased rapidly during the following decade, surpassing densities of nine animals per 100 km^2 in the mid-2000s (Figure 4). The wolf population declined after that peak, averaging approximately five animals per 100 km^2. The cougar population quadrupled in 1987–2016 (Figure 4), an example of predator recovery in the absence of active reintroduction. The abundance of grizzly bears almost doubled (Corradini et al., 2023; Figure 1). Cougars killed more elk than were killed by wolves in 1998–2004, a period of steep decline in elk numbers (Metz et al., 2020; Ruth, 2019). The per capita

kill rate of cougars on elk is double the kill rate by wolves (Ruth, 2019). Grizzly bears have a larger and more additive effect on neonatal mortality than wolves (Barber-Meyer et al., 2008; Griffin et al., 2011). Human harvest had a greater influence on elk numbers than wolves did during the decade after wolf reintroduction (Vucetich et al., 2005). It follows that a suite of predators, including humans, was implicated in reducing the abundance of elk in 1990–2022.

The elk population declined precipitously after the mid-1990s, creating the appearance of a causal mechanism for a trophic cascade from wolves to plants with effects that purportedly extended throughout the ecosystem (e.g., see fig. 4 in Ripple et al., 2014). This mechanism would be consistent with the theory for a simple, linear food chain (Figure 1A). However, the food web of Yellowstone's northern range is not simple. There are several plant communities composed of dozens of species of plants consumed by a multispecies community of large herbivores, known to feed selectively. A resurgent guild of apex predators preyed on elk (Peterson et al., 2014). Seemingly simple "causal" relationships, for example, "wolves caused the decline in the elk population" turned out to be excessive simplifications of a more complex truth (Peterson et al., 2014).

This historical context created an exceptional opportunity to examine whether the restoration of apex predators to a food web reverses the effects of their loss. It is clear there were multiple causes of the transition from the beaver–willow state to the elk–grassland state, but excessive browsing by an elk population released from control by large carnivores has been repeatedly implicated as the primary cause. Long-term experiments are the only way to learn whether the return of apex predators to Yellowstone caused state reversal (Figure 2).

OVERVIEW OF EXPERIMENT

We conducted a 20-year, manipulative experiment to test the hypothesis that the return of large carnivores to the northern range restored the beaver–willow state, providing evidence that restoring apex predators to food webs was able to reverse the conditions that emerged while they were absent. This hypothesis was evaluated against the alternative hypothesis that the absence of disturbance by beavers and persistent browsing by large herbivores stabilized the alternative, elk–grassland state, providing evidence that ecosystems with complex food webs can be resilient to predator restoration. Our experiment was designed to represent the effects of attenuation of browsing ostensibly created by trophic effects of large carnivores, as well as the effects of modification of stream

FIGURE 4 Population densities of wolves (Yellowstone Wolf Project, 2022) on the northern range of Yellowstone Park and population densities of cougars on the northern range and areas immediately adjacent to it (Smith et al., 2023). Population densities of wolves were computed by dividing the total counts on the northern range by its area.

hydrological processes created by beaver dams. We sought to create experimental conditions mimicking the beaver–willow state and compare the growth of willows under those conditions with the growth of willows experiencing ambient conditions on the northern range over the last two decades.

STUDY AREA

The northern range of Yellowstone National Park, USA, is a 100,000-hectare (ha) area used intensively by Yellowstone's largest elk herd during winter (Houston, 1982). This region spans 1923–2076 in elevation and receives 410 mm of average annual precipitation with 44% falling as snow (Wolf et al., 2007). The landscape is rolling hills formed of glacial till with lower elevations dominated by *Artemisia tridentata* Nutt. and *Elymus smithii* Rydb. and higher elevation forest stands of *Pseudotsuga menziesii* Mirbel and *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex Wats. The cool semiarid steppe is punctuated by patches and ribbons of wetter vegetation supported by ground and surface water. Fens and other predominately groundwater wetlands occur as patches throughout the northern range (Lemly & Cooper, 2011). Our study sites were third-order and fourth-order perennial streams of less than 10% gradient with their floodplain hydrologic regimes dominated by the stream surface water. Riparian vegetation was dominated by sedges, grasses, and five species of nonclonal willows: *Salix bebbiana* Sarg., *S. geyeriana* Anderss., *S. drummondiana* Barratt ex Hook., *S. boothii* Dorn, and *S. pseudomonticola* Ball. Aspen (*Populus tremuloides* Michx.) occur on the floodplain margins and adjacent hillslopes.

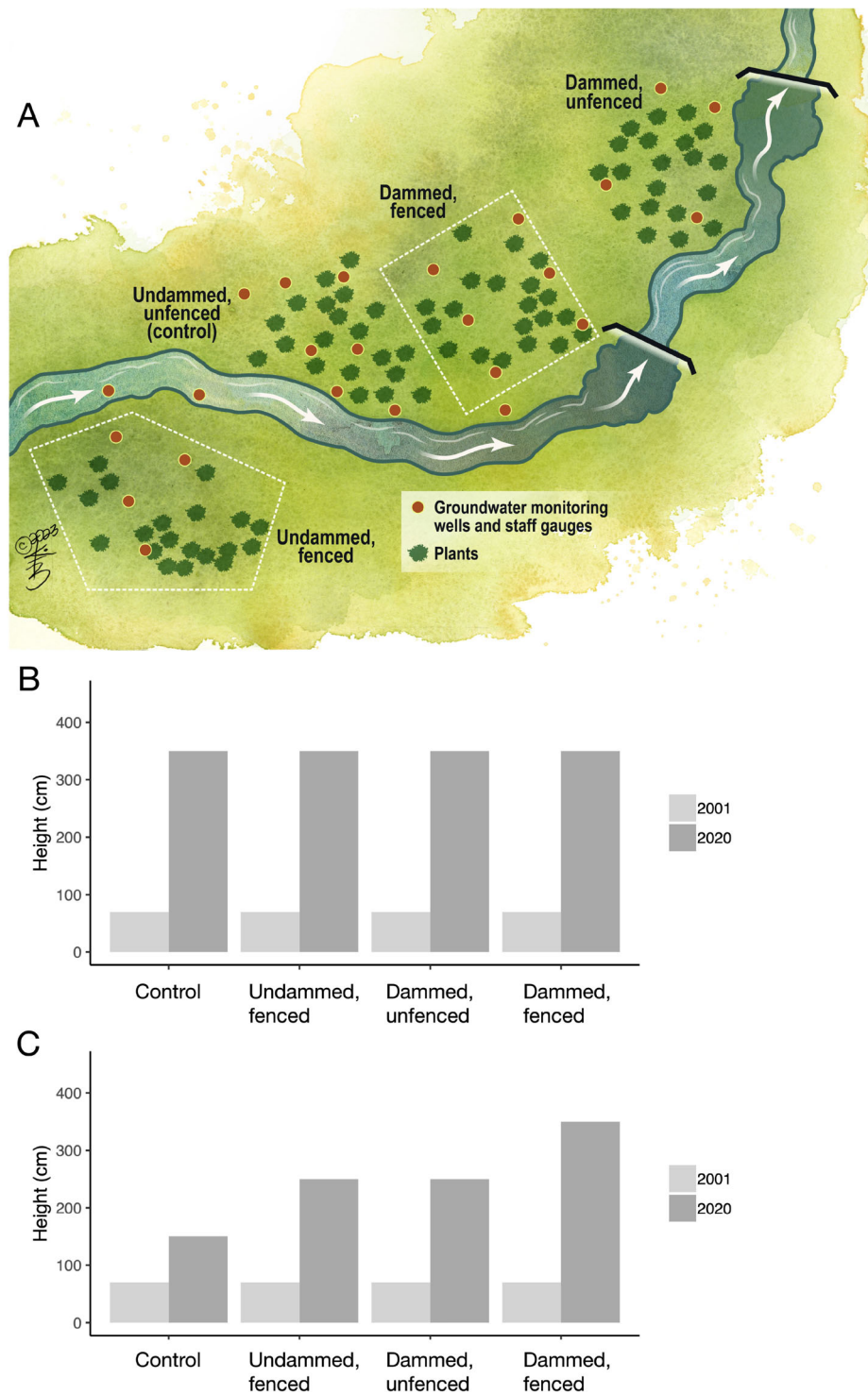## METHODS

Experimental design

We began our experiment in 2001 at four replicated sites along streams on the northern range. Sites were selected that met three criteria: (1) evidence of historic presence of beaver dams and ponds; (2) relatively large populations of *Salix bebbiana*, *S. geyeriana*, *S. drummondiana*, *S. boothii*, and *S. pseudomonticola*, and (3) riparian zones with groundwater recharged by stream water and lacking significant hillslope groundwater inflows. The willow species at the chosen sites do not reproduce clonally and can reach 3–5 m in height. Clonal willow species such as *Salix exigua* Nuttall and *S. planifolia* Pursh were not included in our study

and are not significant components of the riparian vegetation on small streams of the northern range.

Our four experimental sites were along Elk Creek and the West and East Forks of Blacktail Deer Creek. The study streams were 1–3 m wide, up to 1 m deep, with banks 0.5–1.0 m high, except at unstable cutbanks where bank height could exceed 2 m. The vertical banks created two distinct riparian environments: (1) narrow, deeply incised channels, and (2) broad, flat terraces above the banks. Ground surfaces within incised channels were close to the stream water level, while terrace surfaces were 1–2 m above the late summer water table. The streams we studied have low-sinuosity, meandering single-thread channels with a low to moderate gradient, and cobble, gravel, and sand beds. All study sites were within the 1988 fire burned-area perimeter, and charred logs at the Elk Creek site indicated that its floodplain vegetation may have been burned.

Experimental units within each site were four plots of ~0.1 ha. We assigned two levels of herbivory (fenced and unfenced) and two levels of damming (dammed and undammed) to the plots in a full-factorial design to evaluate how these treatments influenced willow height and growth (Figure 5A). Treatment was randomly assigned to plots after measuring pretreatment willow heights in 2001. Browsing was eliminated from half of the plots by surrounding them with fences 2.4 m high. Dams were constructed directly downstream from or adjacent to plots that had been randomly selected to receive elevated water tables (Bilyeu et al., 2008), simulating the effects of natural beaver dams. Thus, each replicated site had four treatment levels: (1) a control plot with no fence or dam, (2) a plot dammed and not fenced, (3) a plot fenced and not dammed, and (4) a plot fenced and dammed (Figure 5A). The design allowed us to evaluate two competing hypotheses (Figure 5B,C):

1. The first hypothesis was that the restoration of apex predators caused a reciprocal transition to the willow–beaver state that prevailed before their extirpation. Under this hypothesis, willows in fenced and control plots would have similar growth rates because the effects of predators on elk numbers and foraging behavior were sufficient to allow rapid willow growth. Under this hypothesis, growth in plots with dams would not differ from growth in controls because reducing browsing was a sufficient condition for range-wide restoration of willow height. This hypothesis predicted no difference in willow heights among the cells in the experiment 20 years after treatments were imposed (Figure 5B). The system did not show hysteresis because the restoration of apex predators allowed the elk–grassland to rapidly return to the

FIGURE 5 The experiment crossed two levels of fences (fenced and unfenced) with two levels of simulated beaver dams (dammed and undammed) at four replicated sites (A). (B) The expected results under the hypothesis that the effects of the restoration of apex predators were reciprocal to effects of their loss from the northern range, allowing the restoration of the beaver–willow state. (C) The alternative hypothesis that the loss of engineering by beavers and continued browsing by large herbivores made the elk–grassland state resilient to the effects of restoration of apex predators. Panel (A) is printed with permission from copyright holder Kate Galloway, KTB Studios, LLC.

beaver–willow state along the same trajectory that created the alternative, elk–grassland state (Figure 2, blue arrows).

2. The competing hypothesis predicted that the alternative elk–grassland state was resilient to the restoration of apex predators and that predator restoration had

not restored the beaver–willow state. In this case, fences would accelerate growth relative to controls because the return of large carnivores to the food web failed to reduce browsing sufficiently to permit rapid growth on control plots. Dams would increase growth relative to controls because dams restored the hydrological conditions, favoring willow growth that historically prevailed along the small stream network but are now absent. The combined effects of dams and fences would exceed their individual effects because both browsing and current hydrological conditions suppress growth. This hypothesis predicted unambiguous differences in willow height among the cells in the experiment 20 years after treatment was imposed (Figure 5C). Under this hypothesis, the system exhibits hysteresis. The restoration of apex predators did not allow the return of the beaver–willow state because changes in the disturbance regime and the morphology of streams that occurred while predators were absent eliminated the environmental conditions needed for willows to establish and grow (Figure 2, tan arrows) and because herbivory remained sufficiently intense to suppress willow growth.

Manipulative experiments provide the gold standard for evidence demonstrating or refuting the operation of trophic cascades (Ford & Goheen, 2015). Our experiment met all but one of the criteria required to reveal the operation of multiple stable states (Petraitis, 2013). We observed the response of a sentinel species to a perturbation of sufficient magnitude to cause state change on experimental sites. These sites were replicated over space for a period of time sufficient to allow differentiation among the responses of the alternative states. The only criterion that we did not meet was reversing the experiment at its conclusion to cause a reversal of state in the different cells of the experiment. Instead, our experiment represents the reversal of the "natural experiment" of the removal of apex predators from the northern range.

Measurements

Approximately 20 willows in each experimental plot were selected at random using a stratified design to ensure equal representation among the three most abundant willow species: *Salix geyeriana*, *S. bebbiana*, and *S. boothii* (Bilyeu et al., 2008). Each plant was marked near its base with a metal tag. Annually, we measured the characteristics of willow in the falls of 2001–2020 and the springs of 2002–2019. We measured the height of each plant as the distance from the ground surface to the tip of the tallest stem. A stem included the previous >1 year growth that

was rooted at the base of the plant. During spring, we counted the total number of shoots and the number of browsed shoots on 3–5 stems per plant. Shoots were defined as the woody tissue that accumulated during the current year's growing season, also called current annual growth. We estimated overwinter browsing intensity as the proportion of shoots on replicate stems on each plant that were browsed. We examined the relationship between the proportion of shoots browsed and plant height to determine whether there was a threshold where plants became sufficiently tall that browsing diminished.
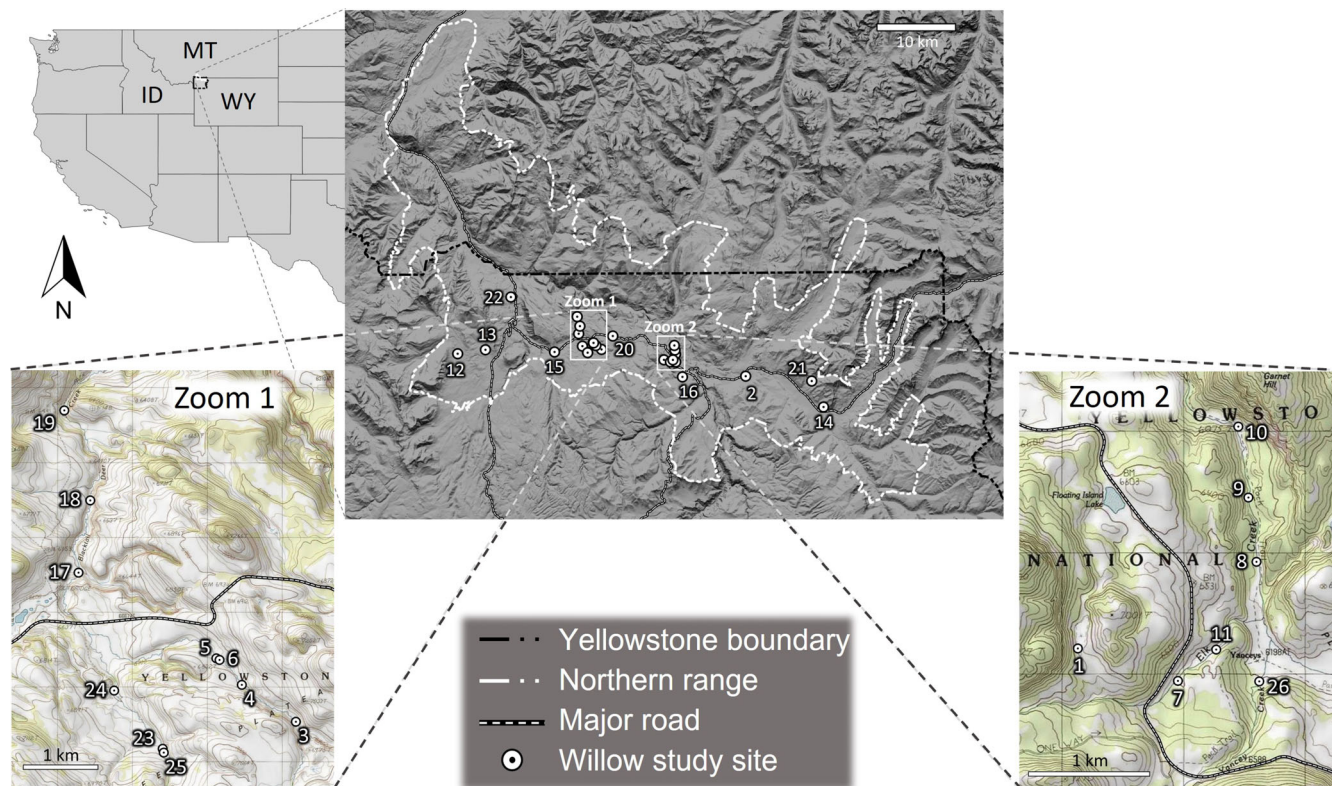
We installed 2–6 groundwater monitoring wells in each experimental plot in July and August 2001 to monitor water table depth and the effects of the simulated beaver dams on the water table. Wells were constructed of fully slotted 3.2-cm diameter PVC schedule 40 pipe and installed by hand augering to a depth ~30 cm below the late summer water table, 120–280 cm deep. We installed steel drive points that could be pounded to a suitable depth where rocky soils prohibited augering to the water table. Following installation, wells were pumped dry several times to develop them, and ensure adequate flow between the well and adjacent soil. We recorded water levels approximately every 2 weeks during the growing season using an electric tape. From 2010 to 2020, at least one well in each experimental plot was equipped with a logging pressure transducer (In-Situ Rugged TROLL 100 Data Logger), that was corrected for atmospheric pressure with a recording barometric pressure logger (In-Situ BaroTROLL Data Logger).

Replication of experimental controls

The inarguable strength of designed experiments is their ability to make unambiguous inferences about causation, inference that cannot be obtained using observational investigations alone. However, the difficulty and expense of establishing experimental manipulations, particularly in a national park, limit the ability to replicate experiments extensively over space, leading to inevitable questions about whether the experiment was representative of the population we seek to understand.

To deal with this potential limitation, we established 21 replications of the experimental controls in 2009 to expand the spatial extent of our measurements on the ambient condition (Figure 6; Appendix S1). Hereafter, we will refer to these replications as "observational sites." The sites were selected randomly from a population of stream reaches that were either known to have been occupied by beavers (Jonas, 1955), had evidence of former beaver occupation such as relic dams and ponds, or were of appropriate size and gradient for damming by

FIGURE 6 Observational and experimental study sites on the northern range in Yellowstone National Park. See Appendix S1 for a key to site names and locations.

beavers. Potential streams were selected based on gradient (less than 10%) and stream order (third and fourth orders). We used a spatially balanced random sampling algorithm (RRQRR) to select from the population of potential sites (Theobald et al., 2007). Details of this sampling design were given by Marshall et al. (2014).

Measurements identical to those taken on the experimental controls were obtained at the observational sites to ensure that experimental controls were representative of the range-wide condition, thereby strengthening our ability to answer core question one, above. The observational sites also increased replications and spatial coverage of our estimates of browsing pressure, which was critical for answering core question two, above. It was essential for us to know how browsing changed over time across the northern range after the recovery of large carnivore populations. We also used observational plots to make inferences on the influence of variation in browsing intensity and water tables on willow growth.

Beaver-occupied sites

Dam building by beavers has been absent from the small stream network of the northern range since the 1920s.

However, in the summer of 2015, beavers built dams, lodges, and food caches on three small streams: West Blacktail, Elk Creek, and Crystal Creek. These three sites were added as additional observational sites to monitor conditions for water level and vegetation response to beaver activity. No beaver activity was observed at the original observational sites. We installed five groundwater wells to measure water table depth and one staff gauge at each site and monitored willow height as in all other observational sites. The natural beaver activity observational sites at West Blacktail and Elk Creeks were distinct and separated from the experimental sites on those same two creeks. Beavers persisted on Elk Creek and the monitored reach of Crystal Creek for only a couple of years before depleting the willows and moving elsewhere. West Blacktail has a large riparian zone and willow population supported in part by hillslope groundwater that has sustained beaver occupancy.

Camera trap data

Understanding how the community of large herbivores reorganized after the guild of large carnivores was restored was key to understanding sources of stability in

the alternative state (question two above). We installed motion-detecting Reconyx camera traps at 13 of the observational sites in 2013 and recorded the images they captured each month through 2016. We visually classified the ungulates by species and counted the number of individuals of each species in each camera image. The independent sampling unit was the site.

Population counts and herbivore biomass

We also examined the composition of the herbivore community using count data for elk (Northern Yellowstone Cooperative Working Group, 2023) and bison (Geremia, 2022) within Yellowstone National Park. Elk counts were usually conducted during the winter and a bison census during the summer. It follows that the elk counts do not inform the size of the population during the growing season, and the bison census may not perfectly reflect the number of bison using the northern range during the winter. However this seasonal bias is likely to be much smaller for bison than for elk. The elk counts were corrected for sightability to prevent underestimation of true population size as a result of animals that were present but not observed (Smith & MacNulty, 2023). Bison counts were not corrected for sightability. However, undercounting is less problematic for bison because they tend to aggregate in large groups in open grasslands during the summer. The count data are vital to link measurements of plant growth to demand for forage by large herbivores and to understand how the herbivore community had changed in the 25 years following wolf restoration. Annual wolf counts were obtained from the Yellowstone Wolf Project (2022).

We estimated the total biomass of elk and bison inhabiting the northern range using a weighted average body mass (Rose & Cooper, 2017) multiplied by the count of individuals in the population, assuming that the age and sex composition of each population was constant. Total forage consumed per day by elk and bison is roughly proportional to total biomass because dry matter intake of ruminants is well approximated as a constant fraction of body mass (Alldredge et al., 1974; Cordova et al., 1978; Holechek & Vavra, 1982).

Analysis

We sought inference about the rates of willow height growth over time in the experiment and at observational sites. We collected our willow data by species, but preliminary analyses revealed that differences among species were not sufficient to justify species-specific analyses. Therefore, we lumped species into a single category for all analyses.

We analyzed the experimental data on height change over time using a Bayesian multilevel model (Gelman & Hill, 2009; Hobbs & Hooten, 2015) structured hierarchically to reflect how the data were collected (Gelman et al., 2013; Zachmann et al., 2021). We fitted a random intercept and time slope (growth rate, in centimeters per year) for each marked plant within each plot to account for the repeated measures structure of the design. Plant-specific slopes and intercepts were modeled as correlated random variables by fitting a variance–covariance matrix for each plot. It is important to understand that fitting treatment intercepts and slopes as random rather than fixed means that our inference applied to all possible sites suitable for damming by beavers on the northern range. In contrast, assuming fixed effects of treatment would dramatically reduce the uncertainty about those effects, but would constrain inference to the four sites that we studied.

We carried out a parallel analysis of observational data, seeking to understand the role of water availability and browsing at large scales. We analyzed observations of willow height over time using a linear model for each marked plant within each site in which time was the predictor variable. Intercepts and growth rates (i.e., time slopes) and their covariance were modeled for each plant within each site. Intercepts and time slopes were drawn from a range-wide hyperdistribution allowing inference to extend to the population of willows on the small stream network. Browsing intensity from observational sites was analyzed with a similar model with a likelihood appropriate for modeling the number of shoots browsed out of the total number of stems on a sample of observed stems.

We regressed the growth rate for each of the observational sites on characteristics of the water table and browsing intensity averaged over 2009–2019. We first conducted univariate analyses of the growth rate predicted by browsing intensity, mean water table depth, standard deviation of water table depth, and the coefficient of variation of water table depth. We then choose among the predictors based on the probability of their slopes overlapping zero in a model, including main effects and two-way interactions. We included predictor variables involving temporal variation in water table depth (standard deviation and coefficient of variation) reasoning that such variation can create periods of water stress not reflected in the mean water table depth.

Camera trap data were compiled to assure independence among photos by finding the maximum number of individuals of a species observed in the series of photographs recorded on a single day at a single site. These

daily maxima (one for each day and site) were then summed across a season to obtain the total number of individuals observed at a site.

We estimated the mean proportion of observations of three herbivore species observed in camera traps during winter and summer using a Bayesian hierarchical model. Each camera trap (i.e., site) was modeled as having its own vector of species proportions drawn from a range-wide distribution of proportion vectors.

We describe the mathematical details of these models, the computational procedures we used to fit them, and methods for model checking in Appendix S2.

RESULTS

Growth rates and heights in the experiment

Raising water tables and eliminating browsing caused dramatic changes in willow heights. The dam treatment raised the mean water table depth by 40 cm in July (Figure 7). The combined effects of the dam and fence treatment tripled the rate of increase in the height of willows in the experiment, accelerating the mean annual increase in the height by 9.7 cm/year (Table 1). Mean growth rates in the fence and dam treatments were three times more rapid than the control growth rate (Figure 8A,B; Table 1). The average height of willows in fenced and dammed plots 20 years after the initiation of the experiment exceeded 350 cm, while the height in controls averaged less than 180 cm (Figure 8C). The probability that the fence effect exceeded zero was 0.88, the dam effect was 0.83, and the dam and fence effect was
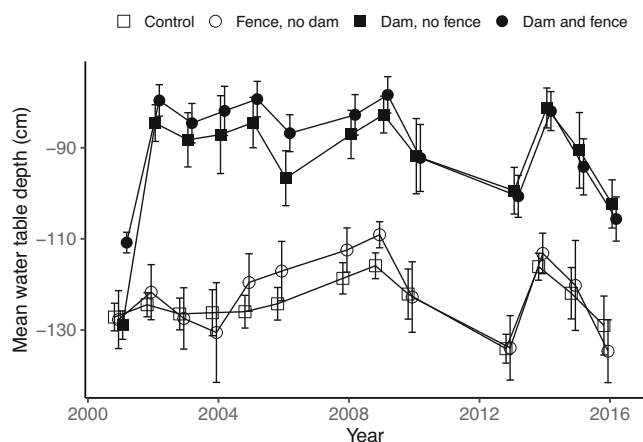
0.99 (Table 1). It is notable that dam treatment and fence treatment had effects of similar magnitude. This suggests that well watered plants could tolerate relatively heavy browsing. It also shows that the absence of engineering by beavers suppressed willow growth to a similar extent as did browsing. Thus, reducing browsing is a necessary but not a sufficient condition for the restoration of willows. We found some evidence that the effect of removing browsing was magnified by the effect of dams (Pr(interaction >1) = 0.69; Table 1), but we could not rule out the possibility that this interaction was zero.

We observed variation among sites in response to treatment (Figure 9). There was virtually no overlap between posterior distributions of willow growth rates in control plots relative to posterior distributions of willow growth rates in dammed, fenced plots at all sites. However, we observed substantial overlap in posterior distributions between control and dammed, unfenced plots at the elk site (Figure 9C), and overlap between the control and fenced plots at the East Blacktail Creek and West Blacktail sites (Figure 9A,B,D). The overlap at the elk site appeared to have resulted from unusually heavy browsing on plants in the dammed, unfenced plot, which was on a heavily used bison trail used for traveling into and out of Yancy's Hole. The upstream East Blacktail Creek dam experienced bank erosion, allowing water to flow around the dam starting in 2011 and, although repairs were made, the effect of the dam was reduced in the dammed and fenced and dammed-not-fenced plots (Figure 9A).

Growth rate and heights at observational sites

The mean growth rate of willows from observational sites and experimental controls was 5.15 cm/year (95% equal-tailed Bayesian credible interval = 3.46, 6.88). Growth rates of willows at observational sites had large among-site variation (Figure 10). However, there was no indication that the mean growth rates of willows on experimental controls differed from the mean growth rates of willows on observational sites across the northern range, allowing the conclusion that the 20-year growth rates of willows on experimental controls were representative of growth rates across the small stream network of the northern range.

The heights of willows in the fall of 2020 at observational sites were similar to the heights on experimental control plots (Figure 11). The mean predicted height was 178 cm. As with growth rates, we observed substantial variation among observational sites in 2020 heights. However, there was no evidence of differences between

FIGURE 7 Measured water table depths in dammed and undammed plots during July. Symbols are means; vertical lines are two standard deviations of the observed mean height.

TABLE 1 Slopes of the regression of height on time (growth rates in centimeters per year) and effect sizes of treatments.

Parameter	Mean	SD	2.5%	97.5%	Pr(>0)
Growth rates (in centimeters per year)					
Control	4.92	1.68	1.79	8.34	0.995
Fence	8.17	1.56	5.15	11.4	1
Dam	8.82	2.72	3.08	13.7	0.996
Fence and dam	14.6	2.13	10.3	18.8	1
Treatment effects on growth rates (in centimeters per year)					
Fence	3.25	3.14	−2.99	9.47	0.876
Dam	3.89	4.42	−5.15	12	0.837
Fence and dam	9.7	3.66	2.39	16.9	0.991
Interaction	2.56	5.71	−8.44	14	0.686

Note: Effect sizes were the difference between the control and treatment slopes. The interaction is the increase in height over the sum of the main effects that occurred when both dam and fence treatments were present. The fence and dam effect was the sum of the fence effect, the dam effect, and the interaction. SD is the standard deviation of the marginal posterior distribution of the mean; 2.5% and 97.5% give upper and lower, equal-tailed Bayesian credible limits.

heights on observational sites and experimental controls, reinforcing the conclusion that experimental plots were representative of the conditions on the northern range.

Browsing intensity

The mean proportion of browsed shoots on unfenced plots in the experiment decreased steeply from a high of 0.62 in 2003 to a low of 0.10 in 2010, and increased thereafter (Figure 12). We also found an increase in the proportion of browsed shoots on observational sites and experimental controls in 2009–2017, although this increase was not as steep as we saw in unfenced experimental plots (Figure 13).

Plants that were <250 cm tall after 2011 experienced browsing levels of about 30% of shoots. Browsing declined to ~20% when plants equaled or exceeded 250 cm, which suggests that some shoots at the top of the plant escaped browsing (Figure 14). However, because we did not measure the heights of browsed shoots, we could not be certain that this reduction in browsing on tall plants was due to shoots being out of reach of ungulates. Tall plants also had many stems, so it is possible that shoots in the middle of the plant escaped browsing.
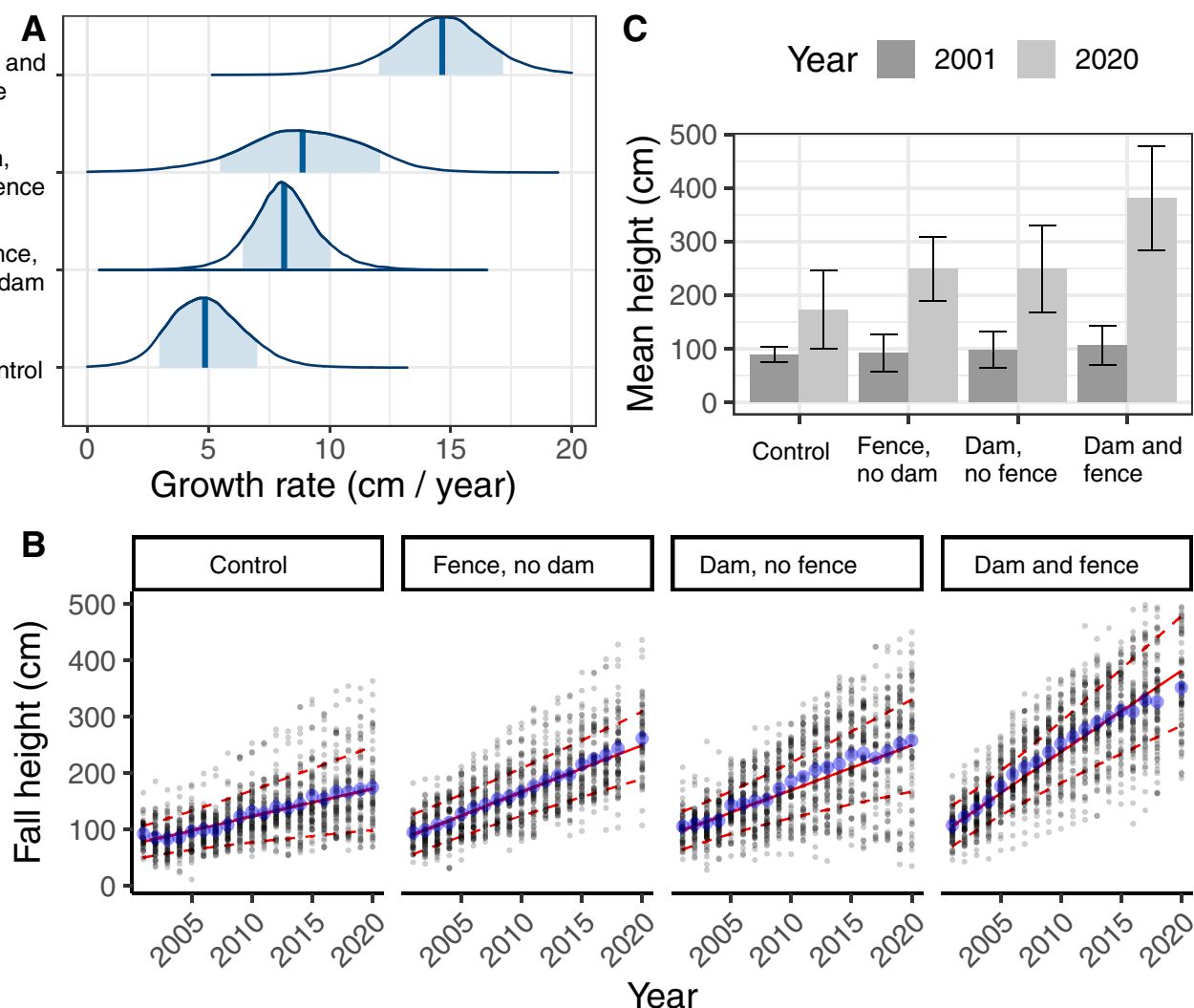
Effects of browsing and water tables on growth rate

We found a negative relationship between the growth rate of willows and the mean proportion of browsed shoots averaged over the years (Figure 15). The growth rate declined by 8 cm per year for each 0.1 change in the proportion of stems browsed (Table 2). We found a positive relationship between growth rate and less negative coefficients of variation in mean water table depth averaged across years (Figure 16), implying that deep and/or variable water tables retarded willow growth. The growth rate increased by 9.3 cm/year for each 0.1 unit increase (less negative) in the average coefficient of variation (Table 2). Including both the proportion of shoots browsed and the coefficient of variation of water table depth in the same model of growth rate with standardized predictor variables revealed the effect of variation in water tables was more than three times stronger than the effect of browsing, reinforcing the conclusion of our experiment that mitigating browsing pressure is not sufficient to allow rapid growth of willows without perennial access to groundwater.

The large herbivore guild

The herbivore community reorganized during the course of our investigations. The estimated elk population declined from more than 15,000 animals in 1995 to fewer than 2000 in 2023 (Figure 17A). The decline in elk numbers coincided with a steady increase in number of bison in the northern range population (Figure 17A) such that bison outnumbered elk after 2012. The total biomass of elk and bison declined steeply from 1995 to 2005, coincident with the decline in elk numbers (Figure 17B). However, ungulate biomass increased from 1.6 Mg in 2010 to 2.1 Mg in 2022. This increase coincided with the increase in bison numbers during the period and could explain the increase in browsing intensity we observed after 2010 (Figures 12 and 13).
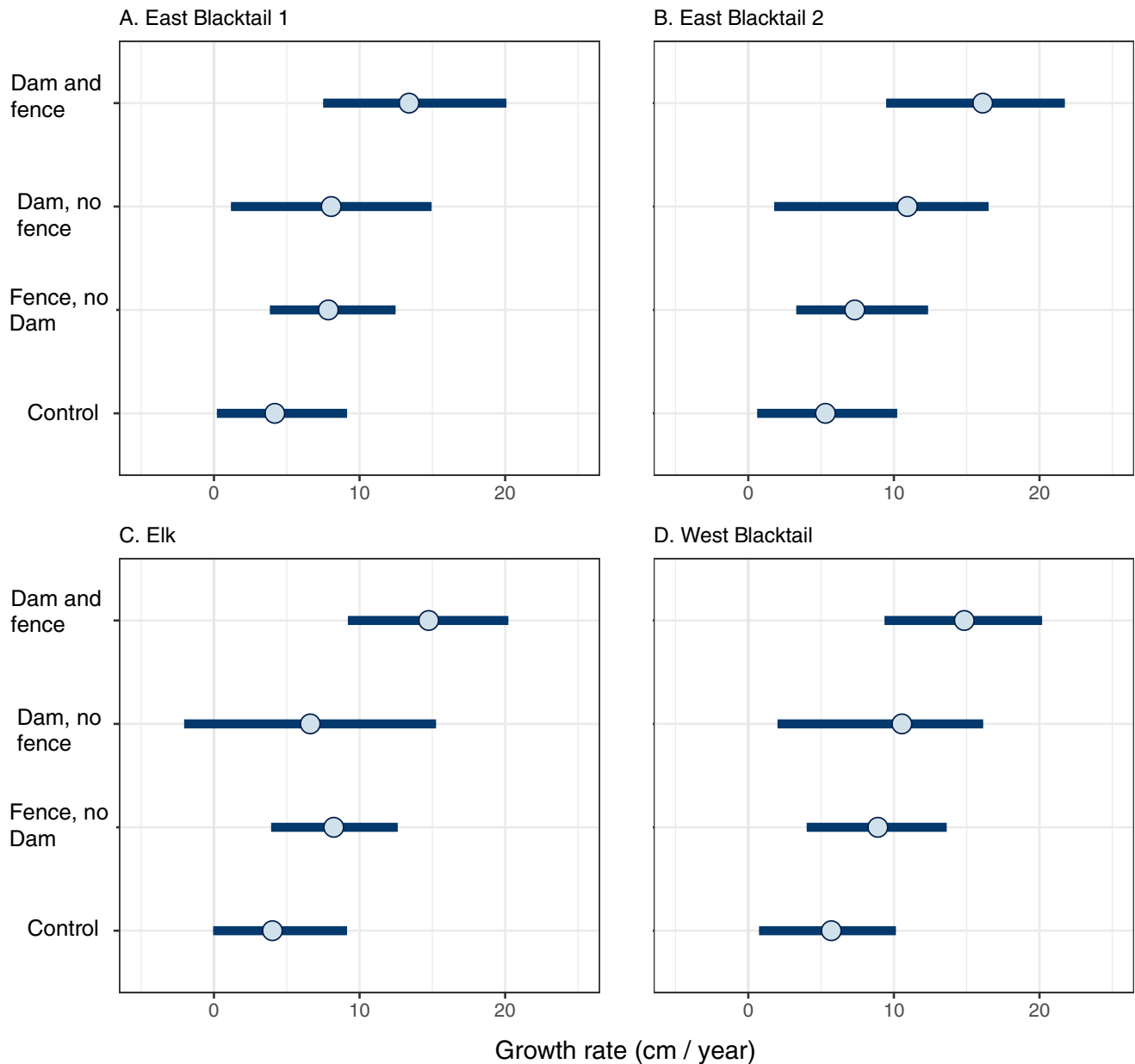
FIGURE 8 (A) Marginal posterior distributions of growth rates (in centimeters per year) in control and treated plots. (B) Fit of the model to observations of willow heights. Gray circles show the heights of individual plants; blue circles are the mean heights averaged across the four replicate sites for each treatment. The solid line shows the prediction of the out-of-sample mean growth rate. Dashed lines are 95% Bayesian credible intervals. (C) Predictions of out-of-sample mean heights of willows in the experiment pretreatment in the fall 2001 and after 19 years of treatment (fall 2020). Vertical lines give 95% equal-tailed Bayesian credible intervals.

Small changes in bison numbers relative to elk can caused large changes in ungulate biomass because bison are 2–3 times heavier than elk. There was a strong negative relationship between wolf numbers and elk + bison biomass before 2009 and no relationship thereafter (Figure 17C). We would not expect the relationship to be strong after 2009 because elk numbers were low and wolves rarely preyed on bison in the northern range (Smith et al., 2000; Tallian et al., 2017). Metz et al. (2020) demonstrated that wolves have regulated the abundance of elk over the last 15 years, but these regulating effects did not appear to extend to the entire community of large herbivores.

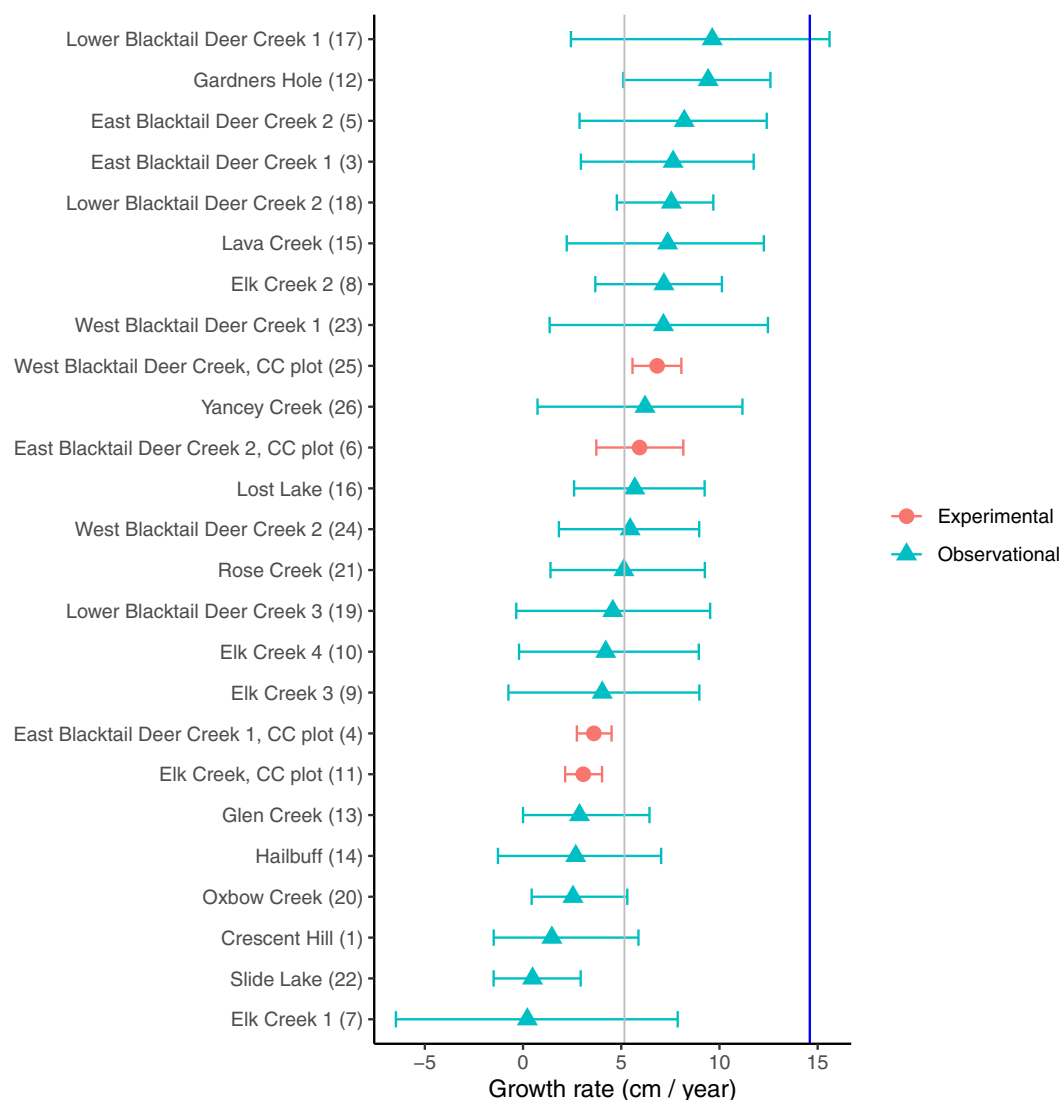Our camera trap data reinforced the idea that the relative frequency of large herbivore species using willows had shifted (Figure 18). Use of willow communities by bison now exceeded the use by elk during the growing season and is equal to elk use during winter. Winter use by moose was roughly half of the use by elk. It might be argued, wrongly, that bison are grazers and will not browse on willows, so their presence in willow communities does not mean they are having any impact on willow growth. Our data suggested otherwise; 20% of all our annual observations of bison in willow communities showed them browsing on willows, suggesting that bison feed on willows at least 20% of the time that they are in willow communities. Waggoner and Hinkes (1986) and Rose and Cooper (2017) showed that willows and other woody deciduous plants can be a substantial component of bison diets.

FIGURE 9 Means (circles) and 95% equal-tailed Bayesian credible intervals for the rate of growth of willows (in centimeters per year) in response to treatment at the four experimental sites.

We are the first to analyze the consequences of a reorganized guild of large herbivores for browsing pressure on willows (Figure 19). We found a positive relationship between browsing pressure and elk population size (Figure 19A) from 2002 to 2008, but no relationship from 2009 to 2022, the period when the total biomass of elk + bison had stabilized. The relationship between bison numbers and browsing intensity (Figure 19B) was complicated by the inverse relationship between elk and bison numbers in 1995–2010 when bison numbers were fewer than 2000 animals (Figure 17A). However, browsing intensity increased in relation to bison abundance after the population exceeded 2000 animals after 2008

(Figure 19B). We observed a strong positive relationship between elk + bison biomass and browsing intensity in all years (Figure 19C). There was a strong positive relationship between wolf numbers and browsing intensity (Figure 19D), indicating that when wolf numbers were high, so was browsing intensity. This somewhat counterintuitive relationship can be explained by the numerical response of wolves to elk: high densities of wolves are positively associated with high densities of elk and hence positively associated with high browsing pressure. However, it is notable that there was no relationship between the number of wolves and browsing pressure after 2008 because of the shift toward a bison-dominated

FIGURE 10 Means and 95% equal-tailed Bayesian credible intervals for willow growth rates at observational sites and experimental control plots. The vertical gray line is the mean of out-of-sample predictions of the growth rate for observational and experimental controls; the vertical blue line is the mean of the marginal posterior distribution of growth rate in the dammed and fenced plots in the experiment. Numbers in parentheses to the right of site names refer to site numbers in Figure 6.

community of large herbivores that was less vulnerable to wolf predation.

Beaver activity in relation to willow height

The average heights of willows in sites with active dam and lodge building by beavers were 79 cm taller than willows at other observational sites, and were only 51 cm shorter than the mean height of willows in dammed, fenced plots (Figure 20). The cause and effect relationship here is that beavers choose sites with tall willows rather than willows that become tall shortly after the beavers had colonized. In total, 76% of the willows in observational sites were shorter than the average at beaver-occupied sites (Figure 20). This is important because sustaining

beaver activity over time requires many sites with adequate supplies of tall willows. Beavers may abandon dams and lodges after a few years of use if the population of tall willows diminishes and they require new sites to colonize (Baker et al., 2005; Wolf et al., 2007). We observed that beavers colonized and then abandoned our elk and Crystal Creek study sites.

DISCUSSION

Did the restoration of apex predators reverse the effects of their loss?

Our two decades of research revealed that the restoration of apex predators to a food web after a long absence
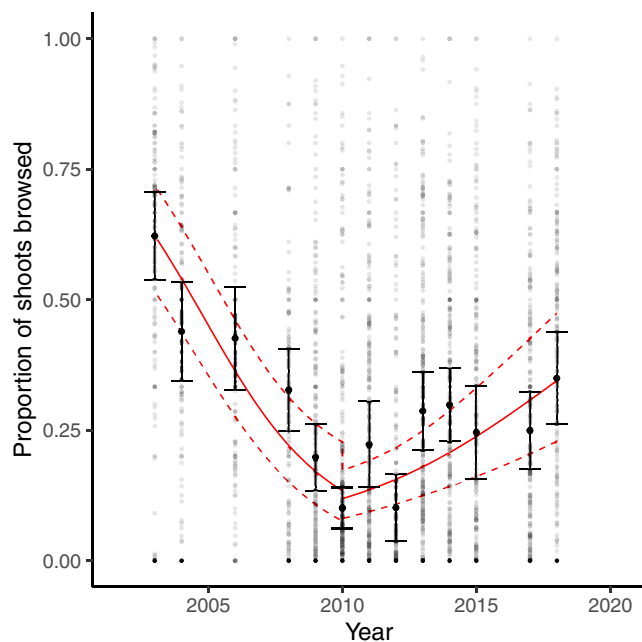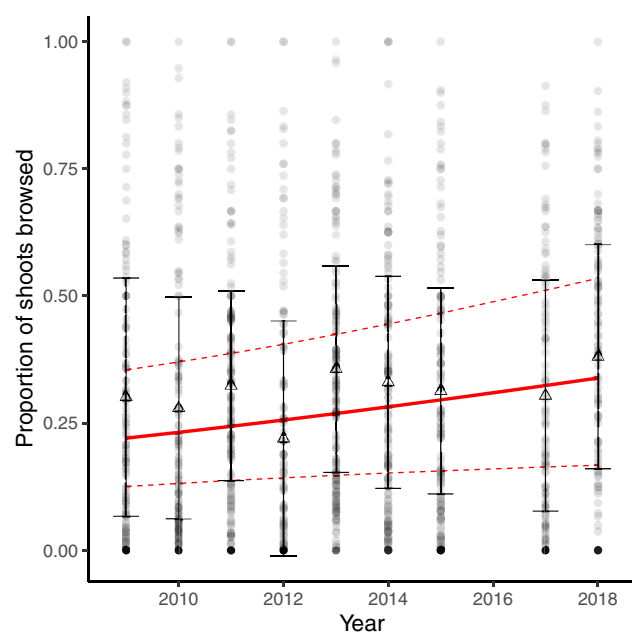
FIGURE 11 Predicted fall heights of willows in 2020 at observational sites and experimental control plots. Horizontal lines are 95% equal-tailed Bayesian credible intervals. The vertical gray line is the mean of out-of-sample predictions of 2020 heights for observational and experimental controls; the vertical blue line is the mean of the marginal posterior distribution of 2020 height in the dammed and fenced plots in the experiment. Numbers in parentheses to the right of site names refer to site numbers in Figure 3.

failed to reverse the effects of their loss from the food web. This absence of reversal could be attributed to effects of slowly changing ecosystem conditions (i.e., "parameters" in the language of Beisner et al. (2003) that emerged while predators were absent from the food web. The elk–grassland state along the small stream network of the northern range in Yellowstone National Park bore the hallmark of an alternative stable state (Folke et al., 2004; Petraitis, 2013; Scheffer et al., 2001): a change in the food web caused the ecosystem to reconfigure to a new state characterized by dramatic shifts in plant communities, an altered disturbance regime, and long-lasting changes in the physical environment. Our experiment provides causal evidence that this alternative state has been stabilized by
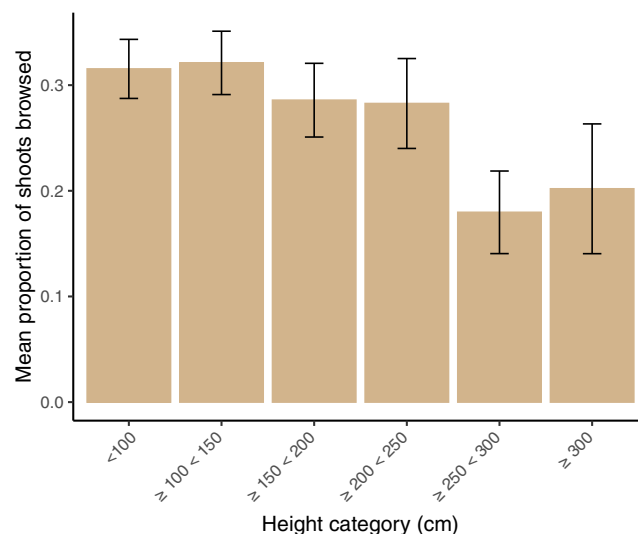
self-reinforcing changes in the hydrologic regime caused by the absence of engineering by beavers and continued effects of browsing by a reorganized community of large herbivores (Figure 8; also see Bilyeu et al., 2008; Marshall et al., 2013). The results of our analyses from observational sites amplify the central result of our experiment, that restoration of the beaver–willow state has been prevented by the interplay of top-down and bottom-up forces, that groundwater influences state transition, and that trophic feedbacks did not operate in a simple, linear fashion. Our results led us to reject the hypothesis that the effects of restoration of apex predators to the food web were reciprocal to the effects of their removal on Yellowstone's northern range (Figures 5 and 8).
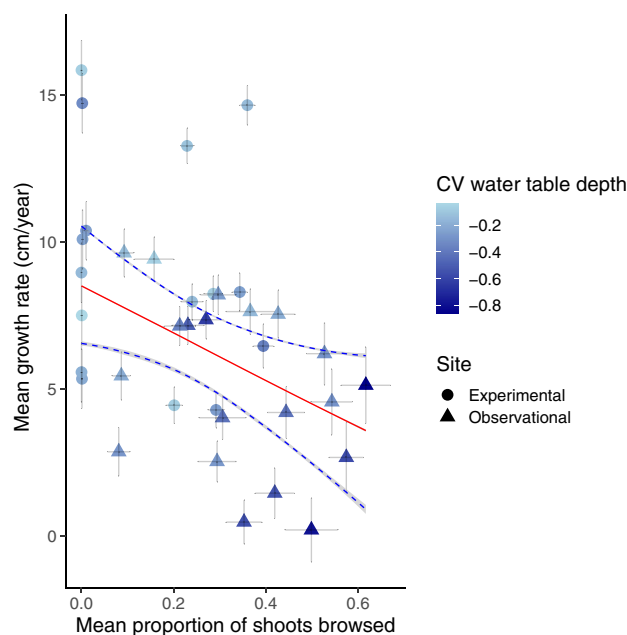
FIGURE 12 Out-of-sample predictions of the mean proportion of all shoots that were browsed (solid line) from willows on unfenced experimental plots. Dashed lines are 95% Bayesian credible intervals. Filled circles are the means of the observations; bars are two standard deviations of the distribution of the means. Grayed points are observations from individual plants.

FIGURE 14 Relationship between the proportion of shoots browsed and fall height of willows after 2011. We limited data to later years of the study to prevent confounding between declining elk numbers and increasing plant height. Vertical bars indicate ± two standard deviations of the mean.

FIGURE 13 Proportion of shoots browsed at observational sites and experimental controls. The solid line is the prediction at the mean of the posterior distribution of site intercepts and slopes. Dashed lines are 95% Bayesian credible intervals. Grayed points are observations of individual plants. Triangles are means of the data across sites and vertical bars are two standard deviations of the distribution of the mean.
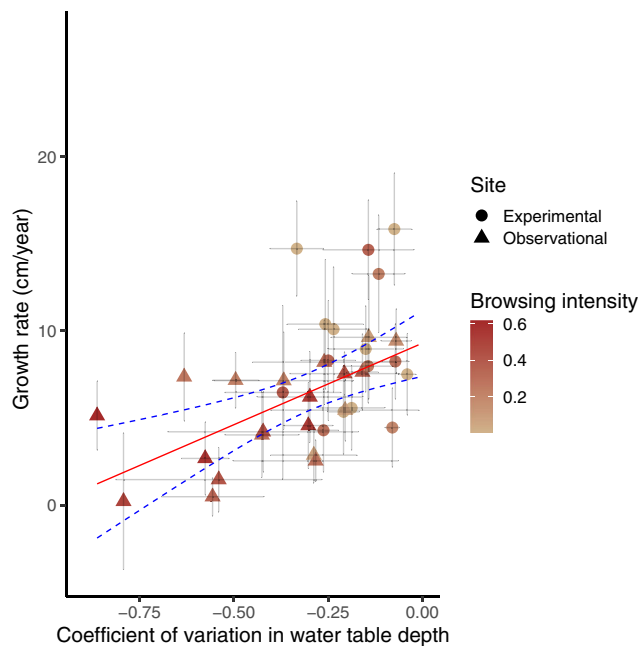

FIGURE 15 Relationship between 20-year growth rates (the time slopes in the regression of height on time) and the 20-year average proportion of stems browsed at experimental and observational sites. The solid line is the out-of-sample prediction of the mean growth rate. Dashed lines are 95% Bayesian credible intervals on the predicted mean. Vertical lines show the standard deviation of the marginal posterior distribution of the mean growth rate. Horizontal lines show two standard deviations of the observed mean proportion of stems browsed.

TABLE 2 Parameters in univariate and multivariate regression of willow growth rates (in centimeters per year) on browsing intensity (Figure 15) and the coefficient of variation in water table depth (Figure 16).

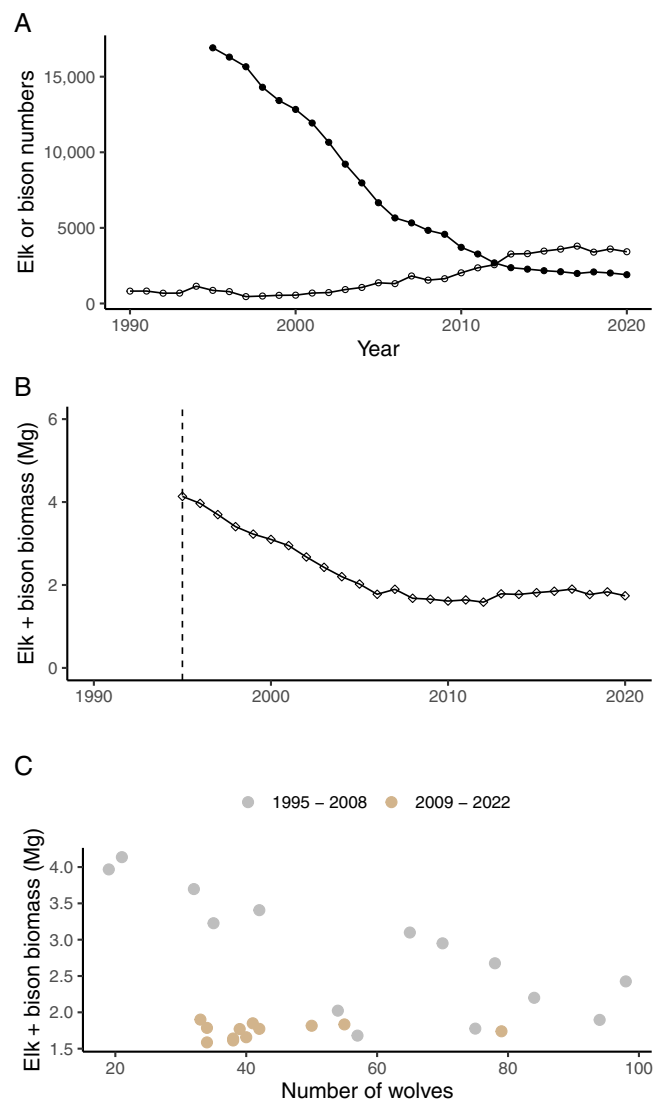| Model and parameter	Mean	SD	2.5%	97.5%	Pr(0 ∉)
Univariate browsing model					
Intercept	8.51	1.01	6.55	10.5	1
Browsing slope	−8	3.19	−14.4	−1.75	0.994
Univariate water table model					
Intercept	9.26	0.961	7.36	11.2	1
Water table CV slope	9.27	2.63	3.99	14.4	0.999
Multivariate browsing and water table model					
Intercept	6.37	0.639	5.18	7.7	1
Browsing slope	−0.607	0.698	−2.03	0.709	0.81
Water table CV slope	2.03	0.922	0.0988	3.75	0.98
Interaction	−0.314	0.816	−1.78	1.41	0.331

Note: The predictor variables were not standardized in the univariate regressions. Predictor variables were standardized in the multivariate regressions to allow comparison of the relative influence of the predictor variable on growth rate. SD is the standard deviation of the marginal posterior distribution of the mean; 2.5% and 97.5% give upper and lower, equal-tailed Bayesian credible limits. Pr(0 ∉) is the probability that the posterior distribution of the parameter does not include zero. There was no evidence of correlation (=0.58) in the predictor variables in the multivariate model.

FIGURE 16 Relationship between 20-year mean growth rates (the time slopes in the regression of height on time) at observational and experimental sites in relation to 20-year coefficients of variation in water table depth (standard deviation of water table depth/mean water table depth, where deeper water tables are more negative). The solid line is the out-of-sample prediction of the mean growth rate. Dashed lines are 95% Bayesian credible intervals on the predicted mean. Vertical lines show two standard deviations of the marginal posterior distribution of the mean growth rate. Horizontal lines show two standard deviations of the observed mean coefficient of variation in water table depth.

The heights of willows in the experimental controls and observational sites averaged 178 cm in 2020 (Figure 11). The mature height of the species of willows we studied can easily exceed 400 cm under favorable growing conditions (Peterson et al., 2020). A widely suggested threshold for restoration of woody deciduous plant communities is that plants exceed 200 cm in height (Kay, 1990; Keigley & Frisina, 1998; Ripple & Beschta, 2007), ostensibly because plants taller than 200 cm may not be subject to browsing on their upper branches. Our observations suggest this threshold may be too low (Figure 14). Browsing intensity did not decline until plants reached ~250 cm. This finding was consistent with Brice et al. (2022) who found that the height of negligible browsing on aspen (*Populus tremuloides*) exceeded 300 cm. We conclude that the mean height of willows 25 years after wolves were reintroduced and other carnivore populations recovered remains well below the heights that would reasonably be expected in a restored community.
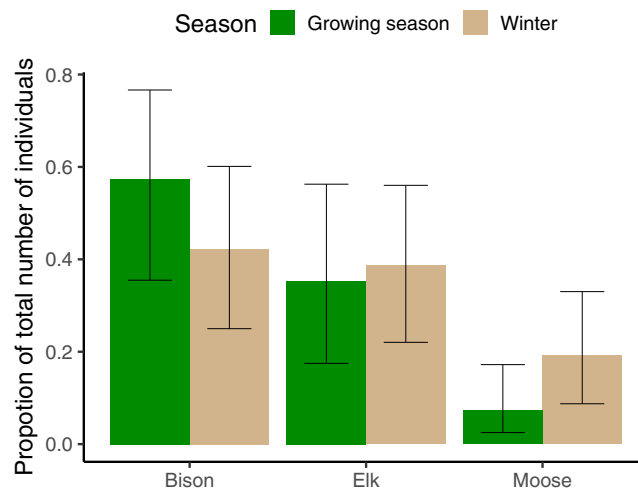
It might be argued that the positive growth rates observed in the experimental controls provide evidence of reciprocal effects of restoration of apex predators because willows did not grow at all before their restoration, so any growth could be interpreted as a state change (Beschta & Ripple, 2016). However, this argument depends on untenable anecdotes that the growth of willows before the 1990s was zero. Some level of positive growth in the controls is the proper null model; willows have evolved to grow tall and there were tall willows on the northern range before the large carnivore guild was

FIGURE 18 Proportion of the total number of individuals of ungulate species observed in camera traps during winter (October–April) and the growing season (May–September) 2013–2016. Vertical lines give 95% Bayesian credible intervals.

FIGURE 17 (A) Changes in elk and bison population size on the northern range within Yellowstone National Park from 1990 to 2020 (open circles = bison, closed circles = elk). (B) The corresponding change in elk + bison biomass. The dashed vertical line shows the year that the gray wolf was reintroduced to the northern range. (C) The relationship between elk + bison biomass and numbers of wolves on the northern range.

restored (Singer et al., 1994). The operative question about the stability of the alternative, elk–grassland state is not "Did willows grow at all after the restoration of apex predators?" but rather "Did willows grow as rapidly as they would have grown if the willow–beaver state had been restored by predator restoration?" Our experimental results provide an unambiguous answer to this question: the loss of hydrologic engineering by beavers on small streams and persistent browsing continue to suppress willow growth in the northern range (Figures 8 and 10).
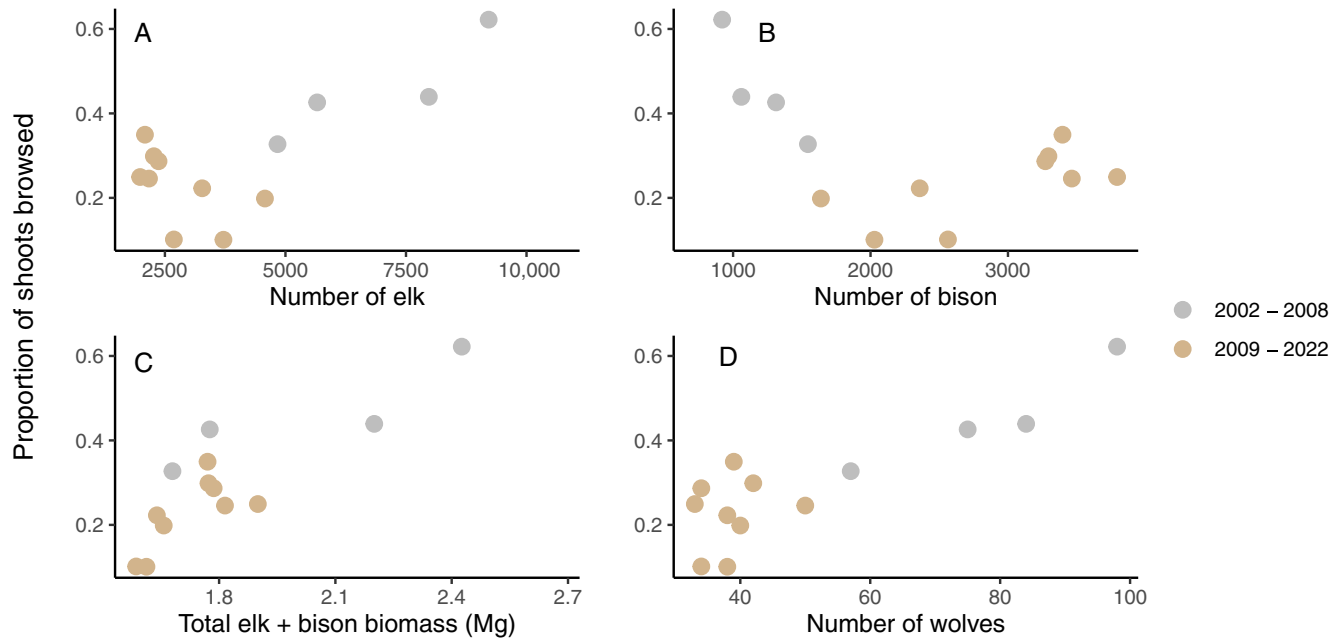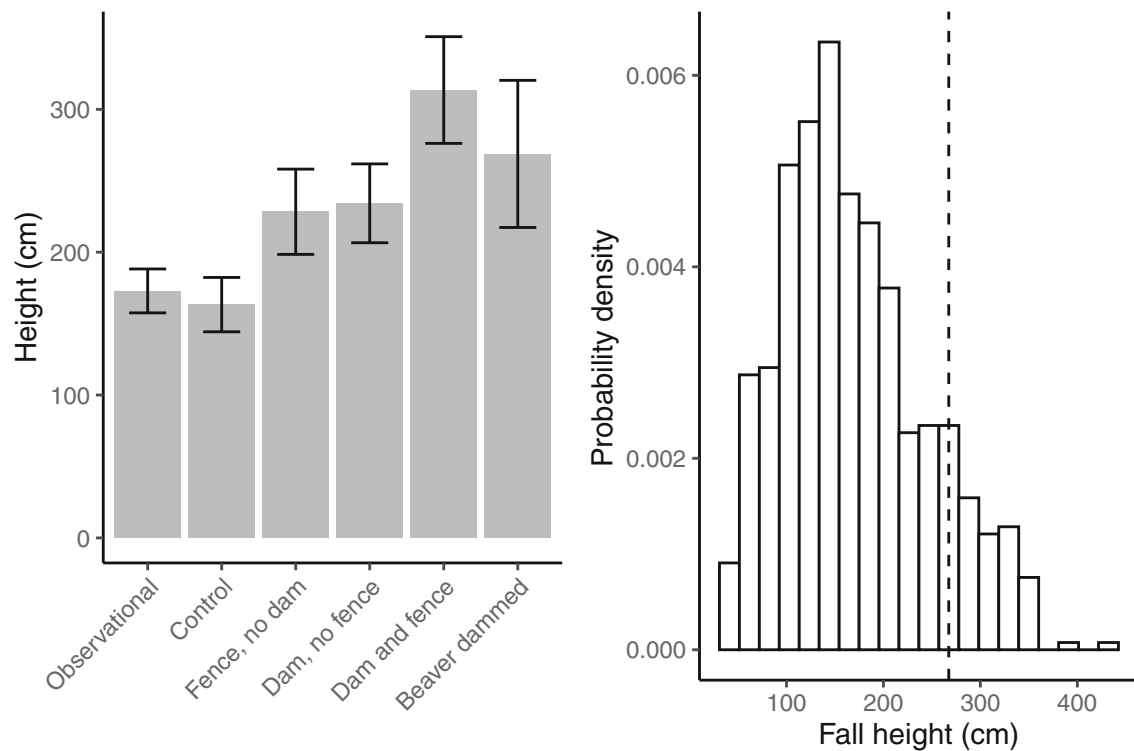
It could also be argued that state change is simply a matter of time scale, that willows are in the "early stages

of recovery" (Beschta & Ripple, 2016), decades after large carnivores were restored to the system. It may be that slow but positive growth rates observed in the experimental controls and observational sites might eventually allow willows to recover height to match current heights in the dammed-fenced plots. This would require an additional 40 years of growth, if the current linear rates of growth are predictive (Figure 10). We cannot rule out this potential trajectory. Nor is it possible to rule out several alternative trajectories:

1. A linear model fit of the data on willow height over time with no indication of decelerating growth rates. However, there is reason to believe that growth rates of willows on the northern range may decline to zero in the future. Willows in control plots had smaller leaves, smaller shoots, more branch junctions, and lower annual growth rates than willows in the dammed, fenced plots (Johnston et al., 2007). The smaller shoots that grew on these willows lacked the ability to transport water efficiently to support the subsequent year's growth. There is a natural progression of declining annual growth as the difficulty of transporting water to the plant's apex increases, as woody plants approach their final height (Ryan & Yoder, 1997). This happens because the wood of each subsequent year is appended to prior growth, resulting in an unavoidable drop in hydraulic connectivity. Annual declines in shoot size and hydraulic connectivity occur more quickly in locations of higher water stress, limiting the final height a plant can attain (Ryan & Yoder, 1997).

FIGURE 19 Browsing intensity measured as the mean proportion of shoots browsed at observational sites and control plots at experimental sites in relation to (A) numbers of elk, (B) numbers of bison, (C) combined biomass of elk and bison, and (D) numbers of wolves on the northern range in 2002–2018. Elk + bison biomass decline stopped in 2008.

FIGURE 20 Mean heights of willows on sites with active dam and lodge building by beavers relative to heights of willows in the experiment and at observational sites (left panel). Vertical bars indicate two standard deviations of the distribution of the mean. Histogram of heights of willows on observational sites and experimental controls in 2016–2019 (right panel). The vertical line shows the mean height of willows at sites with active disturbance by beavers. Sites with beaver activity ($n = 3$) were established during the year after dams were built and were not part of the original sample of observational sites.

2. The future of the herbivore community is unknown, but we show that ungulate biomass and browsing intensity are increasing (Figures 12, 13 and 17C). The composition of the community is also changing. Our camera trap data and Yellowstone National Park counts of elk and bison point to dramatically increased importance of bison as herbivores in the northern range. A trajectory that cannot be eliminated from the possible alternatives is the a reset to a short-stature willow state as a result of increases in herbivory by bison. In addition, moose are becoming more abundant on the northern range and are willow herbivory specialists, particularly in summer.

3. A severe winter that causes increased browsing (Creel & Christianson, 2009) could reduce the height of willows, reversing height gains that accrued over many years.

4. Finally, it remains unknown whether the recent dam building by beavers on some streams can be sustained without landscape-wide increases in willow height. Dam building by beavers outside the park where bison are absent has increased far more rapidly over the last two decades than dam building within the park (Tyers, 2020). Inside the park, beavers persisted on Elk Creek for only 1–2 years, on Blacktail Deer Creek north of the park highway for only 2 years, and on Crystal Creek for 3–5 years before abandoning our study sites. The beavers on Crystal Creek moved up the drainage to an aspen grove. The loss of beaver activity at all of these sites appeared to be caused by an insufficient quantity of willows of suitable sizes after the sites were occupied for a few years.

The willow–beaver state may not return to the northern range, even in the fullness of time. Entire stands of willow died in the early to middle decades of the 20th century as a result of excessive browsing (Chadde & Kay, 1991; Peterson et al., 2020). These stands were replaced by grasslands where it is virtually impossible for willow to establish and grow (Painter et al., 2014). Although the future state of the northern range is uncertain, our results make clear that the current state does not resemble the state that prevailed before large carnivores were extirpated from the northern range.

Spatial scale is important to the interpretation of forces stabilizing alternative states (Petraitis, 2013). Spatial scale and spatial variation are inseparable ecological concepts (Hobbs, 2003; Palmer & White, 1994; Ritchie, 2010). Our observational studies were conducted at a sufficiently broad spatial scale and for a sufficiently long time to reveal enormous variability in willow growth. It is clear from this long-term, large-area data set that brief studies conducted at a small number of locations could reveal all possible patterns in willow growth: rapid positive increments, no change, or steep declines. This also means that individual patches could be accurately characterized as "tall willows," resembling those in the willow–beaver state. There are examples of these in our data (also see Painter et al., 2014; Singer et al., 1994). It is too easy for human perception unaided by broad-scale observations to see these localized examples as proof that the state of riparian communities has changed dramatically across the entire range. Inference from spatially extensive, statistically reliable samples shows otherwise.

Comparison with other studies of willows in the northern range

Others have studied willow growth in the northern range and it was important that we compared our findings to theirs. The results of Beyer et al. (2007) offered correlational evidence of the reciprocal effects of wolf restoration. Beyer and colleagues used growth ring analysis to make inference on stem diameter growth rates of willows, finding increased rates of growth in the 5 years following wolf restoration relative to the previous 5 years. This increase could not be explained with weather and hydrologic variables alone. However, it should be noted that the mid-1990s, when wolves were reintroduced, had the highest snowpack and stream flows on record. This led to the most significant cottonwood recruitment events of the 20th century on the Lamar River and other streams, and probably stimulated higher willow growth due to increased water availability (Rose & Cooper, 2017). Moreover, half of the sites studied by Beyer et al. were on streams too large to be dammed by beaver, so they would not be expected to be influenced by effects of changes in the hydrologic regime experienced on the smaller streams. The conclusions of Beyer et al. agreed with a similar study conducted by Marshall et al. (2014): trophic, topographic, hydrologic, and climatic variables acted together to explain changes in growth ring area through time. Marshall et al. (2014) inferred that "... changes in growth of woody deciduous plants following the reintroduction of wolves cannot be explained by the trophic cascade model alone." The conclusions of Beyer et al. (2007) and Marshall et al. (2014) aligned with our findings (Table 2) that hydrology and browsing act together to limit willow growth.

Tercek et al. (2010) arrived at similar conclusions, explaining spatial variation in willow height on the basis of resource limitation. Tall willows grew on sites with greater water availability, more rapid net soil nitrogen mineralization, greater snow depth, lower soil respiration

rates, and cooler summer soil temperatures than sites with short willows. Tercek et al. concluded that bottom-up forces shaped the response of willows to reduced browsing where it occurred. These findings are consistent with the theory of water transport limitations to tree height (Ryan & Yoder, 1997) as well as willow morphology observed in our experimental sites (Bilyeu et al., 2008; Johnston et al., 2007). We also found that heights of willows on observational sites were well predicted by use of groundwater (Johnston et al., 2011).

Singer et al. (1994) studied willow heights at 15 sites in 1990–1994. We previously compared (Marshall et al., 2013) the willow height distributions of our data to the pre-wolf data. However, the characteristics of the Singer et al. sites were different from our experimental and observational sites being located predominantly along rivers and streams too large to be dammed by beavers, so we would not expect their hydrologic regime to have changed as a result of beaver abandonment. Two of the sites were at substantially higher elevations than the elevation of our sites. Most importantly, we discovered recently that the Singer et al. protocol for measuring willow height differed fundamentally from ours: they measured the height of the tallest willow in a stand rather than a random sample of heights. This caused problems for reliable inference on range-wide heights (Brice et al., 2022). Singer et al. did find results for browsing similar to ours, with high levels of annual variation and the proportion of stems browsed ranging from 32% to 59%.

Painter et al. (2014) revisited seven of the sites studied by Singer et al. (1994) and concluded that the mean heights of willows at the end of the growing season increased by approximately 100 cm over the nearly three decades since the Singer measurements (Painter et al., 2014; Figure 3A). This translates to a mean growth rate of ~4 cm per year, well within the credible intervals of the growth rates we observed for observational sites and experimental controls (Figure 10). Painter also found evidence that some patches grew tall (>300 cm); which is consistent with our observations of high spatial variability in willow heights, particularly where groundwater subsidies from adjacent hillslopes maintained water availability.
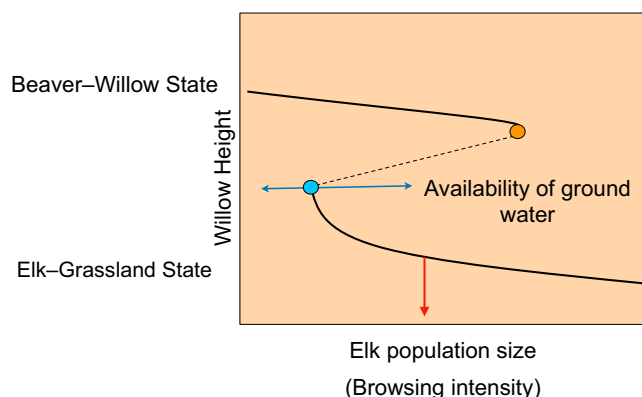
One result presented by Painter et al. (2014) confirmed our finding that changes in hydrology and continued browsing pressure have stabilized the alternative elk–grassland state. The researchers compared the heights of willows in meadows in 2017 with heights at approximately the same locations before wolves were introduced. They found no evidence of any change in height. Willow heights remained <50 cm, a finding that Painter et al. attributed to the suppression of growth by browsing. We agree that browsing is likely to be part of the cause, but we also surmise that limited access to groundwater was partially responsible for height suppression. The loss of beaver activity from small streams that were historically present at these sites is why these willows are now found in meadows. Willows do not naturally establish in meadows because they require bare and wet mineral substrate for seed germination and their hydrophilic growth requirements mean that they must establish along dynamic streams (Wolf et al., 2007). The conversion of the willow–beaver state to the elk–grassland state was manifest by the conversion of riparian corridors with beaver activity to meadows that have lacked beaver activity in many areas of Yellowstone (Houston, 1982, appendix V).

Other workers measured height change in willows on the northern range and concluded that reintroduction of wolves to Yellowstone restored willow communities via a trophic cascade (Beschta & Ripple, 2010, 2016; Ripple & Beschta, 2006). How can these starkly different conclusions be reconciled with the findings reported here? The studies of Ripple and Beschta were limited in spatial and temporal extent. Ripple and Beschta used a nonrandom sampling design biased toward plants that had the best access to groundwater at their sample sites (Johnston et al., 2011). Their design exaggerated the indirect effect of predators on woody deciduous plants (Brice et al., 2022) and failed to allow inference to the population of willow heights on the northern range (Ripple & Beschta, 2006). Many of their study sites were in riparian zones of large rivers that did not experience a state change resulting from the loss of engineering by beavers (Ripple & Beschta, 2006). Thus, it is not surprising that nonrandom sampling at a few sites over a few years produced results that differed from ours. Moreover, Beschta and Ripple (2016) misrepresented the findings of other studies (Bilyeu et al., 2008; Johnston et al., 2011; Marshall et al., 2013) in support of the trophic cascade idea. For example, Marshall et al. (2013) concluded "The 70-year absence of predators from the ecosystem changed the disturbance regime in a way that was not reversed by predator reintroduction. We conclude that predator restoration may not quickly repair effects of predator removal in ecosystems," a conclusion that was ignored in the selective-citation of evidence from Marshall et al. (2013) in Beschta and Ripple (2016).

Implications for ecological theory and conservation practice

Our work contributes a new, compelling example (Figure 21) of hysteresis in ecosystems, "the condition of more than one stable state" (Scheffer & Carpenter, 2003,

FIGURE 21 The small stream network of Yellowstone's northern range following the restoration of apex predators demonstrates hysteresis because a slowly changing environmental variable, stream incision that reduced availability of groundwater, prevented the elk–grassland state from reverting to the elk–beaver state when browsing pressure was reduced in response to predation-induced reductions herbivore biomass. Thus, the system failed to return to the beaver–willow state via the pathway that led to the alternative state, the loss of the apex predator guild. The movement of the system to the right of the orange point illustrates the state change that occurred in the absence of apex predators. Herbivore biomass must move to the left of the blue point to return to the originating state. Availability of groundwater controls the strength of hysteresis, shifting the threshold for restoration (the blue dot) to the right with high availability of groundwater and shifting it to the left with low availability of groundwater. Sufficiently high levels of browsing by a reorganized guild of large herbivores that are not subject to predation by large carnivores, illustrated by the red arrow, could prevent the return to the beaver–willow state despite predator restoration.

p. 651) where slowly changing conditions in the ecosystem (Figures 1 and 2) prevent the return of the alternative to the original state along the pathway that led to the initial state transition. We show with experimental and observational evidence that the elk–grassland state is stabilized by the interplay of browsing intensity controlled by elk population size (a rapidly changing state variable; sensu Beisner et al., 2003) and reduced availability of groundwater due to stream incision and the absence of engineering by beavers (a slowly changing parameter, sensu Beisner et al., 2003). The continued shift in the composition of the herbivore community toward dominance by bison that are not vulnerable to predation suggests that browsing pressure will continue to prevent return to the beaver–willow state. The biomass of large herbivores after 2008 was sufficiently high (Figure 17B) that browsing intensity (Figure 19C) will probably maintain the slow growth rates of willow (Figure 15).

Variable strength of hysteresis explains spatial variation in willow growth rates and heights across the landscape (Figures 10 and 11). Willows on sites with low coefficients of variation in groundwater grew relatively rapidly despite high browsing intensity (Figures 15 and 16). We surmise that the return to the beaver–willow state could occur at higher levels of browsing at those sites, moving the blue dot in Figure 21 to the right and weakening hysteresis. Our experiment showed that browsed willows in the dammed and unfenced plots could grow as rapidly as unbrowsed plants that were in fenced plots without dams (Figure 8C). Johnston et al. (2007) provided a mechanistic explanation for this result. Johnston et al. (2011) showed that access to groundwater explained spatial variation in willow heights, thereby explaining why willows might show local, patchy restoration where water availability is high, for example, in areas of groundwater seeps or along big rivers. These results also suggest that building simulated beaver dams as a management intervention could plausibly accelerate restoration of the beaver–willow state by providing a habitat suitable for rapid willow growth and by providing bare and wet sediments needed for willow establishment (Cooper et al., 2006; Pollock et al., 2014; Wohl, 2021). However, a reorganized guild of large herbivores may maintain browsing intensity at sufficiently high levels now and in the future (for example, at the red arrow in Figure 21) that conditions for return to the beaver–willow state simply do not exist (as in Petraitis, 2013; Figures 3–5).

A major impediment to developing and testing rigorous theory in ecology is that the meaning of terms such as trophic cascade and alternative stable state are used with increasing imprecision after the originating ideas were put forward. The events in Yellowstone following the reintroduction of wolves offer an example (Peterson et al., 2014). The original definition of a trophic cascade implied broad, lasting effects across an entire community, effects that were "pervasive," caused by "runaway consumption," creating "downward dominance through the food chain" so that removal of a predator, or presumably the addition of a predator after its absence, causes "precipitous change in the system" (Strong, 1992). Later Polis (1999) specified that "...a trophic cascade occurs when changes in carnivore abundance alter the distribution and abundance of plants on a community-wide basis." The definition was expanded to include the indirect effects of carnivores on individual plant species (Schmitz et al., 2000) and made broader still to include any "indirect species interactions that originate with predators and spread downward through food webs" (Ripple et al., 2016).

The concept has become so broad that virtually any indirect effect of carnivores on plants, no matter how localized or transient, can be cited as evidence for a

trophic cascade. Most of the evidence supporting claims of indirect effects of restored predators on plants in willow communities on the northern range has been restricted to a small number of sites chosen without randomization, obtained over brief intervals of time, and analyzed without appropriate random effects (Beschta & Ripple, 2007, 2016; Ripple & Beschta, 2006, but also see Beyer et al., 2007; Marshall et al., 2014). This evidence might support site-specific, transient effects of predators on plants, but the evidence fails to support the conclusion of widespread, enduring changes in willow communities caused by predator restoration. Instead, the increase in browsing intensity and ungulate biomass from 2010 to 2020 after a long period of decline (Figures 12, 13 and 17B) implies that the forces shaping the trajectory of the ecosystem are more accurately characterized as transient dynamics (Frank et al., 2011; Hastings et al., 2018; Neubert et al., 2004; Shriver et al., 2019) than a trophic cascade.

We contend that demonstrating a trophic cascade with reciprocal effects on the ecosystem requires showing that the replacement of a predator to the food web caused a persistent, "pervasive" (sensu Strong, 1992) reduction in herbivore biomass or a change in herbivore feeding behavior that allowed a demonstrable, system-wide increase in height, biomass or productivity of willows relative to what would have been seen if the predator had not been replaced. Our experiment and observational studies show conclusively that willows have not grown nearly as rapidly as would be expected if the beaver–willow state had been restored and have not reached heights that are widely viewed as a threshold for restoration. It is clear that wolves alone did not cause a lasting reduction in herbivory that has benefited plants because human harvest, other predators, and serial drought were responsible, at least in part, for declines in elk abundance (MacNulty et al., 2020; Peterson et al., 2014; Vucetich et al., 2005) and because the community of large herbivores has reorganized that such herbivore biomass remains high and is increasing (Figure 17B). It has become clear that there is no credible evidence for behaviorally mediated, indirect effects of wolves on plants in Yellowstone (Creel & Christianson, 2009; Cusack et al., 2020; Kauffman et al., 2010; Kohl et al., 2018; Stahler & MacNulty, 2020), an empirical result well anticipated by theory (Schmitz, 2010). We conclude that the restoration of apex predators to Yellowstone should no longer be held up as evidence of a trophic cascade in riparian plant communities of small streams on the northern range.

What about the theory of alternative stable states? Our work reinforces the predictions of theory (Folke et al., 2004) that ecosystem states that emerge after the alteration of food webs can persist even when the food web is reconfigured to its original condition. A shift between alternative stable states requires evidence of a change from one basin of attraction to another across an entire ecosystem, a change that is relatively abrupt in time (Petraitis, 2013). The "History" section above suggests that tall willows were eliminated within two decades of the loss of predators from the northern range. An "abrupt" change to tall willows across the northern range should occur in approximately the same amount of time. The gradual change in the system over many decades is not evidence of a change between stable states. If it were, then plant succession would qualify as a regime shift. Change in isolated patches within the ecosystem (e.g., Painter et al., 2014) should not be viewed as evidence of a state change, but rather as expected spatial and temporal variation, which we have shown to be important (Figure 10).

These results have important implications for the conservation of the world's large carnivores. Claims of ecosystem restoration resulting from a trophic cascade following the restoration of the gray wolf to Yellowstone (e.g., Beschta & Ripple, 2009, 2010; Ripple & Beschta, 2004, 2006, 2007; Ripple & Beschta, 2012; Ripple et al., 2014) have been used to justify translocation of wolves to their unoccupied, former range in many areas of the world (e.g., McKee, 2019; McKenna, 2018; Mooney, 2019; Oregonian Staff, 2019; Weiss et al., 2007). Careful scrutiny has revealed these claims to be exaggerated or false (Bilyeu et al., 2008; Brice et al., 2022; Creel & Christianson, 2009; Cusack et al., 2020; Johnston et al., 2011; Kauffman et al., 2010; Marshall et al., 2013; Stahler & MacNulty, 2020; Winnie, 2012, this study). Confronting ideas with evidence is, of course, the way science moves forward. However, it is difficult if not impossible to correct inaccurate claims promoted in the popular media (reviewed by Marris, 2017; Mech, 2012) that wrongly influence conservation management and policy, as well as the perceptions of the public. There are good reasons to restore apex predators to food webs (Phillips, 2020), but rapid ecosystem restoration cannot be assured among them (Allen et al., 2017; Brice et al., 2022; this study). The promotion of ecosystem restoration by restoring apex predators suggests there is a "quick fix" for losing them from food webs. We have shown that the ecosystem state that emerged following the loss of large carnivores from the food web resisted reversal after they were restored. It is clear that maintaining the ecosystem services of large carnivores by preventing their extirpation may be a more successful strategy than trying to restore those services after a long absence of apex predators from the food web.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Cooper & Hobbs, 2023a) are available in Dryad at https://doi.org/10.5061/dryad.sqv9s4n7n. Code (Cooper & Hobbs, 2023b) is available in Zenodo at https://doi.org/10.5281/zenodo.8417500.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.