ECOLOGY

Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers

Thomas D. Gable[1]*, Sean M. Johnson-Bice[2], Austin T. Homkes[1], Steve K. Windels[1,3], Joseph K. Bump[1]

Gray wolves are a premier example of how predators can transform ecosystems through trophic cascades. However, whether wolves change ecosystems as drastically as previously suggested has been increasingly questioned. We demonstrate how wolves alter wetland creation and recolonization by killing dispersing beavers. Beavers are ecosystem engineers that generate most wetland creation throughout boreal ecosystems. By studying beaver pond creation and recolonization patterns coupled with wolf predation on beavers, we determined that 84% of newly created and recolonized beaver ponds remained occupied until the fall, whereas 0% of newly created and recolonized ponds remained active after a wolf killed the dispersing beaver that colonized that pond. By affecting where and when beavers engineer ecosystems, wolves alter all of the ecological processes (e.g., water storage, nutrient cycling, and forest succession) that occur due to beaver-created impoundments. Our study demonstrates how predators have an outsized effect on ecosystems when they kill ecosystem engineers.

INTRODUCTION

Apex predators can directly and indirectly affect the behavior, spatial distribution, and abundance of prey populations, which may create cascading effects through lower trophic levels (1) and ultimately alter ecosystem processes such as energy flow and nutrient cycling (2, 3). Large predators are thought to have outsized ecological effects primarily by reducing the abundance of their prey (i.e., density-mediated) or by altering the behavior of their prey via fear (i.e., behaviorally mediated)—both of which can indirectly affect lower trophic levels via trophic cascades (4–6). For example, orcas (*Orcinus orca*) reduce sea otter (*Enhydra lutris*) abundance, which has cascading effects on kelp forest communities (density-mediated trophic cascade) (7), while hawks (*Accipiter* spp.) alter the foraging behavior of jays (*Amphelocoma wollweberi*), which increases the breeding success of hummingbirds (*Archilochus alexandri*) (behaviorally mediated trophic cascade) (8). Quantifying the ecological impact of predators is valuable for understanding the functional role of predation in ecosystems and how that role changes in the face of anthropogenic factors that negatively influence large predator populations (e.g., habitat loss and fragmentation and climate change) (9). The ecological role of large predators and their purported ability to reshape entire ecosystems are frequently the primary justification for large predator conservation, restoration, and reintroduction (10, 11).

In North America, gray wolves (*Canis lupus*) are one of the premier examples of how large terrestrial predator populations can transform ecosystems through trophic cascades, although the extent to whether the mechanism is density- or behaviorally mediated is debated (5, 11, 12). Many have suggested that wolf-induced trophic cascades are the result of a landscape of fear (behaviorally mediated), whereby wolves alter the spatial and temporal distribution of ungulate prey by instilling fear (13, 14). In northern Yellowstone National Park, USA, the primary study site of the wolf–trophic cascade litera-

ture (6), the landscape of fear has supposedly led to pronounced changes in the duration, location, and intensity of ungulate browsing (13–15). Cumulatively, these changes were thought to reduce ungulate over-browsing in riparian areas, which led to increases in wildlife populations [e.g., songbirds and beavers (*Castor canadensis*)] dependent on riparian vegetation (5, 14). Further, the subsequent regrowth of riparian vegetation reduced erosion and ultimately affected the morphology and hydrology of streams by stabilizing stream banks (16–18). This proposed ecological cascade—which was popularized in the online video "How Wolves Change Rivers," viewed more than 42 million times at the time of writing—has been used to garner support for, and justify the conservation and recovery of, wolf populations worldwide (11, 19). However, whether wolves have the capacity to alter ecosystems as drastically as suggested has been increasingly questioned and criticized (6, 11, 19, 20). Moreover, recent research suggests that wolves primarily affect ecosystems through direct predation rather than indirectly through a landscape of fear (15, 21).

Compared to the substantial dossier of Yellowstone research, relatively few studies have examined how wolf predation in boreal ecosystems—about 17% of Earth's land surface area (22)—affects lower trophic levels and ecosystem processes (23). Wolves in boreal ecosystems rely on a different prey base than wolves in more arid, mountainous regions of North America (e.g., Greater Yellowstone Ecosystem). Wolves in boreal ecosystems generally rely, in part, on beavers during the summer for food (24). Because beavers are ecosystem engineers that markedly alter ecosystems (Table 1) by damming waterways and creating impoundments that can persist for centuries (25–27), there is potential for wolves to affect large-scale ecological processes through predation on beavers. For wolves to have such an effect, they would likely have to either (i) decrease beaver, and therefore impoundment, densities through predation (i.e., reducing survival and reproduction); (ii) kill dispersing beavers, thereby altering the spatial and temporal distribution of newly created or recolonized beaver impoundments; (iii) kill certain beaver colony members (e.g., breeding individuals) that lead to increased colony abandonment and consequently, pond/dam failure (28); or (iv) alter the foraging or pond-creating behavior of beavers via a landscape of fear [i.e., nonconsumptive risk effects; (29)]. Given that both wolves

[1]Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, St. Paul, MN 55801, USA. [2]Department of Biological Sciences, University of Manitoba, 50 Sifton Road, Winnipeg, Manitoba R3T 2N2, Canada. [3]Voyageurs National Park, 360 Highway 11 E, International Falls, MN 56649, USA.
*Corresponding author. Email: thomasd.gable@gmail.com

Table 1. Summary of the ecological benefits that ecosystem engineering by beavers creates in wetland and riparian ecosystems. All values (e.g., 200% greater, 2× higher) are in relation to reference (unmodified) sites sampled from the same study or are in relation to sampled characteristics before ecosystem engineering by beaver. Although beavers can have deleterious (or no) effects on ecosystems, we focus on the ecological benefits here for simplicity.

Ecological benefits	Description of benefits due to ecosystem engineering by beavers
Ecosystem services	
Water runoff attenuation	Reduce peak stream discharge 30–100% (*67, 68*); increase water residence time up to 230% (*69*)
Groundwater recharge	Stabilize and even elevate groundwater levels (*70–72*)
Water purification	Greater pH values, acid-neutralizing capacity in ponds (*73–75*)
Sediment deposition	Sedimentation rates up to 0.28 m year^{-1} and 171 m^3 year^{-1}; up to 2000–6500 m^3 total sediment (*76–78*)
Carbon (C) sequestration	Sequester and deposit C within sediment layers (*79*); up to 200% greater C storage (*80*)
Nitrogen (N) sequestration	Increase N soil concentration up to 72% (*81*); remove 5–45% of watershed N loading (*82*)
Habitat alterations	
Stream geomorphology	
Reduce incision	Restore incised stream systems (*83, 84*)
Channels and pools	Increase channel diversity (*49, 85*); increase number (up to 1.4×) and depth (up to 1.6×) of pools (*86*)
Habitat heterogeneity	Increase habitat heterogeneity at local (site) (*87*), stream (*88*), and landscape (*84*) scales
Water storage	Increase area of surface water on landscape up to 9× (*89*); store 2.5–11 km^3 of water globally (*44*)
Benefits to plants and animals	
Mitigate effects of climate	Pond water buffers against effects of temperature increase, drought for animals (*89*)
Wildlife	
Large mammals	Provide aquatic food resources and thermal cooling benefits (*90, 91*)
Semi-aquatic mammals	Provide den sites, shelter, and food resources (*92–94*); increased abundance and species richness (*95*)
Small mammals	Abundance 75–300% greater (*96, 97*)
Bats	Foraging activity and use of beaver ponds 4–8× greater (*98, 99*); up to 1/3 of roosts in ponds (*100*)
Raptors	83% of osprey (*Pandion haliaetus*) nests located in beaver ponds (*91*)
Waterfowl	Up to 3.4× greater species richness (*101*), 10× higher brood density (*102*), and 50× greater abundance (*103*)
Passerines	Species richness 1.3–2× greater (*104, 105*); provide essential snag tree cavities for nests (*106*)
Amphibians	Account for up to 81–100% of breeding sites (*107*); annual production can increase 1.2–23× (*108*)
Reptiles	Species richness up to 1.6× greater and species diversity 1.4× greater (*109*)
Fish	
Salmonids	Increase fish density up to 0.8/m, juvenile survival up to 52%, and production up to 175% (*86*)
Other species	Abundance up to 3× greater and species richness 1.2× greater (*52, 110*)
Invertebrates	
Aquatic	Species richness up to 1.25–1.4× (*111, 112*), biomass density 2–5× (*113*), and abundance 235% greater (*97*)
Terrestrial	Abundance up to 26–60% greater (*87, 97*)
Both	Pond succession influences community assemblages, increasing β-diversity at regional scale (*53*)
Plants	
Aquatic	Biomass density up to 20× greater (*112*); species richness and diversity increase with pond age (*114*)
Herbaceous	Increase species diversity up to 28% and species richness 33–93% (*115, 116*)
Undifferentiated	Increase cumulative (148%) and mean (46%) species richness (*117*)

and beavers are well studied and sympatric throughout most circumpolar boreal ecosystems, it is surprising that there is no information about how this apex predator–ecosystem engineer dynamic influences ecological processes (*28*). Here, we describe how wolves directly alter the persistence, and likely spatial distribution, of beaver ponds in a southern boreal ecosystem through predation on dispersing beavers. By affecting where and when beavers can engineer ecosystems, wolves alter all of the ecological processes (e.g., water storage, nutrient cycling, sediment deposition, and forest succession; Table 1) that beaver-created impoundments affect.

Study area

This research was conducted as part of the Voyageurs Wolf Project, a research project studying wolf-prey interactions in the Greater Voyageurs Ecosystem (GVE), which is a 1812-km² southern boreal ecosystem in northern Minnesota, USA (Fig. 1). The GVE (48°30′N, 92°50′W) borders Ontario, Canada to the north and the Boundary Waters Canoe Area Wilderness to the east. Voyageurs National Park constitutes the northern portion of the GVE, whereas the central and southern portions of the GVE are predominantly a mix of U.S. Forest Service, state-owned, and commercial forest land (30). The GVE is part of the Laurentian Mixed Forest Province and is typified by dense forests (coniferous, deciduous, and mixed) and abundant wetlands, lakes, and bogs interspersed with rocky outcrops and ridges from past glacial activity (31). Timber or wildlife harvest is not permitted in Voyageurs National Park but is common outside of the park. Annual precipitation varies relatively little in the GVE, with an average precipitation of 62 cm (43 cm rain and 19 cm snow) (32). Topographic relief is not substantial (maximum topographic relief is ~90 to 95 m; Fig. 1) throughout the GVE, but the mosaic of rock ridges, small draws, and lowlands provides ideal habitats for beavers to create dams that impound large areas (33).

The GVE has sustained a dense beaver population for >40 years with colony densities across the GVE generally >0.47 to 1.0 colonies/km² (34, 35). As a result, beavers have markedly altered the landscape of the GVE by creating dams and impounding waterways. For example, a total of 7175 beaver-created impoundments (both occupied and unoccupied) were visible from 2019 high-resolution aerial imagery of the GVE, and beavers have impounded ~13% of the terrestrial landscape of Voyageurs National Park (36). The beaver population has remained relatively stable for >30 years, suggesting that the population is at natural carrying capacity, although annual fluctuations in beaver population density do occur (34, 37).

The GVE has maintained high wolf densities (35 to 45 wolves/1000 km²) for >30 years (38–40) with wolf packs occupying the entirety of the GVE. White-tailed deer (*Odocoileus virginianus*) are the primary annual prey of wolves in the area. Beavers, because of their abundance, are important seasonal prey for wolves in the GVE, with beaver constituting up to 42% of wolf pack diets during the ice-free season (April to October) when beavers are vulnerable to predation (41). Predation of beavers is widespread among wolf packs despite variation in beaver density between wolf pack territories (41). For example, beaver constituted 33% of the ice-free season diet of a pack in the lowest beaver density area (0.47 colonies/km²) of the GVE (35). Although individual wolf packs can remove an estimated 38 to 42% of the beaver population within their territory, there is no evidence to suggest that wolves suppress or reduce beaver population densities in the GVE (28, 35).

MATERIALS AND METHODS

To assess the ecological effects of wolf predation on dispersing beavers, we (i) quantified wolf predation on dispersing beavers; (ii) estimated how wolf predation affects the creation, recolonization, and persistence of beaver ponds; and (iii) examined how wolf predation affects the number of ponds and volume of surface water stored in the GVE. To do so, we searched clusters of GPS locations (20-min fix interval) from GPS-collared wolves to locate where wolves killed dispersing beavers and to estimate kill rates of wolves on dispersing beavers. When wolves killed dispersing beavers that had recently
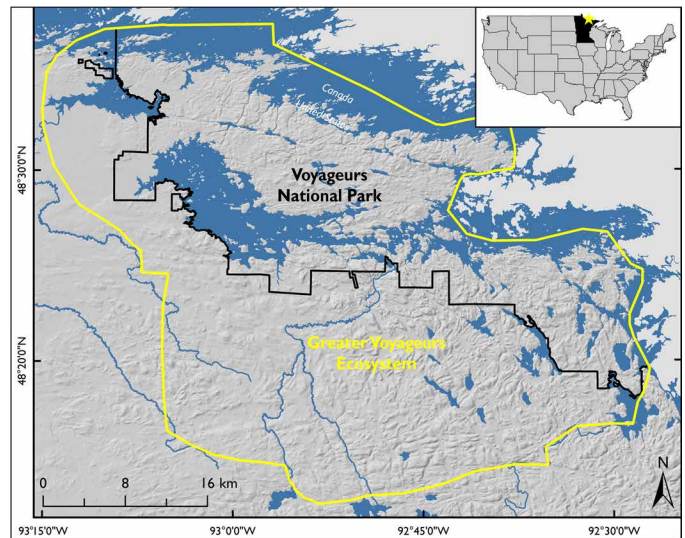

Fig. 1. Map of the GVE (yellow polygon) in northern Minnesota, USA, which is a 1812-km² southern boreal ecosystem (48°30′N, 92°50′W). Voyageurs National Park (black polygon) constitutes the northern portion of the GVE, whereas the central and southern portions of the GVE are predominantly U.S. Forest Service, state-owned, and commercial forest land. The GVE is typified by dense forests (coniferous, deciduous, and mixed) and abundant wetlands, lakes, and bogs interspersed with rock outcrops and ridges from past glacial activity. The GVE has sustained high densities of wolves (35 to 45 wolves/1000 km²) and beavers (>0.47 to 1 colony/km²) for >30 years.

settled in an area—as determined by a newly constructed dam or a repaired existing dam—we monitored the fate and occupancy of that pond annually both on foot and through aerial surveys. We compared the fate of these "wolf-altered ponds" (i.e., where a dispersing beaver created or recolonized a pond and was subsequently killed by a wolf) with newly established "reference ponds" (i.e., where a dispersing beaver created or recolonized a pond) to assess how wolves affected the creation, recolonization, and persistence of beaver ponds. To evaluate the ecological effects of this process, we estimated the number of ponds that wolves alter annually in the GVE by using mean wolf density in the GVE, kill rates of wolves on dispersing beavers that had recently created or recolonized ponds, and the mean number of ponds maintained by a beaver colony in the GVE. We then used bootstrapping to bound the uncertainty around our estimates and to describe how the number of beaver ponds altered by wolves would be expected to change with parameter variability (details below).

Clusters and kill rates

During 2015 to 2019, we captured 30 wolves and fit them with 20-min fix-interval GPS collars (Institutional Animal Care and Use Committee protocol: MWR_VOYA_WINDELS_WOLF). In 2015, two wolves were fitted with collars that took fixes every 4 to 12 hours [see (40) for more details]. We searched clusters of GPS locations from collared wolves during April to November to identify predation events. We considered a cluster to be ≥2 consecutive locations within a 200-m radius of one another (42). When at clusters, we systematically searched for evidence of a predation event (40). When we found remains of a wolf-killed beaver, we assessed whether the beaver was a colony beaver (i.e., associated with an established beaver

colony), a not-settled dispersing beaver (i.e., not associated with a colony or pond), or a settled dispersing beaver (i.e., associated with a recently created or recolonized dam/pond and occupying a wetland). Criteria used to classify a wolf-killed beaver in this way are outlined in Supplementary Materials and Methods. Because we were conservative in our assessment of what classified as a dispersing beaver and the status (settled versus not settled) of the disperser, we are confident that the beavers examined in our analysis were dispersing individuals. Because of our criteria, we likely excluded some dispersing beavers from our analysis. We used this information to estimate the percent of wolf-killed dispersing beavers that were settled when killed (denoted as $P_{settled}$ in the modeling approach described below).

We were only able to estimate kill rates of wolves on dispersing beavers (dispersing beavers per wolf per day) in 2018 and 2019, which is when we searched all clusters of GPS locations from 12 collared wolves. Individual kill rates were determined by dividing the number of dispersing beavers killed by a wolf in 2018 and 2019 by the number of days we searched clusters for that wolf. The mean kill rate (denoted as KR_{wolf} below) was assumed to be representative of the wolf population in the GVE for 2018 and 2019. We determined the total number of dispersing beavers a typical wolf would kill in the GVE by multiplying the kill rate by the typical number of days a year that beavers are available to wolves (213 days; average ice-free season, 1 April to 31 October) (beavers are rarely killed during winter months). We did not determine kill rates for wolves followed from 2015 to 2017 because we only searched a subset of GPS clusters, and there is currently no reliable method to extrapolate wolf kill rates of small prey in summer from only a subset of searched GPS clusters. We used a nonparametric bootstrap to construct percentile-based 95% confidence intervals (CIs) for our estimate of kill rate.

Beaver pond fate
To understand how wolf predation of recently settled dispersing beavers affected the persistence of newly created or recolonized ponds, we compared the fate of "wolf-altered" and "reference" ponds. Reference ponds were newly created or recolonized ponds (<6 months old) with fresh beaver activity. Specifically, we considered a reference pond to be either (i) a newly created impoundment that was >100 m from the nearest active pond and in habitat that had not been previously impounded by beavers based on aerial imagery and evidence at the impoundment (e.g., old cuttings and berm from an old dam) or (ii) a recolonized impoundment that had drained due to dam failure >1 year before being recolonized and was >500 m from the nearest active colony identified during the previous fall's aerial survey. We used these criteria to ensure that reference ponds were those established by dispersing beavers and not beaver colonies that simply moved a small distance up or downstream. Because of our criteria, which were conservative, we likely excluded ponds established by dispersing beavers from our analysis. Reference ponds were identified opportunistically on foot during May to September from 2015 to 2019 when searching clusters and conducting other fieldwork (we hiked >25,000 to 27,000 km in >15,000 hours of fieldwork over this 5-year period). Hence, reference ponds should be a representative sample of newly created or recolonized ponds and represent the fate of all newly created/recolonized ponds in the GVE during the study period. We used data from reference ponds to estimate the proportion of newly created or recolonized beaver ponds in the GVE that

remain occupied until fall of the year they are created or recolonized (denoted as P_{occ} below). Reference ponds could become inactive for a variety of reasons (e.g., secondary dispersal or death of disperser via predation, disease, or starvation), but we had no way to assess this. Still, it is likely that a certain, potentially substantial, proportion of reference pond failure is attributable to wolf predation.

We assessed the fate of wolf-altered and reference ponds using aerial surveys in mid-to-late October during 2015 to 2019 (see Supplementary Materials and Methods for details of aerial survey method). We also assessed the status of all wolf-altered ponds on foot 2 to 6 months after the predation event occurred, and reference ponds were visited multiple times per ice-free season. We quantified pond persistence by determining the percent of wolf-altered and reference ponds that remained active from the summer (May to September) until the fall aerial survey of that year. Further, we monitored the status of wolf-altered and reference ponds via fall aerial surveys in each subsequent year after the pond was colonized, which allowed a preliminary examination of the potential longer-term (1 to 4 years) effects of wolf predation on pond persistence and colonization.

Impact of wolf predation on pond creation and water storage
We then estimated how wolves affect annual beaver pond creation/recolonization and surface water storage in the GVE. Our general approach was to estimate the number of ponds altered per year (*PA*) by wolves by estimating the number of ponds that would have been created or recolonized by dispersing beavers had they not been killed by wolves. Specifically, we first estimated the total number of dispersing beavers killed by wolves per year in the GVE, then determined what proportion of those wolf-killed dispersers had started creating or recolonizing ponds, and from there estimated the number of ponds (*PA*) those dispersers would have created or recolonized had they not been killed; this is represented by Eq. 1

$$PA = W_{pop} \times KR_{wolf} \times P_{settled} \times BP_{beaver} \times P_{occ} \tag{1}$$

where W_{pop} is the number of wolves in the GVE, KR_{wolf} is the number of dispersing beavers killed per wolf per year, $P_{settled}$ is the proportion of wolf-killed dispersing beavers that started creating or recolonizing a pond before being killed, BP_{beaver} is the number of ponds maintained per active beaver colony in the GVE, and P_{occ} is the proportion of newly created or recolonized beaver ponds that remain occupied until fall of that year in the GVE. We estimated the average number of wolves in the GVE by multiplying the average annual wolf density in the GVE [40 wolves/1000 km²; (*38*, *39*, *43*)] by the total area of the GVE (1812 km²). We estimated BP_{beaver} by recording the number of ponds actively maintained by a beaver colony (we sampled 74 colonies) during summer 2017 and 2018. Beaver colonies commonly maintain one or more ponds that are directly adjacent to the primary pond where their lodge is located.

We then used a parametric and nonparametric bootstrapping approach to bound the uncertainty around our *PA* estimate and to understand how our estimate of *PA* changed with different, plausible parameter values. We did this to minimize the possibility of overestimating the magnitude of the effect wolves might have and to minimize the possibility of erroneously concluding that wolves affected pond creation when they did not. For the nonparametric bootstrapping approach, we generated 100,000 plausible values, given the data collected, for each parameter by doing 100,000 bootstrapping iterations

(i.e., resampling with replacement). In other words, we used the variability in the data collected on each parameter to generate plausible values of those parameters. We also incorporated variability in wolf population size (W_{pop}) in the GVE by generating 100,000 plausible wolf density values. We assumed that wolf densities were uniformly distributed between 35 and 45 wolves/1000 km^2 [wolf densities in the GVE generally fluctuate between 35 and 45 wolves/1000 km^2; (38, 39, 43)] and selected a value from that distribution per each of the 100,000 bootstrap iterations. We then multiplied the values generated during each bootstrap iteration (W_{pop}, KR_{wolf}, $P_{settled}$, BP_{beaver}, and P_{occ}) together (Eq. 1) to yield 100,000 plausible estimates for the total number of ponds that wolves altered (PA) in the GVE. We then selected the 2.5 and 97.5% highest values for our 95% CI of PA. We calculated a 99% CI using the same approach.

The parametric bootstrap approach consisted of generating plausible parameter values from a sample distribution—created using the mean and SE for each parameter—which could be multiplied together to yield plausible estimates of PA. That is, we generated plausible values for each parameter (W_{pop}, KR_{wolf}, $P_{settled}$, BP_{beaver}, and P_{occ}) and multiplied those values together (Eq. 1) to yield a plausible estimate of PA in the GVE. We repeated this 100,000 times to get 100,000 estimates of PA. We should note that plausible W_{pop} values were generated from uniform distribution (distribution range, 35 to 45 wolves/1000 km^2). We then selected the 2.5 and 97.5% highest values for our 95% CI of PA. We calculated a 99% CI using the same approach.

We estimated the volume of surface water wolves displaced by preventing beaver pond creation and recolonization by multiplying the number of ponds wolves altered by the average volume of water stored in beaver ponds in the GVE [2197 m^3 per pond; (44)]. We used this singular estimate of surface water storage from Karran et al. (44)—who only measured a small sample of ponds—to coarsely estimate the overall magnitude of the effect wolves have on water storage; a more intensive study would be needed to provide a more precise estimate of the surface water volume wolves displace each year by killing dispersing beavers.

RESULTS

By visiting 11,817 clusters of GPS locations from 32 wolves in the GVE from 2015 to 2019, we documented 58 dispersing beavers killed by wolves. Eleven of these dispersing beavers (19%; 95% CI = 9 to 29%) had either constructed rudimentary dams ($n = 6$) in an attempt to create a new pond or started to recolonize drained ponds by repairing dams ($n = 5$) that had blown out >1 year prior (i.e., the dam was not functional, and water was freely flowing downstream). Wolves, on average, killed 0.021 dispersing beavers per wolf per day ($n = 12$ wolves in 2018 to 2019), which is 4.5 dispersing beavers per wolf per year (95% CI = 2.7 to 6.4 beavers per wolf per year).

We compared the fate of wolf-altered ponds (i.e., where a dispersing beaver started creating or recolonizing a pond and then was killed by a wolf) with reference ponds (i.e., where a dispersing beaver started creating or recolonizing a pond) to assess how wolves affected the creation, recolonization, and persistence of beaver ponds (Figs. 2 and 3). Of 31 reference ponds, 84% (26 of 31; 95% CI = 71 to 97%) persisted to the fall after beaver colonization in the summer, whereas 0% (0 of 11) of wolf-altered ponds persisted to the fall (Fig. 2). All 11 wolf-altered ponds were nonfunctional by the fall, as the newly constructed or repaired dams had failed, and water was

flowing freely downstream. In other words, after a wolf killed a dispersing beaver that had created or recolonized a pond, our data indicate that the pond remained inactive for >1 year 100% of the time (Figs. 3 and 4). Of 23 reference ponds monitored for >1 year, 57% (13 of 23; 95% CI = 38 to 78%) were active in the fall of the following year, and 69% (11 of 16; 95% CI = 44 to 88%) of reference ponds monitored >2 years were active after the second fall following creation or recolonization (Fig. 2). All wolf-altered ponds were inactive as of fall 2019, except for two pre-existing ponds that were recolonized 1 and 3 years after a wolf killed a dispersing beaver in that pond. Beaver colonies in the GVE maintained an average of 1.7 ponds (95% CI = 1.54 to 1.88).

In total, we estimate that wolves altered the establishment of ~88 ponds per year (95 and 99% nonparametric bootstrap CI = 36 to 162 ponds and 24 to 194 ponds, respectively) and the storage of ~194,000 m^3 of water per year [95% CI = 79,100 to 355,900 m^3; this assumes 2197 m^3 of water stored per pond (44)]. Notably, CIs generated via the nonparametric and parametric bootstrap approaches were nearly identical. Our modeling suggests that these results depend primarily on the number of dispersing beavers killed by wolves and the proportion of wolf-killed dispersing beavers that had started creating or recolonizing ponds (Fig. 4).

DISCUSSION

We have demonstrated that wolves, by killing dispersing beavers that are unable to maintain the dams and ponds they had started creating or recolonizing, are able to alter wetland creation (i.e., beaver pond creation, recolonization, and persistence and water storage; Figs. 2 and 4). Because dispersing beavers are primarily solitary individuals (45), the only way for a newly created or recolonized pond to persist once a wolf kills a dispersing individual is if another dispersing beaver reaches that pond and continues to maintain the dam. Our work suggests that such a scenario is rare and that once a
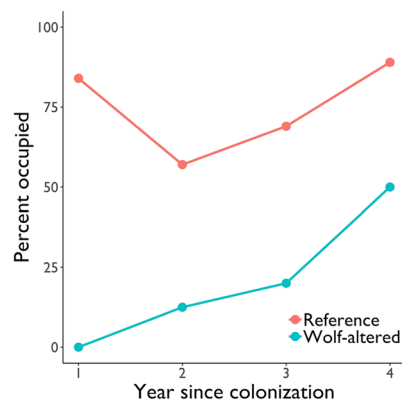

Fig. 2. Occupancy of beaver ponds after creation or recolonization by dispersing beavers in the GVE, Minnesota, USA during 2015 to 2019. Wolf-altered ponds (turquoise line) were ponds where dispersing beavers started creating or recolonizing a pond and then were subsequently killed by a GPS-collared wolf, whereas reference ponds (red line) were ponds that were created or recolonized by dispersing beavers during April to September of that year and identified while conducting fieldwork. Reference ponds are a representative sample of newly created and recolonized ponds in the GVE and thus should reflect the fate of all newly created and recolonized ponds in the GVE. Sample sizes for 1, 2, 3, and 4 "years since colonization" were 31, 23, 16, and 9 for reference ponds and 11, 8, 5, and 4 for wolf-altered ponds, respectively.
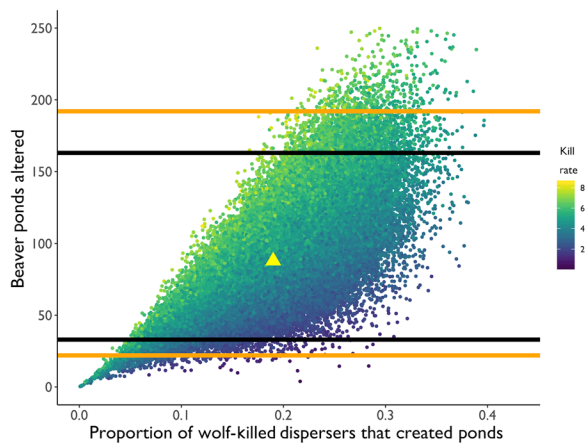
Fig. 3. Relationship between the number of beaver ponds wolves altered per year and the proportion of wolf-killed dispersing beavers that created ponds. Wolf kill rates of dispersing beavers (beavers per wolf per year) are represented in the color spectrum. Mean wolf kill rates of dispersing beavers in the GVE was 4.5 beavers per wolf per year (95% CI = 2.7 to 6.4 beavers per wolf per year), and the proportion of wolf-killed dispersing beavers that created ponds was 0.19 (95% CI = 0.09 to 0.29). The yellow triangle represents our point estimate for the number of beaver ponds prevented (point estimate, 88 ponds). The solid black and orange lines represent the 95 and 99% CI, respectively, of the beaver ponds prevented by wolves. Results were obtained by performing 100,000 parametric bootstraps.

wolf kills a dispersing individual, that newly created or recolonized pond remains unoccupied for the rest of that year. Furthermore, our data suggest that the ecological effects caused by wolves disrupting beaver-mediated wetland creation might last for several years (Fig. 2), but longer-term research is needed to assess the duration of effects.

Although wolves appear to alter beaver pond dynamics, we are not convinced that wolves reduce the total number of newly created and recolonized ponds at the landscape scale. Instead, we think that wolves alter the spatial distribution of newly created and recolonized ponds through time. There is little evidence to suggest that wolf populations are able to control or suppress beaver population densities in the GVE (35) or any other system as beaver population change appears to be independent of wolf predation (28, 37). Instead, wolf predation appears compensatory in the GVE beaver population at the landscape scale (35). Given this, we suggest that wolves likely alter the spatial distribution of 88 (95% CI = 36 to 162) ponds per year, which equates to ~194,000 m³ of total surface water storage or one beaver pond per 21 km² in the GVE. Thus, the ecological importance of wolf predation on beavers might not be in influencing beaver population size but rather by altering the spatiotemporal dynamics of where beavers engineer ecosystems. However, if wolf predation was additive or partially compensatory, then the ecological magnitude of wolf predation on wetland creation and recolonization would only increase because wolves would alter not only the spatial distribution of ponds but also the total number of ponds on the landscape. Hence, wolves appear to alter wetland creation regardless of whether predation is compensatory, partially compensatory, or additive; it is only the magnitude of the effect that would change. Notably, while we assumed that wolves in the GVE are solitary predators that kill beavers individually during the summer (28, 46), the number of ponds wolves alter could change if prevalence of cooperative hunting by wolves during summer increased.

At the pond site scale, wolves radically alter the environment when they prevent the establishment of a new beaver pond or the recolonization of an old pond (Fig. 4). Beavers are predictable agents of disturbance within boreal forest ecosystems (47, 48) due to the flooding associated with beaver engineering (49), and the diverse ecological effects that result from beaver disturbance are exceptionally well documented (Table 1). Wolves, by preventing the creation of entirely new ponds for at least 1 to 2 years, can inhibit site-specific disturbances in boreal forests. That is, wolves prevent the conversion of a forest to a wetland and riparian ecosystem for >1 to 2 years. When wolves kill a dispersing beaver that has recolonized an old pond, they directly affect the trajectory of ecological succession within that site and contribute to the increased environmental heterogeneity common within beaver-altered landscapes (50). Ecological succession generally "resets" with beaver activity (51); thus, wolf prevention of beaver pond recolonization allows succession within that site to continue unabated for at least one to two more years and possibly longer (Figs. 2 and 4).

Although wolf alteration of beaver pond dynamics operates on a localized scale, the effects are likely influential at greater spatial and temporal scales. By influencing pond creation and recolonization, wolves contribute to the dynamic mosaic of abandoned and inundated ponds that increases environmental heterogeneity across space and time (50), ultimately influencing the spatial variation (52), diversity (53), and richness (54) of species. This is similar to other small-scale ecological disturbances, such as tree tip-ups and the forest gaps they create (55, 56), predator-killed carcasses (57–59), predator dens and burrows (60, 61), termite mounds (62), and ant hills (63, 64) that, due to their outsized ecological effects, influence landscape heterogeneity despite operating at small, seemingly trivial scales (57). Even short-term, ephemeral disturbances such as vernal pools are important for biotic communities on landscape scales (65, 66).

Even if wolves only prevent pond creation or recolonization for short-time scales (<2 years), wolves' effect on the spatial distribution of ponds at the landscape scale likely compounds over time because where wolves alter pond creation and recolonization almost certainly varies annually. In other words, wolves likely do not prevent pond creation and recolonization at the same 88 sites year after year but rather alter the creation and recolonization of different ponds each year (although there may be sites where wolves do repeatedly prevent beaver creation or recolonization). Thus, we suggest that wolves' impact on pond creation and recolonization is akin to the cumulative ecological effects of beaver pond creation articulated by Johnston and Naiman (33): "Although the area disturbed by an individual beaver pond is small…the cumulative disturbance of many beaver ponds over time results in extensive alteration" (p.1620). For example, in a 1-year period, wolves might only alter the spatial distribution of 1 pond per 21 km² (88 ponds/year), but over a 10-year period, wolves might affect 1 pond per 2.1 km² (88 ponds/year*10 years). While this example is almost certainly an oversimplification, it illustrates that wolves could have a substantial effect on the distribution of wetlands over time in the GVE and in other systems where wolves and beavers are sympatric [see figure 1 of (28)]. Further, it highlights why long-term research is necessary to determine how interactions between this apex predator and ecosystem engineer ultimately shape wetland dynamics in boreal ecosystems.

Previous work from western North America suggests that wolves facilitate long-reaching behaviorally mediated trophic cascades that ultimately affect riparian ecosystems and the geomorphology of
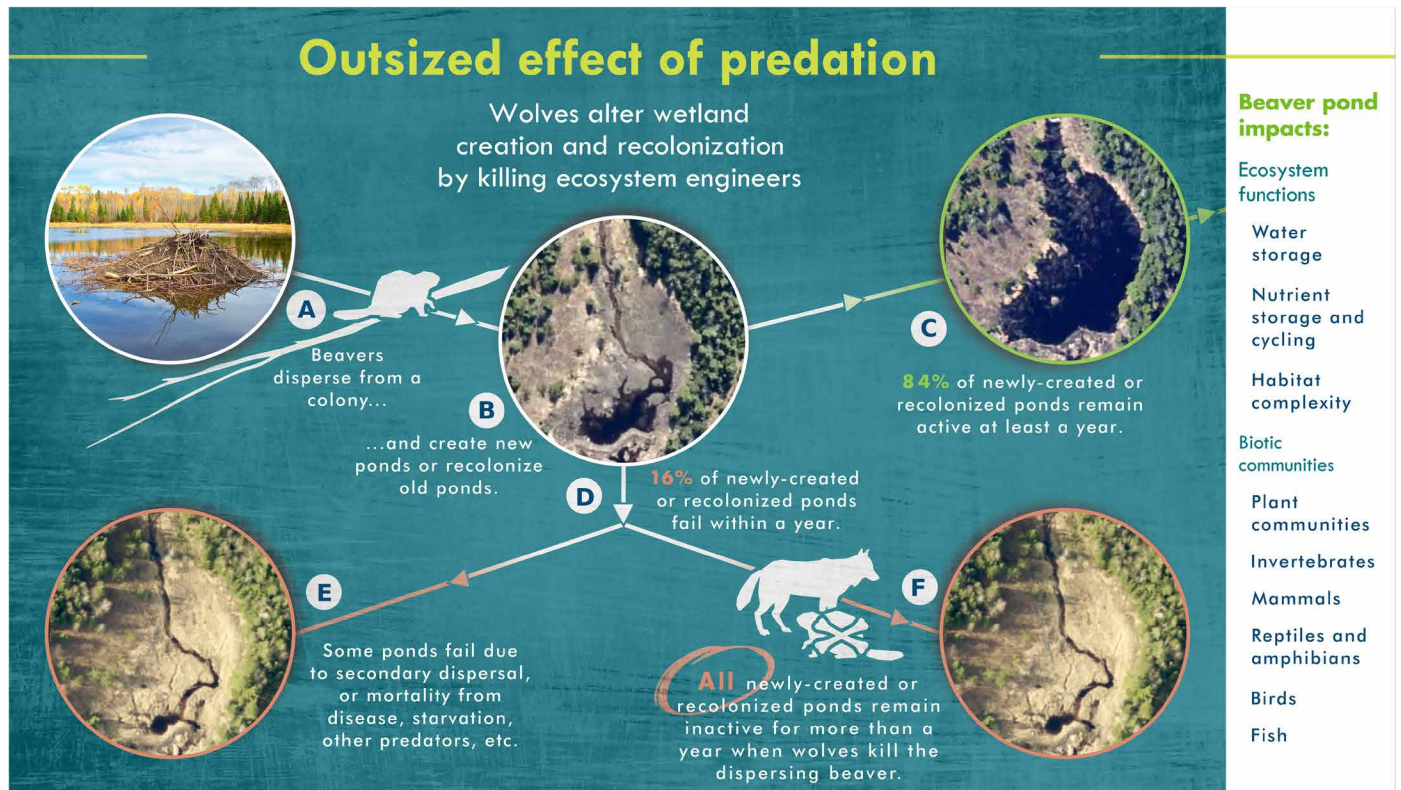
Fig. 4. The fate of ponds created by dispersing beaver in the GVE, Minnesota, USA. Dispersing beavers leave their colony (**A**) and eventually settle in an area where they create a new dam and pond or recolonize an existing pond by repairing a nonfunctional dam on a stream (**B**), either of which creates a new pond. Dispersing beavers in these newly created ponds continue to occupy the pond until the winter of that year 84% of the time (**C**). By creating and occupying the pond, dispersing beavers initiate "ecosystem engineering" that affects multiple species, habitats, ecosystem processes, and aquatic food communities (Table 1). However, 16% of the time, beavers abandon the pond or die before winter of that year (**D**), which causes the dam to fail and the pond to drain (**E** and **F**). An unknown proportion of these pond failures are not related to wolf predation but other causes such as disease, habitat quality, or other predators (e.g., black bears) that either kill the beaver or cause it to abandon the pond (**E**). Wolf predation is responsible for an unknown, but potentially substantial, proportion of these pond failures. After a wolf kills a dispersing beaver that has created or recolonized a pond, our data indicate that the pond remains inactive for >1 year 100% of the time (**F**). Note that photos in (**B**) to (**F**) are of the same pond. Photo credit: Thomas Gable, University of Minnesota. Aerial imagery credit: St. Louis County, Minnesota. Infographic credit: A. Ostman.

waterways (*16*, *18*), but this has been met with skepticism (*11*, *19*). We, however, have identified and provided evidence for a well-defined mechanism by which wolves affect riparian ecosystems directly through predation (Fig. 4). Beavers, through their prolific ecosystem engineering, transform ecosystems wherever they establish ponds, creating abundant habitat for a variety of taxa and affecting large-scale ecological processes such as water storage, sedimentation, nutrient cycling, and carbon sequestration (Table 1) (*26*). If beavers are the natural ecosystem "engineers," creating wetlands across the circumpolar boreal ecosystem, then wolves can be thought of as a factor that directly influences such engineering by altering site-specific beaver construction that, in turn, influences the spatial and temporal distribution of wetlands.

Large predators are thought to primarily have landscape-level ecological effects through density-mediated or behaviorally mediated mechanisms. Here, we described a mechanism by which a large predator, through the outsized effects of direct predation on an ecosystem engineer, affected ecosystems without altering the density or behavior of their prey (although these mechanisms are not mutually exclusive). The functional and numerical responses of predators to prey populations likely influence the ecological magnitude, but

the mechanism itself is independent of predator and prey densities. That is, predators can have outsized ecological effects by killing prey that have a disproportionately large role in ecosystem functioning (e.g., ecosystem engineers). Our work highlights yet another functional role of direct predation in ecosystems and should be helpful for understanding how the conservation and restoration of large predator populations across the world might affect ecosystems.

REFERENCES AND NOTES

1. M. Hebblewhite, C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, P. C. Paquet, Human activity mediates a trophic cascade caused by wolves. *Ecology* **86**, 2135–2144 (2005).
2. O. J. Schmitz, Effects of predator hunting mode on grassland ecosystem function. *Science* **319**, 952–954 (2008).
3. J. K. Bump, C. R. Webster, J. A. Vucetich, R. O. Peterson, J. M. Shields, M. D. Powers, Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. *Ecosystems* **12**, 996–1007 (2009).

4. W. J. Ripple, J. A. Estes, O. J. Schmitz, V. Constant, M. J. Kaylor, A. Lenz, J. L. Motley, K. E. Self, D. S. Taylor, C. Wolf, What is a trophic cascade? *Trends Ecol. Evol.* **31**, 842–849 (2016).

5. W. J. Ripple, R. L. Beschta, Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biol. Conserv.* **145**, 205–213 (2012).

6. A. T. Ford, J. R. Goheen, Trophic cascades by large carnivores: A case for strong inference and mechanism. *Trends Ecol. Evol.* **30**, 725–735 (2015).

7. J. A. Estes, M. T. Tinker, T. M. Williams, D. F. Doak, Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473–476 (1998).

8. H. F. Greeney, M. R. Meneses, C. E. Hamilton, E. Lichter-Marck, R. W. Mannan, N. Snyder, H. Snyder, S. M. Wethington, L. A. Dyer, Trait-mediated trophic cascade creates enemy-free space for nesting hummingbirds. *Sci. Adv.* **1**, e1500310 (2015).

9. E. G. Ritchie, B. Elmhagen, A. S. Glen, M. Letnic, G. Ludwig, R. A. McDonald, Ecosystem restoration with teeth: What role for predators? *Trends Ecol. Evol.* **27**, 265–271 (2012).

10. R. M. Engeman, L. R. Allen, B. L. Allen, Study design concepts for inferring functional roles of mammalian top predators. *Food Webs* **12**, 56–63 (2017).

11. B. L. Allen, L. R. Allen, H. Andrén, G. Ballard, L. Boitani, R. M. Engeman, P. J. S. Fleming, A. T. Ford, P. M. Haswell, R. Kowalczyk, J. D. C. Linnell, L. D. Mech, D. M. Parker, Can we save large carnivores without losing large carnivore science? *Food Webs* **12**, 64–75 (2017).

12. J. A. Estes, J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, D. A. Wardle, Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011).

13. J. W. Laundré, L. Hernández, K. B. Altendorf, Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Can. J. Zool.* **79**, 1401–1409 (2001).

14. W. J. Ripple, R. L. Beschta, Wolves and the ecology of fear: Can predation risk structure ecosystems? *Bioscience* **54**, 755–766 (2004).

15. M. T. Kohl, D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, D. R. MacNulty, Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* **88**, 638–652 (2018).

16. R. L. Beschta, W. J. Ripple, River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA. *Earth Surf. Process. Landf.* **31**, 1525–1539 (2006).

17. R. L. Beschta, W. J. Ripple, The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology* **157–158**, 88–98 (2012).

18. R. L. Beschta, W. J. Ripple, Can large carnivores change streams via a trophic cascade? *Ecohydrology* **12**, e2048 (2019).

19. L. D. Mech, Where can wolves live and how can we live with them? *Biol. Conserv.* **210**, 310–317 (2017).

20. K. N. Marshall, N. T. Hobbs, D. J. Cooper, Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proc. R. Soc. B* **280**, 20122977 (2013).

21. J. J. Cusack, M. T. Kohl, M. C. Metz, T. Coulson, D. R. Stahler, D. W. Smith, D. R. MacNulty, Weak spatiotemporal response of prey to predation risk in a freely interacting system. *J. Anim. Ecol.* **89**, 120–131 (2020).

22. E. S. Kasischke, Boreal ecosystems in the global carbon cycle, in *Fire, Climate Change, and Carbon Cycling in the Boreal Forest. Ecological Studies (Analysis and Synthesis)*, E. S. Kasischke, B. J. Stocks, Eds. (Springer New York, New York, 2000), pp. 19–30.

23. W. J. Ripple, T. P. Rooney, R. L. Beschta, in *Trophic Cascades*, J. Terborgh, J. A. Estes, Eds. (Island Press, Washington, DC, 2009), chap. 9.

24. T. D. Gable, T. Stanger, S. K. Windels, J. K. Bump, Do wolves ambush beavers? Video evidence for higher-order hunting strategies. *Ecosphere* **9**, e02159 (2018).

25. C. G. Jones, J. H. Lawton, M. Shachak, Organisms as ecosystem engineers. *Oikos* **69**, 373–386 (1994).

26. F. Rosell, O. Bozsér, P. Collen, H. Parker, Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Rev.* **35**, 248–276 (2005).

27. C. A. Johnston, Fate of 150 year old beaver ponds in the Laurentian Great Lakes Region. *Wetlands* **35**, 1013–1019 (2015).

28. T. D. Gable, S. K. Windels, M. C. Romanski, F. Rosell, The forgotten prey of an iconic predator: A review of interactions between grey wolves *Canis lupus* and beavers *Castor* spp. *Mammal Rev.* **48**, 123–138 (2018).

29. E. Say-Sallaz, S. Chamaillé-Jammes, H. Fritz, M. Valeix, Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. *Biol. Conserv.* **235**, 36–52 (2019).

30. A. T. Homkes, T. D. Gable, S. K. Windels, J. K. Bump, Berry important? Wolf provisions pups with berries in northern Minnesota. *Wildl. Soc. Bull.* **44**, 221–223 (2020).

31. R. G. Bailey, *Description of the Ecoregions of the United States* (U.S. Department of Agriculture Miscellaneous Publication No. 1391, Washington, DC, 1980).

32. L. W. Kallemeyn, K. L. Holmberg, J. A. Perry, B. Y. Odde, *Aquatic Synthesis for Voyageurs National Park* (U.S. Geological Survey, Information and Technology Report 2003–0001, International Falls, MN, 2003).

33. C. A. Johnston, R. J. Naiman, Aquatic patch creation in relation to beaver population trends. *Ecology* **71**, 1617–1621 (1990).

34. C. A. Johnston, S. K. Windels, Using beaver works to estimate colony activity in boreal landscapes. *J. Wildl. Manag.* **79**, 1072–1080 (2015).

35. T. D. Gable, S. K. Windels, Kill rates and predation rates of wolves on beavers. *J. Wildl. Manag.* **82**, 466–472 (2018).

36. C. A. Johnston, R. J. Naiman, The use of a geographic information system to analyze long-term landscape alteration by beaver. *Landsc. Ecol.* **4**, 5–19 (1990).

37. S. M. Johnson-Bice, J. M. Ferguson, J. D. Erb, T. D. Gable, S. K. Windels, Ecological forecasts reveal limitations of common model selection methods: Predicting changes in beaver colony densities. *Ecol. Appl.*, e02198 (2020).

38. P. J. P. Gogan, W. T. Route, E. M. Olexa, N. Thomas, D. Kuehn, K. M. Podruzny, *Gray Wolves in and Adjacent to Voyageurs National Park, Minnesota: Research and Synthesis, 1987–1991* (U.S. Department of the Interior, National Park Service, Midwest Regional Office, Omaha, NE, 2004).

39. J. Fox, R. O. Peterson, T. Drummer, *Gray Wolf Biology Research in Voyageurs National Park, 1998–2001* (Natural Resource Preservation Program, Project Report #197, International Falls, MN, 2001).

40. T. D. Gable, S. K. Windels, J. G. Bruggink, A. T. Homkes, Where and how wolves (*Canis lupus*) kill beavers (*Castor canadensis*). *PLOS ONE* **11**, e0165537 (2016).

41. T. D. Gable, S. K. Windels, J. G. Bruggink, The problems with pooling poop: Confronting sampling method biases in wolf (*Canis lupus*) diet studies. *Can. J. Zool.* **95**, 843–851 (2017).

42. T. D. Gable, S. K. Windels, A. T. Homkes, Do wolves hunt freshwater fish in spring as a food source? *Mamm. Biol.* **91**, 30–33 (2018).

43. T. D. Gable, S. K. Windels, J. G. Bruggink, S. M. Barber-Meyer, Weekly summer diet of gray wolves (*Canis lupus*) in northeastern Minnesota. *Am. Midl. Nat.* **179**, 15–27 (2018).

44. D. J. Karran, C. J. Westbrook, J. M. Wheaton, C. A. Johnston, A. Bedard-Haughn, Rapid surface-water volume estimations in beaver ponds. *Hydrol. Earth Syst. Sci.* **21**, 1039–1050 (2017).

45. M. Mayer, S. C. Frank, A. Zedrosser, F. Rosell, Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal. *J. Anim. Ecol.* **89**, 577–588 (2020).

46. D. J. Demma, S. M. Barber-Meyer, L. D. Mech, Testing global positioning system telemetry to study wolf predation on deer fawns. *J. Wildl. Manag.* **71**, 2767–2775 (2007).

47. M. M. Remillard, G. K. Gruendling, D. J. Bogucki, Disturbance by beaver (*Castor canadensis* Kuhl) and increased landscape heterogeneity, in *Landscape Heterogeneity and Disturbance*, M. G. Turner, Ed. (Springer New York, New York, 1987), pp. 103–122.

48. P. Nummi, T. Kuuluvainen, Forest disturbance by an ecosystem engineer: Beaver in boreal forest landscapes. *Boreal Environ. Res.* **18**, 13–24 (2013).

49. R. J. Naiman, C. A. Johnston, J. C. Kelley, Alteration of North American streams by beaver. *Bioscience* **38**, 753–762 (1988).

50. S. Kivinen, P. Nummi, T. Kumpula, Beaver-induced spatiotemporal patch dynamics affect landscape-level environmental heterogeneity. *Environ. Res. Lett.* **15**, 094065 (2020).

51. A. M. Little, G. R. Guntenspergen, T. F. H. Allen, Wetland vegetation dynamics in response to beaver (*Castor canadensis*) activity at multiple scales. *Ecoscience* **19**, 246–257 (2012).

52. I. J. Schlosser, L. W. Kallemeyn, Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology* **81**, 1371–1382 (2000).

53. B. M. Bush, C. Stenert, L. Maltchik, D. P. Batzer, Beaver-created successional gradients increase β-diversity of invertebrates by turnover in stream-wetland complexes. *Freshw. Biol.* **64**, 1265–1274 (2019).

54. A. Stein, K. Gerstner, H. Kreft, Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **17**, 866–880 (2014).

55. J. W. McClure, T. D. Lee, Small-scale disturbance in a northern hardwoods forest: Effects on tree species abundance and distribution. *Can. J. For. Res.* **23**, 1347–1360 (1993).

56. J. L. Hart, J. D. Grissino-Mayer, Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA. *Plant Ecol.* **201**, 131–146 (2008).

57. J. K. Bump, R. O. Peterson, J. A. Vucetich, Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology* **90**, 3159–3167 (2009).

58. C. C. Wilmers, D. R. Stahler, R. L. Crabtree, D. W. Smith, W. M. Getz, Resource dispersion and consumer dominance: Scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecol. Lett.* **6**, 996–1003 (2003).

59. J. M. Barry, L. M. Elbroch, M. E. Aiello-Lammens, R. J. Sarno, L. Seelye, A. Kusler, H. B. Quigley, M. M. Grigione, Pumas as ecosystem engineers: Ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. *Oecologia* **189**, 577–586 (2019).

60. D. J. Eldridge, W. G. Whitford, Badger (*Taxidea taxus*) disturbances increase soil heterogeneity in a degraded shrub-steppe ecosystem. *J. Arid Environ.* **73**, 66–73 (2009).

61. T. Gharajehdaghipour, J. D. Roth, P. M. Fafard, J. H. Markham, Arctic foxes as ecosystem engineers: Increased soil nutrients lead to increased plant productivity on fox dens. *Sci. Rep.* **6**, 24020 (2016).

62. J. M. Dangerfield, T. S. McCarthy, W. N. Ellery, The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *J. Trop. Ecol.* **14**, 507–520 (1998).

63. P. J. Folgarait, S. Perelman, N. Gorosito, R. Pizzio, J. Fernández, Effects of *Camponotus punctulatus* ants on plant community composition and soil properties across land-use histories. *Plant Ecol.* **163**, 1–13 (2002).

64. J. Frouz, V. Jilková, The effect of ants on soil properties and processes (Hymenoptera: Formicidae). *Myrmecol. News* **11**, 191–199 (2008).

65. P. H. Zedler, Vernal pools and the concept of "isolated wetlands". *Wetlands* **23**, 597–607 (2003).

66. D. D. Williams, *The Biology of Temporary Waters* (Oxford Univ. Press, Oxford, 2006).

67. A. Puttock, H. A. Graham, A. M. Cunliffe, M. Elliott, R. E. Brazier, Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Sci. Total Environ.* **576**, 430–443 (2017).

68. R. K. Meentemeyer, D. R. Butler, Hydrogeomorphic effects of beaver dams in Glacier National Park, Montana. *Phys. Geogr.* **20**, 436–446 (1999).

69. M. Majerova, B. T. Neilson, N. M. Schmadel, J. M. Wheaton, C. J. Snow, Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream. *Hydrol. Earth Syst. Sci.* **19**, 3541–3556 (2015).

70. C. J. Westbrook, D. J. Cooper, B. W. Baker, Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resour. Res.* **42**, W06404 (2006).

71. D. J. Karran, C. J. Westbrook, A. Bedard-Haughn, Beaver-mediated water table dynamics in a Rocky Mountain fen. *Ecohydrology* **11**, e1923 (2017).

72. C. A. Johnston, R. J. Naiman, Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. *Landsc. Ecol.* **1**, 47–57 (1987).

73. M. E. Smith, C. T. Driscoll, B. J. Wyskowski, C. M. Brooks, C. C. Cosentini, Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Can. J. Zool.* **69**, 55–61 (1991).

74. B. E. Margolis, M. S. Castro, R. L. Raesly, The impact of beaver impoundments on the water chemistry of two Appalachian streams. *Can. J. Fish. Aquat. Sci.* **58**, 2271–2283 (2001).

75. L. A. Błędzki, J. L. Bubier, L. A. Moulton, T. D. Kyker-Snowman, Downstream effects of beaver ponds on the water quality of New England first- and second-order streams. *Ecohydrology* **4**, 698–707 (2010).

76. R. J. Naiman, J. M. Melillo, J. E. Hobbie, Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* **67**, 1254–1269 (1986).

77. D. R. Butler, G. P. Malanson, Sedimentation rates and patterns in beaver ponds in a mountain environment. *Geomorphology* **13**, 255–269 (1995).

78. M. M. Pollock, T. J. Beechie, C. E. Jordan, Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surf. Process. Landf.* **32**, 1174–1185 (2007).

79. E. Wohl, Landscape-scale carbon storage associated with beaver dams. *Geophys. Res. Lett.* **40**, 3631–3636 (2013).

80. C. A. Johnston, Beaver pond effects on carbon storage in soils. *Geoderma* **213**, 371–378 (2014).

81. R. J. Naiman, G. Pinay, C. A. Johnston, J. Pastor, Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* **75**, 905–921 (1994).

82. J. G. Lazar, K. Addy, A. J. Gold, P. M. Groffman, R. A. McKinney, D. Q. Kellogg, Beaver ponds: Resurgent nitrogen sinks for rural watersheds in the Northeastern United States. *J. Environ. Qual.* **44**, 1684–1693 (2015).

83. M. M. Pollock, T. J. Beechie, J. M. Wheaton, C. E. Jordan, N. Bouwes, N. Weber, C. Volk, Using beaver dams to restore incised stream ecosystems. *Bioscience* **64**, 279–290 (2014).

84. D. Burchsted, M. D. Daniels, R. Thorson, J. Vokoun, The river discontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. *Bioscience* **60**, 908–922 (2010).

85. A. M. Gurnell, The hydrogeomorphological effects of beaver dam-building activity. *Prog. Phys. Geogr.* **22**, 167–189 (1998).

86. N. Bouwes, N. Weber, C. E. Jordan, W. C. Saunders, I. A. Tattam, C. Volk, J. M. Wheaton, M. M. Pollock, Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Sci. Rep.* **6**, 28581 (2016).

87. N. J. Willby, A. Law, O. Levanoni, G. Foster, F. Ecke, Rewilding wetlands: Beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philos. Trans. R. Soc. B* **373**, 20170444 (2018).

88. J. M. Smith, M. E. Mather, Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshw. Biol.* **58**, 1523–1538 (2013).

89. G. A. Hood, S. E. Bayley, Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biol. Conserv.* **141**, 556–567 (2008).

90. D. Müller-Schwarze, *The Beaver: Its Life and Impact* (Cornell Univ. Press, Ithica, NY, 2011).

91. S. K. Windels, Beavers as engineers of wildlife habitat, in *Beavers: Boreal Ecosystem Engineers*, C. A. Johnston, Ed. (Springer New York, New York, 2017), pp. 239–268.

92. G. J. Knudsen, *Relationship of Beaver to Forests, Trout and Wildlife in Wisconsin* (Wisconsin Department of Conservation Technical Bulletin No. 25, Madison, WI, 1962).

93. F. A. LeBlanc, D. Gallant, L. Vasseur, L. Léger, Unequal summer use of beaver ponds by river otters: Influence of beaver activity, pond size, and vegetation cover. *Can. J. Zool.* **85**, 774–782 (2007).

94. C. L. Mott, C. K. Bloomquist, C. K. Nielsen, Within-lodge interactions between two ecosystem engineers, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*). *Behaviour* **150**, 1325–1344 (2013).

95. P. Nummi, W. Liao, O. Huet, E. Scarpulla, J. Sundell, The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. *Glob. Ecol. Conserv.* **20**, e00701 (2019).

96. D. E. Medin, W. P. Clary, *Small Mammals of a Beaver Pond Ecosystem and Adjacent Riparian Habitat in Idaho* (U.S. Department of Agriculture Research Paper INT-445, Intermountain Research Station, Ogden, UT, 1991).

97. M. McCaffery, L. Eby, Beaver activity increases aquatic subsidies to terrestrial consumers. *Freshw. Biol.* **61**, 518–532 (2016).

98. M. Ciechanowski, W. Kubic, A. Rynkiewicz, A. Zwolicki, Reintroduction of beavers *Castor fiber* may improve habitat quality for vespertilionid bats foraging in small river valleys. *Eur. J. Wildl. Res.* **57**, 737–747 (2011).

99. P. Nummi, S. Kattainen, P. Ulander, A. Hahtola, Bats benefit from beavers: A facilitative link between aquatic and terrestrial food webs. *Biodivers. Conserv.* **20**, 851–859 (2011).

100. M. A. Menzel, T. C. Carter, W. M. Ford, B. R. Chapman, Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the Upper Coastal Plain of South Carolina. *Am. Midl. Nat.* **145**, 112–119 (2001).

101. P. Nummi, S. Holopainen, Whole-community facilitation by beaver: Ecosystem engineer increases waterbird diversity. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **24**, 623–633 (2014).

102. P. Nummi, A. Hahtola, The beaver as an ecosystem engineer facilitates teal breeding. *Ecography* **31**, 519–524 (2008).

103. M. C. McKinstry, P. Caffrey, S. H. Anderson, The importance of beaver to wetland habitats and waterfowl in Wyoming. *J. Am. Water Res. Assoc.* **37**, 1571–1577 (2001).

104. J.-C. Aznar, A. Desrochers, Building for the future: Abandoned beaver ponds promote bird diversity. *Écoscience* **15**, 250–257 (2008).

105. A. M. Grover, G. A. Baldassarre, Bird species richness within beaver ponds in south-central New York. *Wetlands* **15**, 108–118 (1995).

106. W. B. Rendell, R. J. Robertson, Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. *Condor* **91**, 875–885 (1989).

107. J. M. Cunningham, A. J. K. Calhoun, W. E. Glanz, Pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. *J. Wildl. Manag.* **71**, 2517–2526 (2007).

108. N. E. Karraker, J. P. Gibbs, Amphibian production in forested landscapes in relation to wetland hydroperiod: A case study of vernal pools and beaver ponds. *Biol. Conserv.* **142**, 2293–2302 (2009).

109. B. S. Metts, J. D. Lanham, K. R. Russell, Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the Upper Piedmont of South Carolina. *Am. Midl. Nat.* **145**, 54–65 (2001).

110. J. W. Snodgrass, G. K. Meffe, Influence of beavers on stream fish assemblages: Effects of pond age and watershed position. *Ecology* **79**, 928–942 (1998).

111. G. A. Hood, D. G. Larson, Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. *Wetlands* **34**, 19–29 (2014).

112. A. Law, F. McLean, N. J. Willby, Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshw. Biol.* **61**, 486–499 (2016).

113. D. M. McDowell, R. J. Naiman, Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia* **68**, 481–489 (1986).

114. A. M. Ray, A. J. Rebertus, H. L. Ray, Macrophyte succession in Minnesota beaver ponds. *Can. J. Bot.* **79**, 487–499 (2001).

115. C. B. Anderson, C. R. Griffith, A. D. Rosemond, R. Rozzi, O. Dollenz, The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile: Do exotic beavers engineer differently in sub-Antarctic ecosystems? *Biol. Conserv.* **128**, 467–474 (2006).

116. J. P. Wright, C. G. Jones, A. S. Flecker, An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**, 96–101 (2002).

117. A. Law, M. J. Gaywood, K. C. Jones, P. Ramsay, N. J. Willby, Using ecosystem engineers as tools in habitat restoration and rewilding: Beaver and wetlands. *Sci. Total Environ.* **605-606**, 1021–1030 (2017).

Citation: T. D. Gable, S. M. Johnson-Bice, A. T. Homkes, S. K. Windels, J. K. Bump, Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. *Sci. Adv.* **6**, eabc5439 (2020).

Science Advances

Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers

Thomas D. Gable, Sean M. Johnson-Bice, Austin T. Homkes, Steve K. Windels and Joseph K. Bump

ARTICLE TOOLS	http://advances.sciencemag.org/content/6/46/eabc5439
SUPPLEMENTARY MATERIALS	http://advances.sciencemag.org/content/suppl/2020/11/09/6.46.eabc5439.DC1
REFERENCES	This article cites 104 articles, 4 of which you can access for free http://advances.sciencemag.org/content/6/46/eabc5439#BIBL
PERMISSIONS	http://www.sciencemag.org/help/reprints-and-permissions

Use of this article is subject to the Terms of Service