Supplemental File S1

Predator decline and shifting baselines: Are the landscapes we study a "sick patient"?

By William J. Ripple, Christopher Wolf, Robert L. Beschta, Apryle D. Craig, Zachary S. Curcija, Erick J. Lundgren, Lauren C. Satterfield, Samuel T. Woodrich, Aaron J. Wirsing

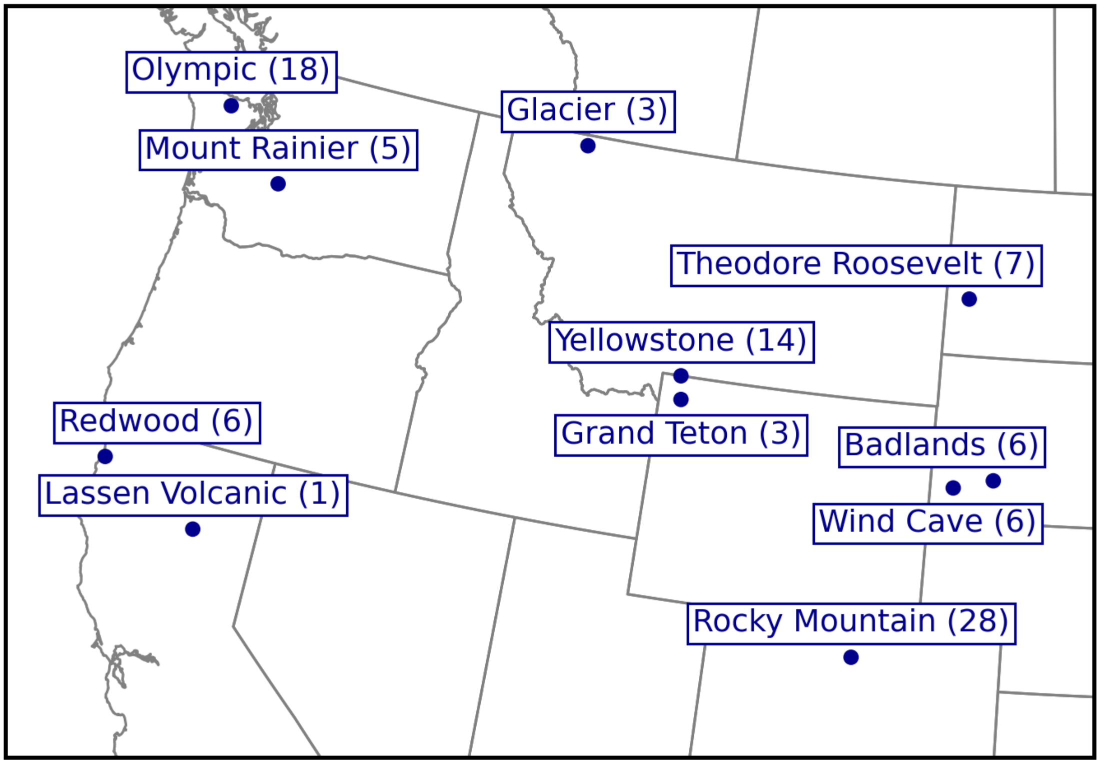

Figure S1. Locations of national parks. We considered all national parks in the Western United States where wolves were historically present. For each park, the number of associated theses and journal articles that we obtained is shown in parentheses.

Table S1. Summary of observations regarding ungulates and plants following the displacement/extirpation of large predators in three northwestern US national parks. Source: Beschta and Ripple (2009).

National Park	**Summary of observations**
Olympic National Park (western portion of the park)	With wolves functionally extirpated by 1910 and a hunting ban on elk that began in 1905, the Olympic peninsula's elk population began to rapidly increase and significant browsing of riparian shrubs was observed within a decade (Bailey 1918). As herbivory impacts continued, palatable shrub and tree species were increasingly unable to grow above the browse level of elk (Murie 1935, Schwartz 1939, Newman 1954). A deterioration of plant communities led park service biologist E.L. Sumner to surmise that wolves had likely been an essential ‘‘natural check” preventing elk over-population (Sumner 1938). He further indicated: ‘‘Unless some substitute for this now absent controlling factor is provided, serious destruction of certain plants and even their total elimination in certain places through inability to reproduce will no doubt occur.”
Yellowstone National Park (northern winter range)	By 1920, and perhaps earlier, wolves had been functionally extirpated from Yellowstone's northern elk winter ranges. Approximately a decade later, Rush (1933) found that the northern range was ‘‘badly overgrazed”, sheet erosion was occurring, and much of the ‘‘rich top soil” had washed away. Subsequently, Grimm (1939) concluded that herbaceous plants became depleted each winter due to over-utilization by ungulates. His studies of aspen indicated that excessive browsing by elk threatened the ‘‘existence of aspen on the winter range.” Even though the Park Service reduced elk numbers in an attempt to lessen their foraging impacts, by the mid-1950s the cumulative effects of grazing and trampling by elk had removed lush thickets of willows from meadows, impacted sagebrush, and depleted aspen stands ‘‘that cannot be replaced while elk consume reproduction” (NPS 1956). Bunchgrasses, which normally comprised the bulk of an elk's diet, were also in ‘‘poor condition.” The diminishment of northern range plant communities led A. Leopold (1949) to simply conclude: ‘‘Thus the Yellowstone has lost its wolves and cougars, with the result that elk are ruining the flora, particularly on the winter range.”
Wind Cave National Park	Journal records of naturalist G.B. Grinnell during the 1874 Custer expedition to the Black Hills chronicled abundant large carnivores, ungulates, berry-producing shrubs, wildflowers, and beaver along their route (Ludlow 1875). For example, serviceberry, a browse species that today is uncommon in the park, was ‘‘very abundant, both in the form of low bushes in open, dry, sparse copses and as thickets in the valleys.” Grinnell also noted ‘‘almost all the streams which we passed were dammed in many places by beaver.” However, discovery of gold in 1874 and a rush of miners to the Black Hills were soon followed by large herds of cattle and sheep. Thus, large predators were quickly removed from the landscape. By the mid-1880s continuous grazing by livestock had resulted in a ‘‘dangerous depletion of the range” and thus ‘‘beaver had begun to disappear and their dams began to let go” (Palais 1942). When the park was established in 1905, it inherited not only an area generally devoid of large predators, but one where native plant communities had experienced several decades of intensive herbivory by domestic ungulates (Smith unpublished[1]).

[1] Smith J. Rare Tree and shrub survey in Wind Cave National Park. Hot Springs, SD: Wind Cave National Park Files. Unpublished.

Table S2. Species in the American West affected by coyote predation as listed by the U.S. Fish and Wildlife Service and species of concern according to Natural Heritage programs. Adapted from Table 1 in Ripple et al. (2013).

Common name	**Scientific name(s)**	**Status**
Black-footed ferret	*Mustela nigripes*	Endangered
Pygmy rabbit	*Brachylagus idahoensis*	Endangered
San Joaquin kit fox	*Vulpes macrotis mutica*	Endangered
Columbian white-tailed deer	*Odocoileus virginianus leucurus*	Endangered
Least tern	*Sterna antillarum*	Endangered
Whooping crane	*Grus americana*	Endangered
Olympic marmot	*Marmota olympus*	Species of concern WA
Swift fox	*Vulpes velox*	Species of concern CO, MT, NM, WY
Sandhill crane	*Grus canadensis tabida*	Species of concern CO, OR, WA
Snowshoe hare	*Lepus americanus, Lepus americanus klamathensis, Lepus americanus seclusus, Lepus americanus tahoensis*	Species of concern NM, CA, WY
Long-billed curlew	*Numenius americanus*	Species of concern CO, OR
Yellow-bellied marmot	*Marmota flaviventris*	Species of concern NM

Table S3. List of theses and journal articles analyzed. From left to right, the table columns show the thesis/dissertation or article identification number, associated national park, year of publication, university or journal name, author(s), title, taxonomic group(s) considered, whether or not the historical presence of wolves was considered, and a quote about wolves (or other large carnivores), if applicable. In the "Wolves?" column, theses and articles where only large carnivores other than wolves were considered by the authors are marked with an asterisk. Thesis number 32 covers two national parks: Theodore Roosevelt and Wind Cave. We have not included references in quotes in our references list; these papers can be identified using the associated document.

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
41 theses								
1	Badlands	2006	South Dakota State University	Russell, Todd A.	Habitat Selection by Swift Foxes in Badlands National Park and the Surrounding Area in South Dakota	swift fox	no	
2	Badlands	2007	South Dakota State University	Schroeder, Greg M.	Effect of Coyotes and Release Site Selection on Survival and Movement of Translocated Swift Foxes in the Badlands Ecosystem of South Dakota	swift fox	no	
3	Badlands	2011	South Dakota State University	Sasmal, Indrani	Population Viability Analysis of Swift fox (Vulpes velox) at the Badlands National Park	swift fox	no	
4	Badlands	2017	South Dakota State University	Nevison, Sarah Ann	Swift Foxes in Southwestern South Dakota: Assessing the Current Status of a Reintroduced Population	swift fox	no	
5	Glacier	1955	University of Montana	Hawley, Vernon Duane	Ecology of the marten in Glacier National Park	American marten	no	
6	Glacier	1968	University of Montana	Koterba, Wayne Douglas	Analysis of the North Fork Valley grasslands in Glacier National Park Montana	herbaceous vegetation	no	
7	Glacier	1981	University of Montana	Burnett, Gary W.	Movements and habitat use of American marten in Glacier National Park Montana	American marten	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
8	Lassen Volcanic	2007	California State University System	Kirk, Thomas A.	Landscape-scale habitat associations of the American marten (Martes americana) in the greater southern Cascades region of California	American marten	yes	Page 5: "Several top mammalian predators have been extirpated from this region including grizzly bear (Ursusarctos), gray wolf (Canis lupus) and wolverine (Gulo gulo) (USDA 2001)."
9	Mount Rainier	1970	Oregon State University	Schamberger, Melvin	Mammals of Mount Rainier National Park	small mammals	yes	Pages 80-81: "At present, the wolf is thought to be absent from the park, but may perhaps wander down from the North Cascades in the future."
10	Mount Rainier	1970	Central Washington University	Meredith, Don H.	Subalpine Cover Ecology of Eutamias amoenus, Eutamias townsendii and other small Mammals in Huckleberry Park, Mount Rainier National Park	small mammals	no	
11	Mount Rainier	1973	Oregon State University	Henderson, Jan A	Composition, distribution and succession of subalpine meadows in Mount Rainier National Park	understory	no	
12	Mount Rainier	1987	Oregon State University	Cooper, Kevin Craig	Seasonal movements and habitat use of migratory elk in Mount Rainier National Park	elk	no	
13	Olympic	1979	Oregon State University	Jenkins, Kurt Jeffrey	Home range and habitat use by Roosevelt elk in Olympic National Park, Washington	elk	yes	Page 4: "Local politicians established a bounty on cougars; concurrently, settlers depleted wolf populations to protect the diminishing elk herds and to protect livestock."

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
14	Olympic	1982	Oregon State University	Leslie, David M.	Nutritional ecology of cervids in old-growth forests in Olympic National Park, Washington	elk	yes	Page 8: "Wolves, Canis lupus, were extirpated from the Olympic Peninsula by the 1920s."
15	Olympic	1986	Oregon State University	Schroer, Gregory L.	Seasonal movements and distribution of migratory Roosevelt elk in the Olympic Mountains, Washington	elk	no	
16	Olympic	1993	Oregon State University	Happe, Patricia Jenkins	Ecological relationships between cervid herbivory and understory vegetation in old-growth Sitka spruce-western hemlock forests in western Washington	understory	yes	Page 10: "Due to the public outcry associated with theperceived low elk numbers, bounties were established to control cougar in 1904 (wolves were extirpated by 1930)..."
17	Olympic	2000	University of Washington	Riege, Dennis Alan	Arrested succession in old fields within a temperate rain forest.	range condition	no	
18	Olympic	2005	University of Washington	Fetherston, Kevin L.	Pattern and process in mountain river valley forests	trees	no	
19	Olympic	2008	University of Montana	Griffin, Suzanne Cox	Demography and ecology of a declining endemic| The Olympic marmot	marmot	yes	Page 24: ". . . predator-prey dynamics on the peninsula have been altered by the extirpation of the wolf (Canis lupus) from the peninsula in the early 20th century and the simultaneous arrival of the coyote (C. latrans) . . ."

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
20	Olympic	2008	University of Washington	Stolnack, Scott A.	Patterns of conifer establishment and vigor on montane river floodplains in Olympic National Park, Washington, USA	trees	no	
21	Olympic	2014	University of Washington	Lewis, Jeffrey Charles	Post-Release Movements, Survival, and Resource Selection of Fishers (Pekania pennanti) Translocated to the Olympic Peninsula of Washington.	fisher	no	
22	Olympic	2020	University of Washington	Murphy-Williams, Maia.	Climate Change Impacts in Alpine Meadows: Environmental Factors Correlated with the Decline of the Olympic Marmot (Marmota olympus) Population in Olympic National Park, Washington State	marmot	yes	Page 35: "Without the competition from wolves, invasive coyotes arrived in the Olympics. Predation on the Olympic marmot by coyotes has been shown in previous research to be a significant factor in marmot decline (Figure 1) (Witczuk et al. 2013, Griffin et al. 2008)."
23	Redwood	2010	California State University System	Teraoka, Emily	Structure and composition of old-growth and unmanaged second-growth riparian forests at Redwood National Park, USA	trees	no	
24	Redwood	2016	Texas State University – San Marcos	Kolbe, Nicholas R.	Density-Dependent Not - Independent Factors Influence Roosevelt Elk Recruitment in the Bald Hills of Redwood National Park	elk	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
25	Rocky Mountain	2013	Colorado State University	Kaczynski, Kristen Mannix	Riparian willow decline in Colorado: interactions of ungulate browsing, native birds and fungi	shrubs	yes	Page 13: "Elk populations have increased since the early 1900's due to the extirpation of wolves, while moose were introduced into Colorado in the late 1970's
26	Rocky Mountain	2015	Colorado State University	Craig, Apryle Dawn	Impacts of elk management and riparian condition on songbirds in Rocky Mountain National Park	shrubs	yes	Abstract: ". . . riparian willow (Salix spp.) communities in Rocky Mountain National Park (RMNP) are declining as a result of a trophic cascade involving the local extinction of wolves (Canis lupus) and an exponential increase in elk (Cervus elaphus)."
27	Rocky Mountain	2019	Colorado State University	Laurel, DeAnna J.	Effects of beaver engineering on downstream fluxes in Colorado mountain streams	shrubs	yes	Page 15: "Wolves were hunted to extinction in Rocky Mountain National Park during the 1920s and the numbers of elk and moose within the national park rose steadily during the 20th century."

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
28	Rocky Mountain	2021	Colorado State University	Contento, Taryn Elizabeth	Willow growth response to altered disturbance regimes in Rocky Mountain National Park: herbivory, water levels, and hay production	shrubs	yes*	Page 6: "Increased herbivory from native species is often caused by mass extinction that led to the loss of apex predators and subsequent growth of prey species population that feed on riparian vegetation (Berger et al., 2001).
29	Theodore Roosevelt	1988	Montana State University	Sullivan, Mark Gerald	Distribution, habitat use, and food habits of reintroduced elk in Theodore Roosevelt National Park, North Dakota	elk	yes*	Page 32: "The cow-calf ratio in September 1985 was 45:100. This was less than expected for an area devoid of large predators."
30	Theodore Roosevelt	1989	Montana State University	Westfall, Jerry Allen	The ecology of reintroduced elk in Theodore Roosevelt National Park, North Dakota	elk	no	
31	Theodore Roosevelt	1998	Montana State University	Lewis, Stephen Thomas	Evaluation of habitat use by a transplanted bighorn sheep herd in Theodore Roosevelt National Park	bighorn sheep	no	
32	Theodore Roosevelt and Wind Cave	2010	Texas State University – San Marcos	Miller, Shelley D.	Comparative Study of the Spatial Organization and Zoogeomorphic Effects of Black-tailed Prairie Dogs	prairie dog	no	
33	Wind Cave	1998	South Dakota State University	Bauman, Peter J.	The Wind Cave National Park Elk Herd: Home Ranges, Seasonal Movements, and Alternative Control Methods	elk	yes*	Page 6: "Currently, natural regulation of elk populations in WICA is not feasible, principally because there are few suitable predators found in this relatively small, fenced park (Varland et al. 1978)."

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
34	Wind Cave	2001	South Dakota State University	Duckwitz, Jeremy J.	Small Mammal Survey of Wind Cave National Park.	small mammals	no	
35	Wind Cave	2004	South Dakota State University	Sievers, Jaret D.	Factors Influencing a Declining Pronghorn Population in Wind Cave National Park, South Dakota	pronghorn	no	
36	Wind Cave	2007	South Dakota State University	Chronert, Jamie M.	Ecology of the Coyote (Canis latrans) at Wind Cave National Park.	coyote	yes	Page 1: "Several explanations have been put forth for coyote expansion across North America, including the extirpation of wolves . . . In Yellowstone National Park, for instance, the extirpation of gray wolves may have permitted higher coyote population densities . . . (Crabtree and Sheldon 1999)."
37	Yellowstone	1966	Colorado State University	Oldemeyer, John Lee	Winter ecology of bighorn sheep in Yellowstone National Park	bighorn sheep	no	
38	Yellowstone	1968	Colorado State University	Woolf, Alan	Summer ecology of bighorn sheep in Yellowstone National Park	bighorn sheep	no	
39	Yellowstone	1981	Montana State University	Tyers, Daniel Bruce	The condition of the northern winter range in Yellowstone National Park : a discussion of the controversy.	range condition	yes	Page 86: "One was the near elimination of the grey wolf and mountain lion that disturbed the mutually beneficial relationship between predators and plant eaters.

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
40	Yellowstone	1990	Utah State University	Kay, Charles E.	Yellowstone's Northern Elk Herd: A Critical Evaluation of the "Natural Regulation" paradigm	range condition	yes	Page 2: "...government agents eliminated all wolves and most mountain lions from the park by the late 1920s. After this had been accomplished, the Park Service came to believe that its eradication of native predators had permitted the northern elk herd to irrupt and overuse its range."
41	Yellowstone	1994	Montana State University	Sikes, Derek Scott	Influences of ungulate carcasses on Coleopteran communities in Yellowstone National Park, USA	scavengers	no	
55 journal articles								
42	Badlands	1998	Journal of Wildlife Management	Biggins, DE; Godbey, JL; Hanebury, LR; Luce, B; Marinari, PE; Matchett, MR; Vargas, A	The Effect of Rearing Methods on Survival of Reintroduced Black-Footed Ferrets	black-footed ferret	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
43	Badlands	2013	Conservation Genetics	Sasmal, Indrani; Jenks, Jonathan A.; Waits, Lisette P.; Gonda, Michael G.; Schroeder, Greg M.; Datta, Shubham	Genetic Diversity in a Reintroduced Swift Fox Population	swift fox	yes	Page 93: "The species declined during the mid-1800s, largely due to habitat loss and poisoning targeted at wolves (Canis lupus) and coyotes (Canis latrans)."
44	Grand Teton	1991	Applied Animal Behaviour Science	Boyce, MS	Migratory Behavior and Management of Elk (Cervus-Elaphus)	elk	yes	Page 243 :The major predator on elk in Jackson Hole was the wolf {Canis lupus) before its extirpation during the 1920s (Weaver, 1979)."
45	Grand Teton	1996	Canadian Journal of Zoology-Revue Canadienne De Zoologie	Smith, BL; Anderson, SH	Patterns of Neonatal Mortality of Elk in Northwest Wyoming	elk	no	
46	Grand Teton	1998	Journal of Wildlife Management	Smith, BL; Anderson, SH	Juvenile Survival and Population Regulation of the Jackson Elk Herd	elk	no	
47	Mount Rainier	1999	Journal of Range Management	Sharrow, SH; Kuntz, DE	Plant Response to Defoliation in a Subalpine Green Fescue Community	range condition	no	
48	Olympic	1993	Northwest Science	Schroer, GL; Jenkins, KJ; Moorhead, BB	Roosevelt Elk Selection of Temperate Rain-Forest Seral Stages in Western Washington	elk	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
49	Olympic	1994	Northwest Science	Woodward, A; Schreiner, EG; Houston, DB; Moorhead, BB	Ungulate-Forest Relationships in Olympic-National-Park - Retrospective Exclosure Studies	range condition	no	
50	Olympic	1996	Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere	Schreiner, EG; Krueger, KA; Happe, PJ; Houston, DB	Understory Patch Dynamics and Ungulate Herbivory in Old-Growth Forests of Olympic National Park, Washington	range condition	no	
51	Olympic	2008	Ecohydrology	Beschta, Robert L.; Ripple, William J.	Wolves, Trophic Cascades, and Rivers in the Olympic National Park, USA	trees	yes	Page 118: "Gray wolves (Canis lupus) were extirpated in the early 1900s from the Olympic Peninsula of northwestern Washington."
52	Olympic	2013	Journal of Mammalogy	Witczuk, Julia; Pagacz, Stanislaw; Mills, L. Scott	Disproportionate Predation on Endemic Marmots by Invasive Coyotes	marmot	yes	Page 711: "One unknown but potentially important factor is the absence of gray wolves, extirpated from the Olympic Peninsula about 1930 (Scheffer 1995)."
53	Olympic	2015	Journal of Zoology	Witczuk, J.; Pagacz, S.; Gliwicz, J.; Mills, L. S.	Niche Overlap Between Sympatric Coyotes and Bobcats in Highland Zones of Olympic Mountains, Washington	marmot	yes	Page 2: "The subsequent increase in coyote abundance closely paralleled a dramatic decrease and eventual extinction of the wolf Canis lupus population (Scheffer, 1995)."

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
54	Olympic	2017	Earth Surface Processes and Landforms	East, Amy E.; Jenkins, Kurt J.; Happe, Patricia J.; Bountry, Jennifer A.; Beechie, Timothy J.; Mastin, Mark C.; Sankey, Joel B.; Randle, Timothy J.	Channel-Planform Evolution in Four Rivers of Olympic National Park, Washington, USA: The Roles of Physical Drivers and Trophic Cascades	range condition	yes	Page 1011: ". . . to investigate whether physical or trophic-cascade-driven ecological factors – excessive elk impacts after wolves were extirpated a century ago – are the dominant drivers of channel planform in these gravel-bed rivers."
55	Olympic	2021	Ecosphere	Woodward, A.; Jenkins, K. J.; Harmon, M. E.	Plant Community Succession Following Ungulate Exclusion in a Temperate Rainforest	range condition	yes	Page 3: ". . . the hypothesis that wolf extirpation has created a trophic cascade whereby elk numbers are adversely impacting river morphology through their negative effects on riparian forest vegetation (Beschta and Ripple 2008)."
56	Redwood	2014	Journal of Mammalogy	Starns, Heath D.; Ricca, Mark A.; Duarte, Adam; Weckerly, Floyd W.	Climatic and Density Influences on Recruitment in an Irruptive Population of Roosevelt Elk	elk	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
57	Redwood	2015	California Fish and Game	Kolbe, Nicholas R.; Weckerly, Floyd W.	Home-Range Overlap of Roosevelt Elk Herds in the Bald Hills of Redwood National Park	elk	no	
58	Redwood	2018	California Fish and Game	Tolliver, James D. M.; Weckerly, Floyd W.	Abundance, Habitat and Occupancy of Roosevelt Elk in the Bald Hills of Redwood National Park	elk	no	
59	Redwood	2021	Basic and Applied Ecology	Weckerly, Floyd W.; Kolbe, Nicholas R.; Schmidt, Kristin N.; Bensen, Keith J.	Prescribed Fire Has Slight Influence on Roosevelt Elk Population Dynamics	elk	no	
60	Rocky Mountain	1997	Ecography	Baker, WL; Munroe, JA; Hessl, AE	The Effects of Elk on Aspen in the Winter Range in Rocky Mountain National Park	aspen	yes	Page 155: "Major predators, such as gray wolf canus lupus and grizzly bear Ursus arctos, were extirpated before park establishment."

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
61	Rocky Mountain	1997	Landscape Ecology	Stohlgren, TJ; Coughenour, MB; Chong, GW; Binkley, D; Kalkhan, MA; Schell, LD; Buckley, DJ; Berry, JK	Landscape Analysis of Plant Diversity	range condition	no	
62	Rocky Mountain	1999	Landscape Ecology	Suzuki, K; Suzuki, H; Binkley, D; Stohlgren, TJ	Aspen Regeneration in the Colorado Front Range: Differences at Local and Landscape Scales	aspen	no	
63	Rocky Mountain	1999	Oecologia	Alstad, KP; Welker, JM; Williams, SA; Trlica, MJ	Carbon and Water Relations of *Salix Monticola* in Response to Winter Browsing and Changes in Surface Water Hydrology: An Isotopic Study Using $\delta^{13}C$ and $\delta^{18}O$	willow	no	
64	Rocky Mountain	2001	Journal of Range Management	Menezes, RSC; Elliott, ET; Valentine, DW; Williams, SA	Carbon and Nitrogen Dynamics in Elk Winter Ranges	willow	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
65	Rocky Mountain	2001	Oecologia	Peinetti, HR; Menezes, RSC; Coughenour, MB	Changes Induced by Elk Browsing in the Aboveground Biomass Production and Distribution of Willow (*Salix Monticola* Bebb): Their Relationships With Plant Water, Carbon, and Nitrogen Dynamics	willow	no	
66	Rocky Mountain	2002	Climatic Change	Wang, GM; Hobbs, NT; Singer, FJ; Ojima, DS; Lubow, BC	Impacts of Climate Changes on Elk Population Dynamics in Rocky Mountain National Park, Colorado, USA	elk	yes*	Page 206: "Many of these areas lack large capable predators."
67	Rocky Mountain	2002	Journal of Wildlife Management	Lubow, BC; Singer, FJ; Johnson, TL; Bowden, DC	Dynamics of Interacting Elk Populations Within and Adjacent to Rocky Mountain National Park	elk	yes	Page 773: ". . . but 2 major predators (wolves [Canis lupus] and grizzly bears [Ursus arctos]) have been eliminated from this system. . ."
68	Rocky Mountain	2002	Journal of Wildlife Management	Zeigenfuss, LC; Singer, FJ; Williams, SA; Johnson, TL	Influences of Herbivory and Water on Willow in Elk Winter Range	willow	yes	Page 788: " Large predators and some herbivores have been eliminated. . ."
69	Rocky Mountain	2002	Landscape Ecology	Peinetti, HR; Kalkhan, MA; Coughenour, MB	Long-Term Changes in Willow Spatial Distribution on the Elk Winter Range of Rocky Mountain National Park (USA)	willow	yes*	Page 352 "...possibly due in part to predator eradication. . ."

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
70	Rocky Mountain	2003	Landscape Ecology	Kaye, MW; Stohlgren, TJ; Binkley, D	Aspen Structure and Variability in Rocky Mountain National Park, Colorado, USA	aspen	no	
71	Rocky Mountain	2003	Environmental Management	Weisberg, PJ; Coughenour, MB	Model-Based Assessment of Aspen Responses to Elk Herbivory in Rocky Mountain National Park, USA	aspen	yes	Page 167: "Prior to their extirpation, wolves may have limited the RMNP herd to fluctuations within a range of 300–800 elk (Coughenour 2001)."
72	Rocky Mountain	2004	Journal of Wildlife Management	Schoenecker, KA; Singer, FJ; Zeigenfuss, LC; Binkley, D; Menezes, RSC	Effects of Elk Herbivory on Vegetation and Nitrogen Processes	range condition	yes*	Page 837: "The elimination of large predators, disruption and loss of migration routes, and the creation of artificial forage sources in towns and developed areas have contributed to possible overabundance and/or overconcentrations of elk in some areas (Wagner et al. 1995)."
73	Rocky Mountain	2005	Western North American Naturalist	Bender, LC; Cook, JG	Nutritional Condition of Elk in Rocky Mountain National Park	elk	no	
74	Rocky Mountain	2005	Ecological Applications	Kaye, MW; Binkley, D; Stohlgren, TJ	Effects of Conifers and Elk Browsing on Quaking Aspen Forests in the Central Rocky Mountains, USA	aspen	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
75	Rocky Mountain	2005	Rangeland Ecology & Management	Baker, BW; Peinetti, HR; Coughenour, MB	Resilience of Willow Stems After Release From Intense Elk Browsing	willow	yes	Page 575: "The elimination of large predators has reduced predation risk in some riparian areas. . ."
76	Rocky Mountain	2005	Canadian Journal of Botany-Revue Canadienne De Botanique	Gage, EA; Cooper, DJ	Patterns of Willow Seed Dispersal, Seed Entrapment, and Seedling Establishment in a Heavily Browsed Montane Riparian Ecosystem	willow	yes*	Page 685: "However, because elk in Rocky Mountain National Park lack predators, there appears to be no effective constraint on browsing."
77	Rocky Mountain	2005	Ecological Applications	Baker, BW; Ducharme, HC; Mitchell, DCS; Stanley, TR; Peinetti, HR	Interaction of Beaver and Elk Herbivory Reduces Standing Crop of Willow	willow	yes*	Page 111: "Large herbivores congregate in these areas because they lack disturbance from large predators. . ."
78	Rocky Mountain	2008	Forest Ecology and Management	Binkley, Dan	Age Distribution of Aspen in Rocky Mountain National Park, USA	aspen	yes*	Page 797: "increased browsing that may have resulted from extirpation of predators. . ."
79	Rocky Mountain	2008	Journal of Environmental Management	Bradford, John B.; Hobbs, N. Thompson	Regulating Overabundant Ungulate Populations: An Example for Elk in Rocky Mountain National Park, Colorado	elk	no	
80	Rocky Mountain	2009	Isotopes in Environmental and Health Studies	Menezes, Romulo S. C.	Isotopic Evidence of the Effects of Herbivory and Landscape Position on Plant Nitrogen Sources in a Riparian Ecosystem	willow	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
81	Rocky Mountain	2012	Ecosphere	Baker, Bruce W.; Raul Peinetti, H.; Coughenour, Michael B.; Johnson, Therese L.	Competition Favors Elk Over Beaver in a Riparian Willow Ecosystem	elk	yes	Page 9: "The elk population grew quickly in the absence of wolves (Canis lupus) and grizzly bears (Ursus arctos), which also had been extirpated."
82	Rocky Mountain	2015	Forest Ecology and Management	Kaczynski, Kristen M.; Cooper, David J.	Post-Fire Response of Riparian Vegetation in a Heavily Browsed Environment	range condition	no	
83	Rocky Mountain	2016	Ecosphere	Schweiger, E. William; Grace, James B.; Cooper, David; Bobowski, Ben; Britten, Mike	Using Structural Equation Modeling to Link Human Activities to Wetland Ecological Integrity	range condition	yes	Page 5: "Human activities extirpated (Canis lupus) wolves largely before the park was established."
84	Theodore Roosevelt	2002	Journal of Environmental Management	Irby, LR; Norland, JE; Westfall, JA; Sullivan, MA	Evaluation of a Forage Allocation Model for Theodore Roosevelt National Park	range condition	no	
85	Theodore Roosevelt	2007	Journal of Wildlife Management	Sargeant, Glen A.; Oehler, Michael W., Sr.	Dynamics of Newly Established Elk Populations	elk	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
86	Theodore Roosevelt	2014	California Fish and Game	Sargeant, Glen A.; Oehler, Michael W.; Sexton, Chad L.	Use of Water Developments by Female Elk at Theodore Roosevelt National Park, North Dakota	elk	no	
87	Wind Cave	2007	Frontiers in Ecology and the Environment	Ripple, William J.; Beschta, Robert L.	Hardwood Tree Decline Following Large Carnivore Loss on the Great Plains, USA	oak and cottonwood trees	yes	Page 241: "we conducted a retrospective analysis of large carnivores. . ."
88	Yellowstone	1991	Journal of Wildlife Management	DelGiudice, GD; Singer, FJ; Seal, US	Physiological Assessment of Winter Nutritional Deprivation in Elk of Yellowstone-National-Park	elk	no	
89	Yellowstone	1991	Journal of Applied Ecology	Coughenour, MB	Biomass and Nitrogen Responses to Grazing of Upland Steppe on Yellowstone Northern Winter Range	herbaceous vegetation	no	
90	Yellowstone	1992	Ecology	Frank, DA; McNaughton, SJ	The Ecology of Plants, Large Mammalian Herbivores, and Drought in Yellowstone-National-Park	range condition	no	
91	Yellowstone	1993	Oecologia	Frank, DA; McNaughton, SJ	Evidence for the Promotion of Aboveground Grassland Production by Native Large Herbivores in Yellowstone-National-Park	herbaceous vegetation	no	
92	Yellowstone	1993	Ecological Modelling	Turner, MG; Wu, YG; Romme, WH; Wallace, LL	A Landscape Simulation-Model of Winter Foraging by Large Ungulates	elk	no	

#	National Park	Year	University/ Journal	Author(s)	Title	Taxa	Wolves?	Quote
93	Yellowstone	1994	Ecological Applications	Turner, MG; Wu, YA; Wallace, LL; Romme, WH; Brenkert, A	Simulating Winter Interactions Among Ungulates, Vegetation, and Fire in Northern Yellowstone Park	elk	no	
94	Yellowstone	1994	Biogeochemistry	Frank, DA; Inouye, RS; Huntly, N; Minshall, GW; Anderson, JE	The Biogeochemistry of a North-Temperate Grassland With Native Ungulates - Nitrogen Dynamics in Yellowstone-National-Park	herbaceous vegetation	no	
95	Yellowstone	1994	Journal of Range Management	Singer, FJ; Mark, LC; Cates, RC	Ungulate Herbivory of Willows on Yellowstone Northern Winter Range	willow	yes	Page 435: ". . .since wolves (Canis Lupus) are estirpated. . ."
96	Yellowstone	1994	Canadian Journal of Zoology-Revue Canadienne De Zoologie	Singer, FJ; Norland, JE	Niche Relationships Within a Guild of Ungulate Species in Yellowstone-National-Park, Wyoming, Following Release From Artificial Controls	elk	yes	Page 1383: ". . .the removal of a significant predator, the gray wolf (Canis lupus). . ."

Table S4. Mammal irruptions following predator declines. The table shows the top 10 wild terrestrial mammal species ranked by biomass as given in Greenspoon et al. (2023). The first four columns, taken from Table 1 of Greenspoon et al. (2023), indicate species' common name, scientific name, estimated total biomass in Mt, and estimated total population size. Where applicable, the final column contains a quote and reference related to the species' predators. For information on predator conservation status, see Wolf and Ripple (2017).

Common	**Scientific**	**Mass (Mt)**	**# (M)**	**Status of predators**
White-tailed deer	*Odocoileus virginianus*	2.7	45	"Ungulate irruptions, primarily of deer, began to occur following the occurrence of wolf extinctions, with most of the western irruptions (80 percent) taking place between 1935 and 1945" (Ripple and Beschta 2005)
Wild boar	*Sus scrofa*	1.9	30	n/a
African savanna elephant	*Loxodonta africana*	1.3	0.5	n/a
Eastern gray kangaroo	*Macropus giganteus*	0.6	20	"In Australia, the native Thylacine (*Thylacinus cynocephalus*) was eliminated from the mainland about 5,000 years ago. Livestock grazing was introduced [...], after which the Dingo (*Canis dingo*) was eliminated from much of the mainland, and Indigenous hunting was suppressed [...]. This combination of actions is believed to have reduced predation/hunting pressure on the larger marsupial herbivores, and in combination with [...], has led to significant increases in the distribution and density of many large macropod species, notably the Eastern Grey Kangaroo (Macropus giganteus) [...]" (Gordon et al. 2021)
Mule deer	*Odocoileus hemionus*	0.5	7	"Results from Zion National Park generally affirm Leopold's (1943) interpretation of the mule deer irruption on the Kaibab Plateau of Arizona and its effect on plant communities after cougar and wolf eradication" (Ripple et al. 2010)

Moose	*Alces alces*	0.5	1.5	“In 9 of 10 multiyear, telemetry-based studies in moose–bear–wolf systems, predation (primarily on calves) was the dominant factor affecting moose population dynamics compared with harvest, malnutrition, disease, and adverse weather [...]” (Boertje et al. 2010)
Red deer (elk)	*Cervus elaphus*	0.5	2	“Wolf and lynx predation kept red deer and roe deer below carrying capacity and constantly provided remains for scavengers” (Ordiz et al. 2021)
European roe deer	*Capreolus capreolus*	0.4	20	“[...] found that roe deer densities were significantly lower in areas with sympatric wolves and lynx compared to areas with wolves alone or areas without either predator” (Ripple and Beschta 2012)
Red kangaroo	*Macropus rufus*	0.4	10	“dingo removal was linked to a dramatic increase in red kangaroo abundance” (Hunter et al. 2018)
Common warthog	*Phacochoerus africanus*	0.3	5	n/a

Supplemental Methods

As the basis for our study, we began with a list of all national parks in the continental Northwestern United States west of 100 degrees longitude and between 40 and 49 degrees latitude, yielding an initial total of 13 national parks. We excluded Crater Lake and North Cascades National Parks since they had few wolves historically, resulting in a final total of 11 national parks (Figure S1).

For each national park in our analysis, we searched the Open Access Theses and Dissertations website (OATD; available at OATD.org) for theses and dissertations (hereafter, "theses") using an exact keyword match based on the full name of the national park, which covers titles, abstracts, subjects, etc. We focused on theses and dissertations rather than individual manuscripts because, by definition, these bodies of work represent in-depth field studies where a thorough historical context of the study area would be expected to be presented. To identify scientific journal articles published since 1965, we then searched the Web of Science Core Collection database for "topic" (including titles, abstracts, and keywords) matching each national park name.

For national parks where wolves were extirpated, but have since returned, we only considered theses and articles published when wolves were absent: Yellowstone prior to 1995, Glacier prior to 1985, Grand Teton prior to 1999, and Lassen Volcanic prior to 2015.

OATD indexes theses from a large set of universities and repositories. As of April, 2023, there were over 6.5 million theses indexed on OATD, including some published as early as the late 1700s. We supplemented the list of search results by adding several theses that were not included in the results.

After obtaining initial lists of theses (n = 433) and journal articles (n = 126), we scanned their abstracts in order to remove publications that were not relevant to terrestrial food web ecology. Specifically, we retained publications that were on topics that might be affected by wolf extirpation, only including elk (*Cervus canadensis*) and plants that elk consume, as well as coyotes and coyote prey and smaller predators. We then searched the full text of each remaining publication for the terms "wol", "carn", and "preda" to determine whether (1) the historical presence of wolves was considered, (2) the historical presence of wolves was not considered, but extirpated large carnivores or large predators in general were discussed, or (3) extirpated wolves, large carnivores, or large predators were not discussed at all. In the first two cases, we obtained a relevant short quote from the thesis abstract or full text.

Supplemental References

Bailey V. 1918. Report on investigation of elk herds in the Olympic Mountains, Washington. Olympic National Forest, Olympia, WA.

Beschta RL, Ripple WJ. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142: 2401–2414.

Boertje RD, Keech MA, Paragi TF. 2010. Science and Values Influencing Predator Control for Alaska Moose Management. Journal of Wildlife Management 74: 917–928.

Gordon I, Snape M, Fletcher D, Howland B, Coulson G, Festa-Bianchet M, Caley P, McIntyre S, Pople T, Wimpenny C, others. 2021. Herbivore management for biodiversity conservation: a case study of kangaroos in the Australian Capital Territory (ACT). Ecological Management & Restoration 22: 124–137.

Greenspoon L, Krieger E, Sender R, Rosenberg Y, Bar-On YM, Moran U, Antman T, Meiri S, Roll U, Noor E, others. 2023. The global biomass of wild mammals. Proceedings of the National Academy of Sciences 120: e2204892120.

Grimm RL. 1939. Northern Yellowstone winter range studies. The Journal of Wildlife Management 3: 295–306.

Hunter DO, Lagisz M, Leo V, Nakagawa S, Letnic M. 2018. Not all predators are equal: a continent-scale analysis of the effects of predator control on Australian mammals. Mammal Review 48: 108–122.

Leopold A. 1949. A Sand County almanac and sketches here and there. Oxford University Press.

Ludlow W. 1875. Report of a Reconnaissance of the Black Hills of Dakota, Made in 1874. US Government Printing Office.

Murie OJ. 1935. Report on the Elk of the Olympic Peninsula. Biological Survey.

Newman CC. 1954. Roosevelt Elk of Olympic National Park. National Park Service.

[NPS] National Park Service. 1956. Management Plan for the Northern Elk Herd, Yellowstone National Park, 30 November, 1956. USDI, National Park Service.

Ordiz A, Aronsson M, Persson J, Støen O-G, Swenson JE, Kindberg J. 2021. Effects of human disturbance on terrestrial apex predators. Diversity 13: 68.

Palais H. 1942. The cattle industry in the Black Hills. The Black Hills Engineer 28: 2–107.

Ripple WJ, Beschta RL. 2005. Linking wolves and plants: Aldo Leopold on trophic cascades. BioScience 55: 613–621.

Ripple WJ, Beschta RL. 2012. Large predators limit herbivore densities in northern forest ecosystems. European Journal of Wildlife Research 1–10.

Ripple WJ, Rooney TP, Beschta RL. 2010. Large predators, deer, and trophic cascades in boreal and temperate ecosystems. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, DC, USA 141–161.

Ripple WJ, Wirsing AJ, Wilmers CC, Letnic M. 2013. Widespread mesopredator effects after wolf extirpation. Biological Conservation 160: 70–79.

Rush WM. 1933. Northern Yellowstone elk study. Montana Fish and Game Commission.

Schwartz J. 1939. The Olympic elk study. USDA Forest Service, Olympic National Forest, Olympia, WA.

Sumner E. 1938. Special report of elk in Olympic National Park. USDI National Park Service, San Francisco, California, USA.

Wolf C, Ripple WJ. 2017. Range contractions of the world's large carnivores. Royal Society Open Science 4: 170052.