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Viewpoint

A shifting ecological baseline after wolf extirpation

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Shifting baselines in ecology encapsulate the gradual and often unnoticed alterations in ecosystems over time, leading to a redefinition of what is considered normal or baseline conditions. A wide range of human activities, such as habitat alteration, pollution, invasive species, and climate change, can contribute significantly to these shifts, reshaping the structure and function of ecosystems. Nonanthropogenic factors such as natural evolutionary and geological processes can also play a role in driving these transitions. Identifying the historical ecological baseline, representing the so-called original state before most human impacts, is challenging. It generally requires careful analysis of long-term retrospective data, although research across systems (i.e., space for time substitution) can also provide relevant information (Klein and Thurstan 2016). Nevertheless, recognizing shifting baselines is crucial for effective conservation research and to allow thinking beyond the current state. In the present article, for illustrative purposes, we focus on one type of shifting baseline: the loss of a top terrestrial predator.

Throughout history, human actions have often induced pronounced effects on the behavior, distribution, or density of native animal species (Young et al. 2016). In some instances, we have affected populations and distributions of species and altered food webs; in others, we have simply replaced wild animals with domesticated ones. Over time, humans have hunted and persecuted large predators, causing extirpation or displacement at local scales and reduced numbers and distribution at regional and global scales. The reduction and loss of large terrestrial predators across landscapes has led to various direct and indirect effects, which can have complex and lengthy interaction chains (Ripple et al. 2014).

Trophic cascades, which represent the influences of predators that propagate downward through food webs and across multiple trophic levels, have become increasingly recognized by the scientific community (Estes et al. 2011). Large predator removal or displacement is associated with increases in both large herbivore prey and mesopredator (midsize predator) populations (Ripple et al. 2014). Increases in large herbivores can result in population overshoot, intensified foraging pressure, and reductions or damage to native plants and other basal resources (Beschta and Ripple 2009). Released mesopredator populations can reach high densities, leading to the decline or extirpation of small predators and prey populations and potentially affecting the stability and structure of animal communities (Ritchie and Johnson 2009).

Gray wolves (*Canis lupus*) in North America have experienced a substantial contraction of their historical range, at one point almost disappearing from the contiguous 48 United States. However, their conservation is important in part because of the potential cascading effects wolves can have on lower trophic levels. Namely, the proliferation and changes to behavior and density of large herbivores following the extirpation or displacement of wolves can have major effects on various aspects of vegetation structure, succession, productivity, species composition, and diversity (Soulé et al. 2003), which, in turn, can have implications for overall biodiversity and the quality of habitat for other wildlife.

In the present article, we describe the results of our investigation of publications involving field work in national parks in the US Northwest from the 1950s to 2021 (supplemental figure S1). Our rationale for selecting Western parks is because they contain relatively large intact landscapes with limited confounding anthropogenic influences, and it is a region where trophic cascades have been documented following the loss of predators. Western park biologists' historical observations and age structure data for deciduous trees reveal substantial ecological impacts of ungulates following the removal of gray wolves and other predators (supplemental table S1, figure 1). This has led to declines in long-term tree recruitment, influencing plant communities and ecological processes. The observed impacts in these parks, along with findings from other Western North American studies, suggest broader changes to ecosystem processes and lower trophic levels in areas where gray wolves have been extirpated or displaced (White et al. 1998).

Moreover, in the absence of wolves, high mesopredator densities can be an important driver of ecosystem modification. For example, coyotes (*Canis latrans*) have been identified by the US Fish and Wildlife Service, as well as on state lists of concern, as significant predators of various threatened or endangered vertebrate

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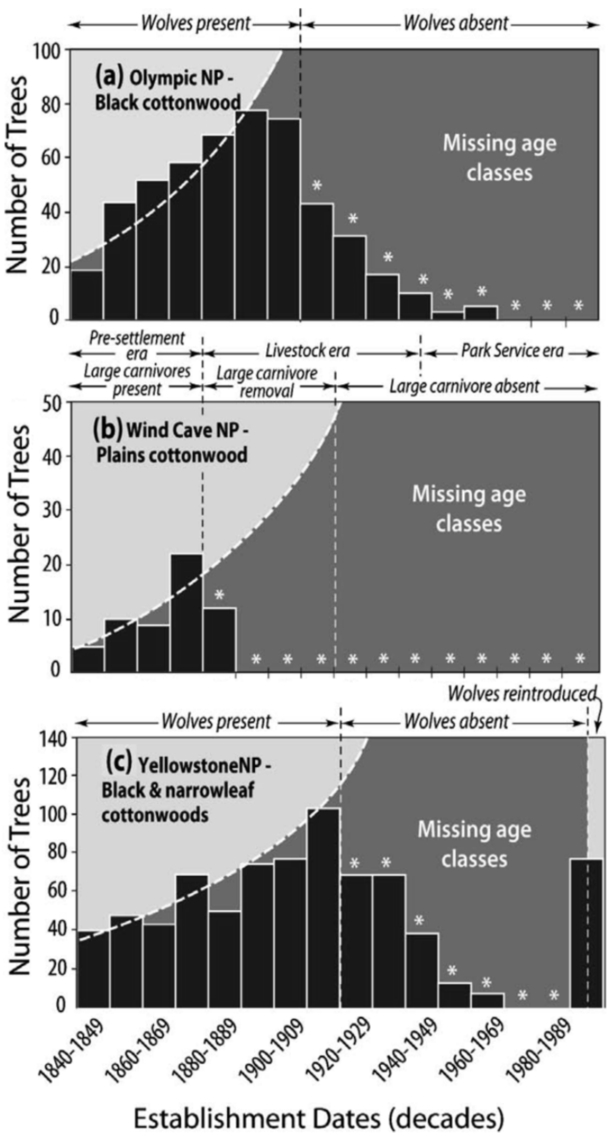

Figure 1. Age structure from 1840 to 2000 for (a) black cottonwood (*Populus trichocarpa*) along river floodplains in western Olympic National Park, (b) plains cottonwood (*Populus deltoides*) in Wind Cave National Park and (c), black cottonwood and narrowleaf cottonwood (*Populus angustifolia*) along floodplains of the Lamar River in the northern range of Yellowstone National Park. Significant decreases (95% lower confidence interval) in observed tree frequencies following the loss of gray wolves and other large predators are indicated by an asterisk (*). Wolf restoration likely contributed to the increase in cottonwoods in 1990–1999 in panel (c). Source: Adapted from Beschta and Ripple (2009).

taxa (supplemental table S2, Ripple et al. 2013). Wolves can reduce coyote populations, thereby mediating their predation of prey and smaller-predator populations, such as rodents, ungulates, small carnivores, leporids, and birds (Newsome and Ripple 2015). Broad changes to lower trophic levels and ecosystem processes have occurred in national parks of the western United States, where wolves or other large predators have been extirpated or displaced (Beschta and Ripple 2009). Therefore, it is crucial to consider the cascading effects of large predator removal when investigating ecological questions within these landscapes. Although there is still debate on the specific extent of the ecological effects resulting from the restoration of wolves, the science is relatively settled regarding the topic of this article, which is about long-term legacy impacts of wolf extirpation. Researchers generally agree that the loss of wolves and other large predators, followed by increased browsing by elk (*Cervus canadensis*), was the main cause for the decline in woody plant communities in many Western parks (White et al. 1998, Beschta and Ripple 2009, Peterson et al. 2020, Hobbs et al. 2024). Our values are to maintain and restore the structure and function of ecosystems using native species whenever possible, including native predators.

Analysis and findings

With the consequences of gray wolf extirpation in mind, we asked if published journal articles and graduate student research (masters theses and PhD dissertations; hereafter, *theses*) included information on the extirpation of wolves in national park study areas in the northwestern United States. For our analysis, we searched the literature for ecology theses and journal articles dealing with 11 national parks in the continental northwestern United States, where wolves had or have been extirpated (for detailed methods, see the supplement). There are two major pathways for wolf-triggered trophic cascades, with one involving the major prey (elk) and the other with the principal mesopredator competitor (coyote; Ripple et al. 2014). Therefore, we further restricted our list to theses and articles involving taxa that might be affected by wolf extirpation, including elk (*C. canadensis*) and plants that elk consume, as well as coyotes and coyote prey and smaller predators. We then searched the full text of each selected publication for the text strings *wol*, *carn*, and *preda* and classified each according to whether it at least partially addressed the historical effects of wolves or other large carnivores (see the supplemental material for our methods). Finally, we identified the taxa or other groups (e.g., small mammals) that may have been affected by the loss of wolves or other top predators.

We identified 96 relevant publications (41 theses and 55 journal articles) across the 11 national parks in our final list, with publication dates ranging from 1955 to 2021 for theses and 1991 to 2021 for journal articles (figure S1, supplemental table S3). The national parks with the most studies were Rocky Mountain (28), Olympic (18), and Yellowstone (14). The taxa studied in these 96 publications could be directly or indirectly affected by the presence or absence of wolves (figure 2). In total, approximately 41% (39 of 96) of the publications mentioned or discussed the historical presence of wolves or large carnivores, but most (approximately 59%) did not (table S3). The results for the theses and journal articles were similar; specifically, 61% (25 of 41) of the theses and 58% (32 of 55) of the articles did not consider the historical presence of large carnivores (table S3).

Implications

By the 1930s, wolves were largely gone from the American West, including from its national parks. Most published ecological research from this region we evaluated occurred after the extirpation of wolves. Therefore, our understanding of plant community succession and structure, animal community dynamics, and ecosystem functions may be affected by shifting baselines—a failure to recall or quantify past ecological conditions or to recognize the effects of large predator loss in contemporary ecosystems (Soga and Gaston 2018). This situation indicates that the scientific community should consider characterizing the historical context and reference conditions when exploring areas where large predators, such as wolves, are absent, functionally extinct, or persist in reduced densities.

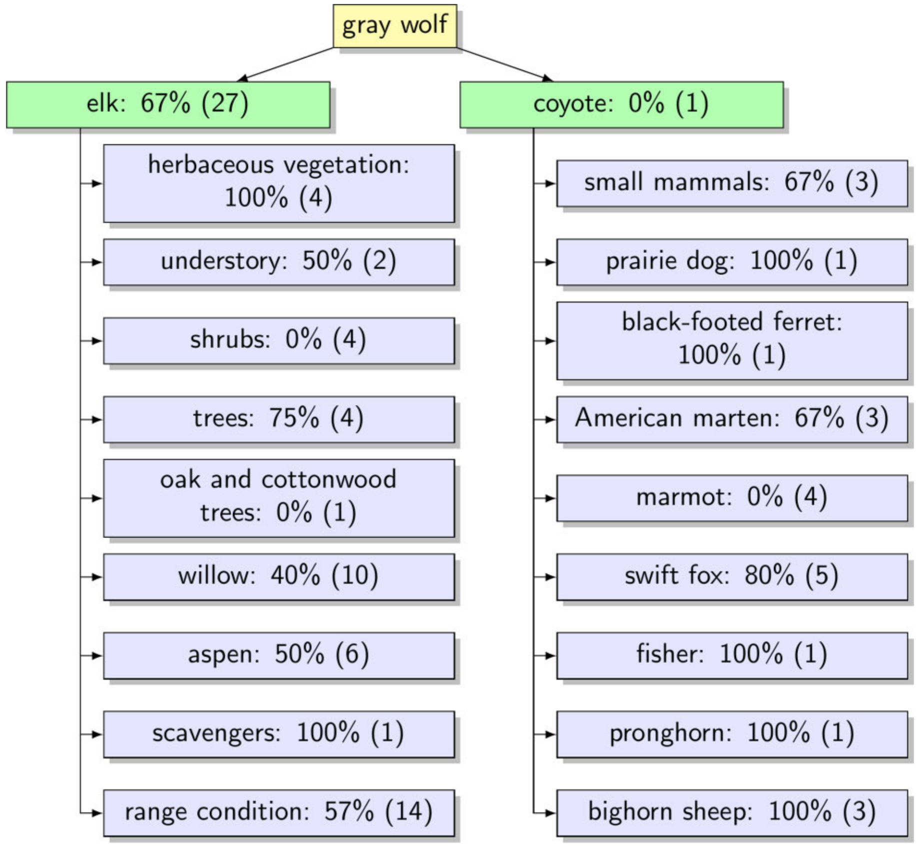

Figure 2. Potential direct and indirect impacts of wolves in 96 national park theses and journal articles. The diagram shows direct and indirect effects of wolves based on taxonomic groups. The numbers indicate the percentages of theses and journal articles that *did not* consider the historical presence of wolves or other larger carnivores followed by the number of associated studies. The included species are gray wolf (Canis lupus), elk (Cervus canadensis), coyote (Canis latrans), prairie dog (genus Cynomys), American marten (Martes americana), marmot (genus Marmota), swift fox (Vulpes velox), fisher (Pekania pennanti), pronghorn (Antilocapra americana), bighorn sheep (Ovis canadensis), aspen (Populus tremuloides), black-footed ferret (Mustela nigripes), oak (Quercus macrocarpa), cottonwood (Populus spp.).

As a starting point for future ecological studies in national parks, we recommend that researchers include a discussion of how the presence or absence of large predators may or may not have influenced their results and conclusions. Obviously, in addition to a loss of predators, there are other potential anthropogenic legacies within national parks that ideally should be considered—most notably, fire suppression, invasion by exotic plants and animals, past overgrazing by livestock, and climate change. Also, wolf-triggered trophic cascades may be context dependent and are not found in all landscapes. To consider the effects of the loss of predators and other potential legacy factors, we recommend researchers investigate park archives to exploit historical data and information to help understand the history of predators and their prey, as well as discriminate among competing explanations for any shifting ecological baselines. National park archives can be a treasure for historical ecological information (e.g., see Ripple et al. 2022).

Studying an altered ecosystem without recognizing how or why the system has changed over time because of the absence of a large predator could have serious implications for wildlife management, biodiversity conservation, and ecosystem restoration, like diagnosing a sick patient without a baseline health exam. Early on, Aldo Leopold concluded that the first rule of restoration is to do no harm and cautioned against apathy to species loss by stating, “To keep every cog and wheel is the first precaution of intelligent tinkering” (Leopold 1949). Therefore, restoration decisions made without consideration of past conditions may themselves continue to alter ecosystems in novel ways. Various national parks in the western United States, which are considered the crown jewels of American wilderness, lack their apex predators, resulting in them being shadows of their supposed ecological integrity (i.e., a sick patient).

Although we have focused our analysis on national parks in the northwestern United States, the same issues likely apply to research conducted in other portions of the United States, as well as in many areas globally, given the widespread and long-term impacts of the decline of large predators and the release of herbivore prey (supplemental table S4). Currently, approximately 40% of all wild terrestrial mammal biomass is concentrated in only 10 species, including five deer species (family Cervidae) and two kangaroo species from the family Macropodidae (Greenspoon et al. 2023). Sympatric gray wolves and bears (*Ursus* spp.) apparently limit the densities of northern hemisphere cervids, which were found to be nearly six times greater in areas without wolves than in areas with wolves (Ripple and Beschta 2012). White-tailed deer (*Odocoileus virginianus*) have the greatest biomass among terrestrial wild mammals, and it is well documented that their populations can irrupt and cause significant browsing impacts following wolf extirpation and land-use change (Rooney and Waller 2003). In parts of Australia, kangaroos have become highly abundant in the absence of their predators, thylacines (*Thylacinus cynocephalus*) and dingoes (*Canis lupus dingo*; Croft and Witte 2021).

Notably, large predator populations are missing or depleted in many marine ecosystems as well (McCauley et al. 2015). For example, a recent global assessment documented widespread depletion of reef sharks, with these predators being functionally extinct in nearly one in five coral reef ecosystems surveyed (MacNeil et al. 2020). The absence of sharks can have consequences for marine ecosystems, including by enabling overabundant green turtle (*Chelonia mydas*) populations that jeopardize seagrass meadows (Heithaus et al. 2014). Therefore, consideration of historical conditions and the implications of large predator absence is also a necessary component of contemporary marine research (Heithaus et al. 2012).

Conclusions

Ecological context can be difficult to establish. Given the plethora of other anthropogenic impacts after European colonization, at the very least, researchers should consider conditions prior to European contact to properly contextualize the current state of most ecosystems. Even then, Indigenous peoples may have had profound effects on some environments relative to their “natural” states, and many of these effects are poorly understood. For example, humans may have contributed to the extinction of megafauna through overhunting at the end of the Pleistocene more than 10,000 years ago (Ripple and Van Valkenburg 2010) and, likewise, may have affected wildlife populations during the Holocene several hundred years ago (Kay 1994). The loss of large predators is only one of many significant changes to our environment, and we encourage researchers to focus not only on predators but on other factors as well.

There are a number of ongoing debates in ecological restoration, including how to handle cases where former keystone species are now extinct, as well as how the potential risks and benefits of nonnative species in ecosystems compare. Although addressing these restoration issues may involve value judgements, sound scientific knowledge of ecosystem processes and functions is also vital. Therefore, protecting Earth’s remaining natural areas can be an important aid to future researchers when studying altered ecosystems. As humanity’s impacts on the biosphere continue to accelerate in the Anthropocene, a better understanding of past conditions and how they have been modified by human actions is crucial for attaining ecology-based restoration goals. The desired state for restoration of a given system likely varies depending on many factors and will require careful consideration and the involvement of many stakeholders and interest groups.

Supplemental material

Supplemental data are available at *BIOSCI* online.

Data Availability

The data underlying this article are available in the article and in its online supplementary material.

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