



Top predators provide insurance against climate change

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Recent research by Wilmers *et al.* shows that top predators might buffer some of the ecological effects of climate change. Top predators can regulate the structure of entire communities and dampen their variability; however, in their absence, prey populations are likely to fluctuate greatly owing to bottom-up factors. Restoring top predators to their natural environment could provide insurance against undesired effects of climate change on ecological communities.

The ecological effects of climate change

Global climate change is an increasing and overarching threat that affects all levels of biodiversity, from species to ecosystems. The response of communities and ecosystems to global climate change is highly unpredictable because of the interactions between local (e.g. local overexploitation and pollution) and global (e.g. biological invasions) stressors. Regardless of the magnitude and the timing of changes, it is possible to predict qualitatively that global warming will increase disease transmission [1], cause species extinctions [2] and range shifts [3], affect the phenology and physiology of organisms, and cause shifts in the structure of communities and ecosystems [4]. Most difficult to predict are shifts in community structure, because of the non-linear nature of species interactions. However, it is likely that compounded perturbations will increase the likelihood of unpleasant ecological surprises, such as trophic cascades and ecosystem phase shifts [5]. This reduces the predictive power of ecological studies and makes it difficult to identify local management actions that can cope with an ever-changing and warmer world.

Can we identify practical short-term management actions to help us prevent greater population and community fluctuations associated with climate change? Recent research by Wilmers and collaborators [6–8] indicates that the presence of top predators might provide one mechanism for ecosystem resistance to climate change. These findings could open the door to practical management actions to restore ecosystem structure, and to enhance the resilience and the ability of ecosystems, and of the species inhabiting them, to adapt to a changing climate.

Top predators as buffers: models

Recent work by Wilmers and collaborators [6,7] indicates that restoring top predators might help buffer the effects of climate change in a forest–grassland ecosystem. Wilmers

and Getz [6] modeled the trophic dynamics of scavengers that depend on winter carrion for survival and reproductive success in Yellowstone National Park. In the Park, the top predator, the gray wolf *Canis lupus* (Figure 1), became ecologically extinct during the 1920s, but was reintroduced in 1995. Before the reintroduction, the non-predation mortality of elk *Cervus elaphus*, the most abundant ungulate in the Park, was greater during severe winters and at the end of moderate winters, but lower during early winter or during mild winters. This winter mortality is caused by a combination of increased metabolic activity and decreased access to food resources buried in deep snow. In the absence of wolves, scavengers such as ravens, eagles, bears and coyotes relied heavily on weather-related elk mortality. However, Wilmers and Getz found that, since 1948, winters are getting shorter. Early snow thaw reduces late-winter elk weather-related mortality and, hence, carrion, causing potential food bottlenecks for scavengers. In addition, the concentration of carrion in a shorter time period during the middle of winter might favor scavenger species that are able to access carrion more easily, such as ravens and bald eagles [9]. Therefore, global warming might increase the survival of elk, with potential cascading effects propagating across the entire ecosystem as winter scavengers switch to other forms of prey at other times of the year.

Once wolves were reintroduced in Yellowstone, they became the primary source of elk mortality throughout the year. Wilmers and Getz's model predicts that the carrion available to scavengers during late winter will decline regardless of the presence of wolves, because of a warming-related reduction in snow depth that enhances elk survival. However, wolves will mitigate this late-winter decline because of the additional predation mortality. The carrion that the wolves generate will also be available throughout winter.

What would happen under uncertain climate change scenarios? Wilmers and collaborators [7] observed 240 wolf-killed elk carcasses in Yellowstone, and incorporated species-specific consumption data in a model to evaluate the effects of wolves under different climate change scenarios as predicted in the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (<http://www.ipcc.ch>). The authors predicted that the stronger the climate anomaly (e.g. El Niño events), the stronger the effects of wolves on buffering carrion availability. Furthermore, regardless of whether the planet is warming or cooling, wolves will dampen the interannual variability in carrion availability. Therefore,

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Figure 1. The gray wolf *Canis lupus* and elk *Cervus elaphus* in Yellowstone National Park. Reproduced with permission from Dan Hartman.

the presence of wolves will enable scavengers to adapt to the effects of global warming over a longer timescale than if wolves were absent.

Top predators as buffers: empirical evidence

The modeling results obtained by Wilmers and collaborators are intriguing and suggest that top predators provide insurance against the ecological impacts of climate change. Wilmers *et al.* [8] conducted an empirical test of this hypothesis using field data from another location, Isle Royale, Michigan. Isle Royale is a National Park harboring a forest ecosystem where wolves are top predators, moose *Alces alces* are a common prey, and balsam fir *Abies balsamea* are the primary winter food resource of the moose. Wilmers *et al.* took advantage of a 50-year time series, and a natural experiment, to determine the role of wolves in buffering the effects of climate variability.

From 1980 to 1982, canine parvovirus (CPV) caused the wolf population in Isle Royale to crash. Wilmers *et al.* quantified the contribution of predation and climate variability [mostly caused by the North Atlantic Oscillation (NAO)] before and after the introduction of CPV. When wolves were abundant, the moose population exhibited slow and steady changes in numbers; when wolf numbers crashed, the moose population displayed a steep increase in numbers in moderate winters, and dramatic declines in severe winters. When wolves were present, top-down regulation (predation) accounted for 38% of the variation in moose population growth rate, whereas bottom-up factors (mostly climate variability) explained only 13%; this ratio was reversed after the wolf population declined, when top-down regulation explained only 1% of the variation, with bottom-up factors accounting for 28%. The switch from top-down to bottom-up regulation resulted in a large increase in the influence of the NAO on moose population dynamics.

The buffering effects of wolves on changes in moose numbers caused by climate variability are likely to cascade through the entire food chain, because an increase in moose abundance results in heavy browsing, and a subsequent decrease in understory fir [10]. Wilmers *et al.*'s [8] results thus suggest that top predators buffer the system against community-wide fluctuations caused by climate variability.

We need the predators back

Are these results general? There is increasing evidence that the loss of top predators can trigger cascades of ecological degradation [11], although a recent meta-analysis suggests that, on average, predators increase the temporal variability of their herbivore prey [12]. Unfortunately, the loss of top predators from most terrestrial and marine ecosystems occurred long before the onset of modern ecology [13–15], which might have hindered our understanding of the importance of top-down control, and overemphasized the importance of bottom-up abiotic factors. The depletion of large predators is still ongoing in some ecosystems (e.g. as a result of bushmeat trade, high-seas and deep-sea fishing; [16]), while we try to undo it in others (e.g. Yellowstone). Regardless of the importance of specific predators in particular systems, Wilmers *et al.*'s findings strongly support the hypothesis that intact food webs including top predators appear to be more resistant to stress. Bottom-up factors thus appear to be more important when food chains are shortened and top-down control is reduced.

The work of Wilmers and collaborators is especially important because they explicitly tested the role of predators in mitigating the effects of global climate change. Their results clearly show that restoring top predators could be crucial for buffering the effects of global warming, and also for reducing uncertainty in an increasingly unpredictable and warmer world.

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