16 Restoring Predators as a Hedge against Climate Change

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Climate change and the loss of ecologically relevant
large terrestrial carnivore populations are two important challenges currently facing conservation practitioners (Ray et al. 2005, Sutherland
et al. 2009). Little attention is given, however, to how these two problems might be related, and how mitigation efforts for each might be
united. Here we explain how predators cannot only influence the cause
of climate change (atmospheric carbon) but also influence—directly and
indirectly—climate impacts on their prey and on entire ecological communities. We draw on an emerging body of work to conceive ways in
which the restoration of large carnivores might provide opportunities for
both carnivore conservation and mitigation of climate change.

Mitigation of Atmospheric Carbon

Hairston et al. (1960) hypothesized that the world is "green" because predators hold herbivores in check, thus allowing plants to thrive.
Fretwell (1977) generalized this idea by suggesting that the parity of a
food chain determines whether plants will be primarily limited in their
biomass by resources or herbivory. He hypothesized that plants in odd-numbered food chains are limited by resources because predators hold
herbivores in check, whereas plants in even-numbered food chains are
limited by herbivory. As most large mammal food webs in terrestrial systems are comprised of three links, theoretically plants in ecosystems with
large mammalian predators should be, at least in part, released from the
pressures of herbivory and should thus become more resource-limited.
While this general phenomenon has been well documented in aquatic
systems (Strong 1992), its broad applicability to terrestrial systems remains a topic of active research (Pace et al. 1999).

This is a challenging question to address because of the difficulty in
experimenting with large mammals and the long time scales over which
terrestrial systems cycle. Additionally, some herbivores are able to escape
predator limitation through either migration or large body size (Sinclair
2003). Recent studies on wolves (*Canis lupus*) and pumas (*Puma con-*

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color) in North America (Berger et al. 2001, Ripple and Beschta 2004a, Beschta 2005, Fortin et al. 2005, Hebblewhite et al. 2005, Ripple and Beschta 2006, Ripple and Beschta 2008) and on jaguars (*Panthera onca*) in the tropics (Terborgh et al. 2001) suggest, however, that the indirect effects of large predators on plant biomass can be substantial if predators are at ecologically relevant densities (Berger and Smith 2005). Most of the above-ground carbon in the biosphere is contained in the tissue of plants. If predators indirectly influence the biomass of plants, what is their potential influence on the ability of plants to sequester atmospheric carbon?

Few mammalian-initiated trophic cascades are as well understood as the one generated by sea otters on kelp forests in nearshore environments (Estes and Palmisano 1974). Sea otters along the North American west coast prey on sea urchins, which in turn feed on kelp. In areas with sea otters, kelp is plentiful. In areas without them, kelp is rare. Recent work by Wilmers et al. (in press) shows that kelp forests throughout the North American range of otters contain 1×10^{10} kg more carbon in total than they would without sea otters. This amounts to an approximately 11% reduction in atmospheric carbon present in the three-dimensional column projected above the otter range, or 43% of the increase in atmospheric carbon since preindustrial times. This substantial amount of carbon would currently fetch in excess of $700 million on the European carbon market.

While the mechanism by which sea otters impact kelp densities is the same as that operating in terrestrial ecosystems (namely, trait and density impacts on prey) the outcome is more extreme. The near-total depletion of plants by herbivores in aquatic environments is made possible by, among other causes, the lack of cellulose (Power 1992), which is indigestible by most herbivores. In terrestrial systems, cellulose comprises much plant matter, so the indirect effects of predators on plant biomass are less than in aquatic systems. Yet it is in cellulose that much of the above-ground biosphere's carbon resides. Coniferous forests and grasslands, for instance, hold nearly 100 and 10 times as much carbon per square meter of earth's surface respectively than do kelp forests. Thus, extrapolating the impact of sea otters to terrestrial ecosystems implies only a 1% to 10% impact of predators on terrestrial plant biomass. While studies attempting to quantify the indirect effects of large terrestrial carnivores on plant biomass at the ecosystem scale have not been conducted to our knowledge, indirect evidence suggests that these influences can be important. For instance, the disappearance of top predators from forest fragments in Venezuela led to a dramatic rise in herbivore numbers and a conse-

quent decline in plant biomass (Terborgh et al. 2001). Similarly, the absence of wolves in eastern North America has led to a fivefold increase in white-tailed deer placing increased pressure on vegetation (Crete 1999). If predators were restored to ecologically effective densities throughout all ice-free portions of the earth's surface, and if they exerted a 1% to 10% impact on plant biomass, they would indirectly help sequester 23 gigatons of atmospheric carbon. This represents roughly 15% of the expected increase in atmospheric carbon over the next 50 years, which is equivalent to one of the seven carbon reduction "wedges" needed to stabilize global CO_2 (Pacala and Socolow 2004); it would currently fetch some $1.6 trillion on the European Carbon Exchange.

This simple calculation illustrates the potential importance of large predators to the global carbon cycle. In practice, the effects of predator repatriation on plant carbon stocks in many places would not be practicable, as a sizeable portion of the earth's land surface has been converted to agriculture and is thereby unsuitable for either native herbivores or predators. Moreover, in many areas large ungulates themselves are being (or have already been) destroyed through overhunting by humans, so there is no need for control of their populations by predator reintroduction. Still, many opportunities, in addition to the sea otter example, might exist for mitigating atmospheric carbon levels by restoring large predators to ecologically effective densities.

Predators as Buffers

Ecologically effective predator populations not only can directly offset atmospheric carbon increases, but also can partially buffer those systems from existing or impending changes in climate. While climate may directly impact dynamics at all levels of a food web, studies of the effects of climate on large mammal food webs have primarily focused on bottom-up pathways (but see Post et al. 1999). That is, changes in climate that impact the timing, growth, and composition of plants in turn influence the quality and quantity of forage for herbivores. Herbivores that are resource-limited, therefore, might be impacted more by a changing climate than are herbivores that are predator-limited. Additionally, the feedback of herbivores on plants and other components of an ecosystem might be driven more by climate in the absence of predators. As we discuss below, these effects might play out over both ecological and evolutionary time scales.

Ecological Time Sscales

Over ecological time scales, predators can act as keystone species by exerting strong top-down control over community dynamics (Power et al.

1996). This maintains biodiversity by suppressing competitively dominant prey (Paine 1966) and possibly by enhancing spatial heterogeneity in prey resource use (Mech 1977). A substantial body of ecological theory now supports the hypothesis that more biodiverse systems are more resilient to outside perturbations (McCann 2000). We hypothesize, then, that ecosystems with keystone species at ecologically functional densities will be more resilient to climate change. Below we explore some of the different mechanisms that operate on ecological time scales and are imposed by predators that might contribute to this role.

Population Dynamics of Prey

The population dynamics of large herbivores that are resource-limited (as in the absence of carnivores) are more likely to be influenced by variation in climate than are the population dynamics of those that are predator-limited (Wilmers et al. 2006). Mild years lead to the buildup of prey populations that then decline rapidly during climatically harsh years. This can lead to overcompensating density dependence and boom-bust cycles in herbivore populations. Populations with boom-bust dynamics are more at risk of extinction than are stable populations of equivalent mean population size, because they risk stochastic extinction during the bust phase of the cycle, and also because they have lower effective population sizes, which makes them less adaptable to novel changes in the environment, such as new diseases.

Examination of ungulate dynamics supports this idea. Reindeer introduced to Saint Matthew Island in the Bering Sea in 1944 in the absence of predators grew to a population of 6,000 individuals in 1960 before crashing to fewer than 42 individuals after food supply shrank dramatically when climate conditions worsened (Klein 1968). The Soay sheep population on Saint Kilda Island, Scotland, displays similar dynamics, though on a shorter time scale. Here the population experiences boom-bust cycles every two to four years as density interacts with climatic conditions to create high-variance population cycles (Coulson et al. 2001). In Greenland, recent analyses have shown that predatorless caribou populations are subject to trophic mismatches between the timing of parturition and phenology of vegetation (Post et al. 2008). In years when the mismatch is greatest, caribou calf production drops as much as fourfold.

A recent analysis of moose population dynamics on Isle Royale, Michigan, suggests that when predators occur at ecologically relevant densities, climate-induced fluctuations in prey populations are dampened. By taking advantage of a disease outbreak in wolves, Wilmers et al. (2006)
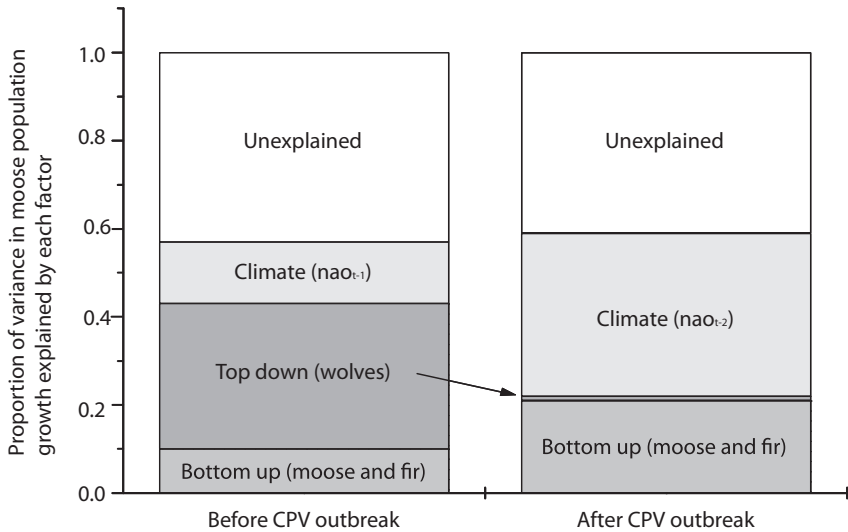
Figure 16.1. Role of canine parvovirus (CPV) outbreak on trophic factors affecting moose population dynamics. Hatched areas represent the variance R_x^2 in moose population growth rate explained by each variable. Before the outbreak of CPV, known biotic factors regulating moose population dynamics are primarily top-down (3:1 ratio) while after outbreak they are primarily bottom-up (28:1). Climate is a small factor governing moose population dynamics when moose are controlled by wolves, and a large factor after wolf populations become decimated by CPV. The arrow indicates the proportion of variation explained by top-down control in the post-CPV period. Redrawn from Wilmers et al. 2006.

showed that when wolves were unaffected by disease and were thus dynamically coupled to moose, they regulated the moose populations. When wolf populations crashed due to the introduction of canine parvovirus (CPV) to the island, however, the moose population mimicked the dynamics of the Saint Matthews caribou herd; they grew to record high numbers before plummeting to very low numbers during a severe winter (figure 16.1).

Ungulate populations in ecosystems where wolves have been extirpated, such as elk in Rocky Mountain and Yellowstone national parks before wolf reintroduction, are often limited by interactions between density and winter severity. Severe winters restrict access to forage and create a food bottleneck that limits the size of ungulate populations. As the climate warms and winters become increasingly mild, ungulate populations in wolf-free systems are predicted to increase in size (Wang et al. 2002, Creel and Creel 2009). This is likely to lead to overgrazing and boom-bust

cycles in ungulate population dynamics, as less frequent severe winters coincide with larger herds and lead to large winter die-offs.

Recent theoretical work has elucidated the mechanisms by which predators, large herbivore life histories, and climate interact to influence ungulate population dynamics. More than 30 years ago, Eberhardt (1977) hypothesized that the vital rates of large vertebrates in different life-history stages change in a predictable sequence as density increases. Juvenile survival declines first, followed by adult fecundity and finally by adult survivorship. By incorporating these features into a stochastic population model, Wilmers et al. (2007b) showed that the level of yearly variation in climatic conditions can have profound impacts on moose population dynamics on Isle Royale. If a good year during which the population grows is followed by a bad year, then density dependence is experienced only in juvenile survivorship and the population declines by a small amount. If a few good years in a row occur before a bad year, then the population can grow to larger densities such that when a bad year strikes, density dependence is experienced in both juvenile survivorship and adult fecundity, thus resulting in a larger population decline. The extreme population crashes occur when many good years in a row are followed by a bad year. This allows the population to grow so large that when a bad year strikes, density dependence is experienced by individuals in all life-history stages, and the population crashes. Paradoxically, then, a higher frequency of good years leads to more dramatic boom-bust cycles, with the population in bust years reaching much smaller sizes than it would given a lower frequency of good years.

Climate can be thought of as a factor that ratchets the negative effects of density dependence up a life-history gradient from declines in juvenile survival through adult fecundity and finally to adult survival. The stronger this ratchet, the less stable the population. If climate becomes increasingly mild (i.e., favorable to herbivores) but more variable over time, as many climate models predict (Boyce et al. 2006), it suggests a strengthening of this ratchet over time.

Large predators can act in opposition to this climate ratchet (figure 16.2). By killing prey and modifying herbivore behavior through fear so that they eat less, predators lower the population growth rates of large herbivores during good years (Wilmers et al. 2007a). This means that when a bad year arrives, the population density is smaller than it would have been without predators, and the consequent decline in population size is smaller. Hence, as in Isle Royale prior to the outbreak of CPV in the wolf population, the model suggests that predators buffer prey popula-
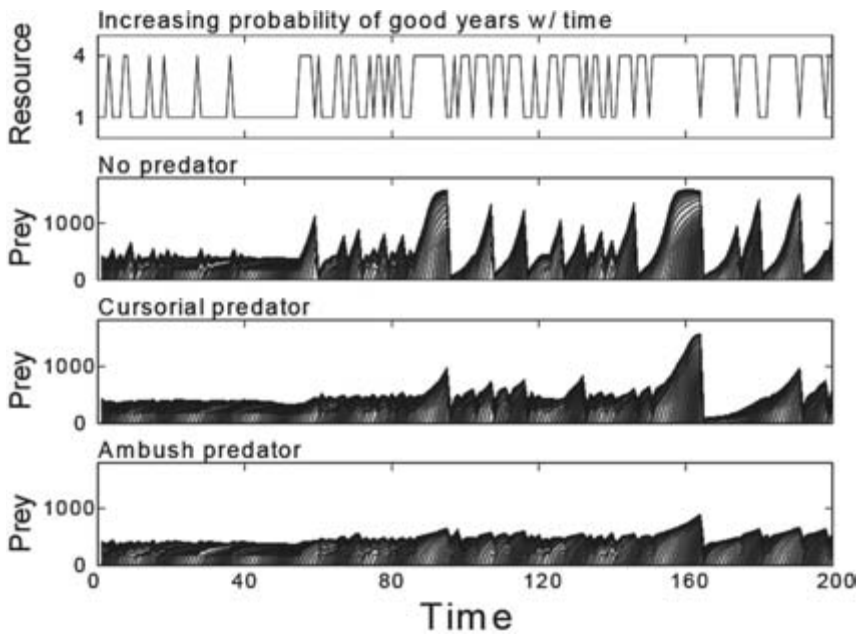
Figure 16.2. Climate change scenario depicting the influence of predation and the increasing frequency of favorable environmental conditions on the population fluctuations of an age-structured prey. As the frequency of favorable years increases, population fluctuations increase in magnitude because favorable conditions allow the population to grow to large densities which, in a poor year, leads to density dependence in multiple vital rates, and finally to a crash. Predators dampen the magnitude of these crashes because they retard the population's growth in good years. A climate change scenario depicting decreasing frequency of favorable conditions through time can be visualized by reading the figure right to left.

tions from the effects of climate, thus resulting in less variable prey population dynamics.

Under certain circumstances, predators might destabilize prey communities. Most famously this has been shown to occur in Fennoscandia rodent populations above 60 degrees latitude (Jedrzerjeski and Jedrzerjewska 1996, Kausrud et al. 2008). This is thought to arise because of inherent time lags associated with reproduction in a specialist predator feeding on a single prey. Below 60 degrees of latitude, the added presence of generalist predators stabilizes prey dynamics. This suggests that low-diversity ecosystems with single specialist predators will be less buffered from climate change than those with more diverse multiple-generalist predators. This example also emphasizes the importance of species diversity in promoting resilience to climate change effects (Kausrud et al. 2008).

Facilitative Effects

Another way in which predators might buffer the impact of climate change on ecological time scales is their influence on community dynamics, via their facilitative effects on scavengers. Wolves, for instance, have been documented to provide winter carrion to more than 40 species of vertebrate scavengers (Paquet et al. 1996, Wilmers et al. 2003b, Selva and Fortuna 2007) and more than 50 species of beetles (Sikes 1998, Wilmers unpublished data). For some species, this predator-derived subsidy can increase overwinter survival and reproduction (Wilmers et al. 2003a). In Yellowstone, the reintroduction of wolves dramatically changed the winter availability of carrion. Before wolf reintroduction, carrion availability was primarily a function of winter severity. During mild winters or at the beginning of winter, very little carrion was available. In contrast, during severe winters or at the end of winter, so much carrion would be available that vertebrate scavengers would be saturated; in the late spring, excess carcasses not exploited by this guild were consumed primarily by invertebrates. After wolf reintroduction, the dominant source of ungulate (in particular, elk) mortality shifted from winter severity to predation by wolves. The effect on carrion availability was that it became more predictable and less variable within and between years (Wilmers et al. 2003a).

The shift in the prime determinant of carrion availability away from winter severity and towards predation by wolves also meant that climate change would have less influence on carrion availability with wolves than without them. Winters in Yellowstone, as in many places across the globe, have been shortening (Wilmers and Getz 2005). This narrowing of the winter season would imply less carrion over a shorter time period in the absence of wolves. With wolves, however, carrion availability is primarily a function of wolf predation, so even as winters grow shorter, carrion is predicted to be available over roughly the same window of time (Wilmers and Getz 2005). Late-winter carrion is also reduced with the presence of wolves in the system (due to a predicted decrease in wolf kill rate), but to a much lesser extent, and over a longer time scale. This conceivably allows scavengers time to adapt to a changing environment over a time scale commensurate with natural processes (figure 16.3).

Predator-mediated carrion supply can also favor some scavenger species over others. The more pulsed and hence abundant a resource is, the more it favors "recruitment specialists" over "competitive dominants" (Wilmers et al. 2003b). Carrion is first consumed by dominant species (e.g., in Yellowstone, coyotes are dominant over eagles and ravens). But if the carrion is so plentiful that dominant species cannot consume it all, recruitment specialists will consume the rest. In Yellowstone, coyotes are

Reduction in scavenge from 1950 to 2000
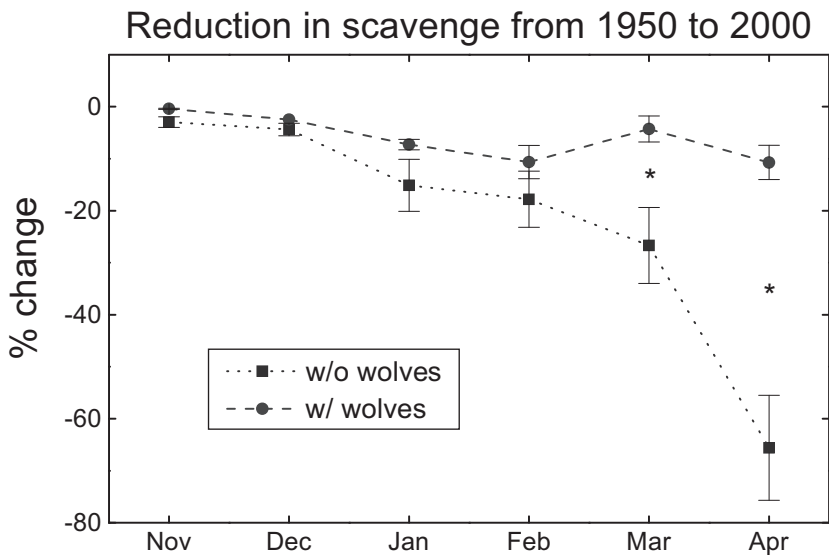
Figure 16.3. Percentage reduction (± SE) in winter carrion available to scavengers due to climate change from 1950 to 2000 under scenarios with and without wolves. The symbol * denotes a significant difference between the two scenarios.

limited to feeding on carrion within a few miles of their home range. If they are saturated with carcasses, bald eagles and ravens, which can recruit from many miles away, will build up their numbers and consume much of the carrion. The presence of wolves, by acting in opposition to the climate-induced pulsing of carrion, will therefore favor competitively dominant species over recruitment specialists.

By extending the time horizon over which winter carrion is available, wolf presence favors species, such as grizzly bears, that have strong seasonal patterns in resource use (figure 16.4). Recent work suggests that as temperatures rise, the buffering effect of wolves on scavengers grows stronger, and in particular on those with strong seasonal use in resources (Wilmers and Post 2006).

Structural Effects
Optimal foraging theory predicts that to maximize fitness, individuals will trade benefits associated with acquiring resources against the costs of acquiring those resources, which often take the form of increased predation risk (Sih 1987, Abrams 1991, Post et al. 2009). Several consequences of this perceived trade-off have been observed in large herbivores. Mech (1977) and later Lewis and Murray (1993) showed that boundaries

between wolf pack territories serve as refuges for herbivore prey. Recently, investigators have shown that elk avoid areas of high predation risk near creeks and rivers (Ripple and Beschta 2004a, Fortin et al. 2005).

Avoidance by large herbivores of areas with high predation risk (Mech 1977, Fortin et al. 2005) can increase spatial heterogeneity in plant composition and biomass. For instance, in Yellowstone and Banff national parks, cascading behavioral interactions appear to be influencing willow stand dynamics (Beyer et al. 2007), but not aspen (Hebblewhite et al. 2005, Kauffman et al. 2010). This increased heterogeneity can increase the resilience of communities in the face of environmental perturbations associated with interannual fluctuations in climate (Allen-Diaz and
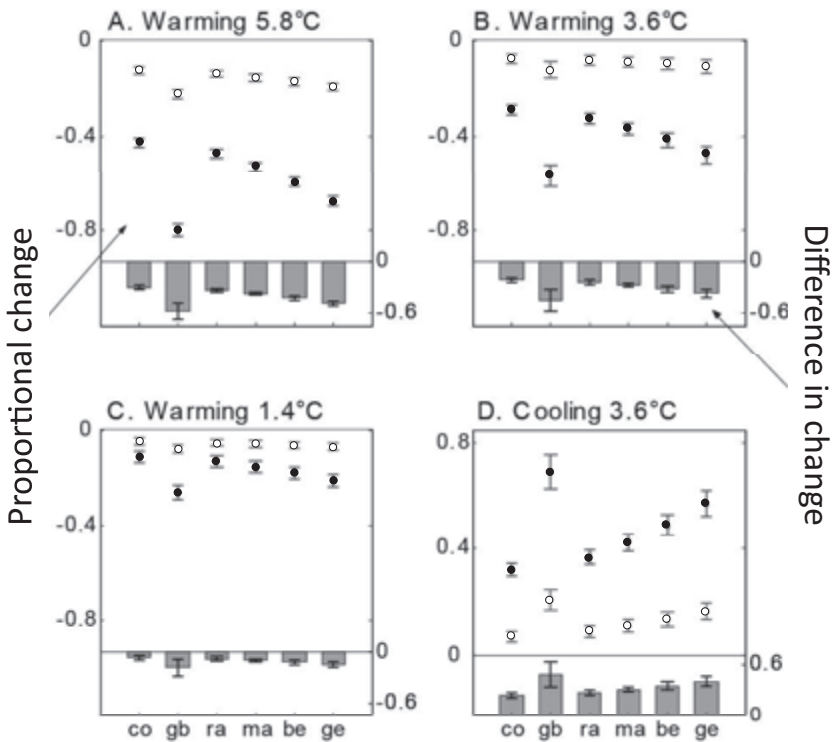
Figure 16.4. Changes in carrion consumption by the six most common scavenger species under (A) maximum, (B) mid-level, and (C) minimum warming, and (D) moderate cooling. Top panels display proportional change in mean carrion abundance ($\pm$ SE) to coyotes (co), grizzly bears (gb), ravens (ra), magpies (ma), bald eagles (be), and golden eagles (ge) from 2000 to 2100 under various climate change scenarios with and without wolves. Bottom panels display differences in availability of carrion to each scavenger species from 2000 to 2100 under scenarios with and without wolves. These graphs illustrate the magnitude of wolf buffering against changes in ENSO.

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Jackson 2000). An evenly grazed meadow, for instance, is more likely to respond uniformly to changes in precipitation or temperature than one with different vegetation heights and the associated differences in shade and soil moisture levels.

This effect is likely to be pronounced in riparian areas, and it can influence other species. The reemergence of wolves and cougars in areas of western North America has led to the return of riparian woody vegetation such as willow and cottonwood in some areas (Beschta 2003, Ripple and Beschta 2004b, Hebblewhite et al. 2005, Ripple and Beschta 2006, Beyer et al. 2007). Areas where riparian woody vegetation is not returning may be indications that the system has entered an alternative stable state, requiring the restoration of beaver to provide higher levels of fine sediment and shallower stream incision profiles necessary for high rates of willow growth (Wolf et al. 2007). Increased riparian woody vegetation provides shade for creeks, keeping water temperatures cool during the hot summer months. This is particularly important for native trout (e.g., *Salvelinus* spp.) that need cool water to survive through summer. While warmer ambient temperatures will raise the temperature of any body of water, shaded areas protected from direct sunlight will warm more slowly. Additionally, by stabilizing stream banks, providing leaf litter to streams, and providing woody debris important for pool formation, increased riparian woody vegetation likely increases habitat quality for native trout (Harig and Fausch 2002).

By shaping the spatial ecology of prey, predators indirectly buffer the base of the food web against climate change. At both population and individual levels and at multiple scales, foragers must constantly evaluate and respond to a shifting mosaic of benefits and costs of foraging in particular areas. And importantly, the trade-offs are not static. For example, predation risk can be spatially and temporally dynamic (Lima and Zollner 1996). Consequently, predator-mediated foraging behavior restricts herbivores from staying in one place (Forester et al. 2007), thus allowing plants to recover from browsing or grazing pressure. This in turn potentially provides them with resources to deal better with climate stressors.

Evolutionary Time

Predators might also drive diversity in foraging behaviors by herbivores over evolutionary time scales. Darimont et al. (2007) used stable isotope analysis to demonstrate that individuals within a black-tailed deer (*Odocoileus hemionus*) population in a coastal rain forest differed considerably in their use of different forest stand types under the risk of predation. Deer were killed by wolves in all areas, but the probability of mortality

increased in types of forest where the protein content of forage plants was higher—consistent with the hypothesis that foragers trade forage quality against the risk of predation. Moreover, individuals that specialized in any one stand type were more likely to be killed. This selection against specialization and individuals' differential responses to risk-reward trade-offs under the risk of predation together explained the observed diversity in foraging behaviors. This is important in the context of climate change because species with generalist life-history strategies are more likely to adapt to a changing climate than are specialists.

Management Implications

As we outline above, there are myriad reasons why managers might consider restoring predators to ecologically effective densities as an adaptive response to climate change. While large predators have recolonized certain areas and been reintroduced to others, this action will generally require a sea change in attitude towards predator management. Currently, predators are often managed for very low densities. This occurs for a number of reasons, chief among which in North America is to control depredation on livestock, and because of a perceived or real notion that large predators substantially suppress game populations.

The management of large game populations and the quota systems that go with it developed over the last century in an era of extremely low predator abundance. In North America, the eradication of wolves, bears, and pumas over large expanses of land meant that wildlife managers could essentially ignore predator effects in setting hunting quotas on deer and elk. Now that the importance of predators to proper ecological function is becoming well accepted in other domains, managers should be further motivated to act, given realized or impending climate change. This could take the form of adjusting hunting quotas (of predators or their prey) or control efforts to levels that can support ecologically effective densities of predators. Moreover, restoration efforts could reintroduce native predators to previously occupied portions of their historic range.

While human hunting might provide an adequate substitute for large carnivores in some situations, the influence of human hunting on ecosystems often has a very different impact than that of large carnivores (Berger 2005). Many of the indirect effects of predators on community structure, for instance, are mediated by behavior rather than by density. In Yellowstone, for instance, elk were managed for very low densities until the park service adopted a policy of natural regulation in the early 1970s (Houston 1982). During that period of low elk population density, however, riparian vegetation did not recover. It was not until reintroduced

wolves altered the "forage quality–predation risk tradeoff" that elk began to avoid valley bottoms, potentially allowing willow and cottonwood to come back. Furthermore, a recent review of the relative importance of trait-mediated interactions (TMIs) and density-mediated interactions (DMIs) showed that TMIs are as strong as DMIs on prey demographics and much stronger on cascading interactions. Density effects attenuate through food chains, while trait effects remain strong (Bolnick and Preisser 2005, Preisser et al. 2005).

Implementing climate change adaptation strategies will require new models that explicitly take predators into account. Conversely, strategies to conserve carnivores should now consider their potential role as hedges against climate change. Indeed, economic incentives or payoffs in the carbon markets of tomorrow might influence carnivore conservation and management. While the legal framework for buying and selling carbon from different sources is still rapidly evolving, it is not inconceivable that the potential carbon sink provided by predators such as sea otters could be sold to fund restoration to ecologically effective densities.

Harvest models that consider predators are needed to implement more effective game management, as discussed above. Predictive models of community response to climate change would also benefit by including strongly interacting species (Soule et al. 2005) such as top predators in order to improve the accuracy of their predictions. Recent empirical work has shown that ignoring species interactions can reverse the predicted response of community composition to climate change (Suttle et al. 2007). Areas with and without top predators may respond very differently, and these differences should be considered in predicting the ecological impacts of increased atmospheric carbon.

This emerging insight into the important role that terrestrial predators serve in buffering ecosystems from global climate change comes at a time when their own future is uncertain. Predators are declining more rapidly than any other food web group. The 2003 IUCN red list of threatened species lists 125 carnivores as threatened with extinction, and carnivores not on the list have, for the most part, experienced dramatic contractions of their range (Laliberte and Ripple 2003). Accordingly, repatriating predators to their historic ranges has enormous potential not only to provide well-known ecological services, but also to improve ecosystem resilience to climate change and drive down atmospheric carbon levels.

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