ECOLOGY

Filtering Wildlife

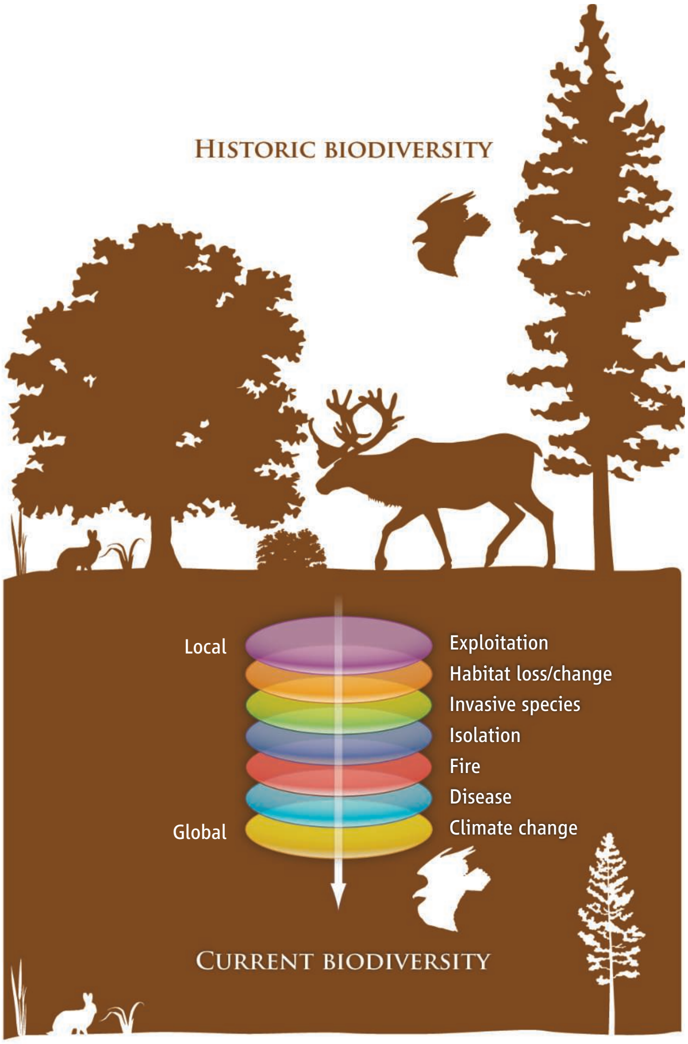
"Extinction filters" help visualize complex threats faced by wildlife in protected areas.

Justin S. Brashares

On 24 April 1903, U.S. President Theodore Roosevelt stood before a crowd outside Gardiner, Montana, and dedicated the world's first national park as a place where "the wild creatures of the Park are scrupulously preserved..." (*1*). Thirty years later, scientists reported the local extinction of Yellowstone National Park's "white-tailed deer, cougar, lynx, wolf, and possibly wolverine and fisher..." (*2*, *3*). More than 100,000 protected areas worldwide now follow in Yellowstone's footsteps, both in their goal of preserving wildlife and in the difficulties they face in achieving this goal. A growing literature highlights the diverse and complex threats faced by wildlife in protected areas, and the pressing need for better tools and monitoring programs for predicting, understanding, and addressing wildlife declines.

Protected areas are the undisputed backbone of wildlife conservation efforts on land and at sea. Analysts often use the pace and scale of their creation to assess global conservation strategies (*4*). Yet conservation biologists have long warned that even well-managed protected areas will lose species over time, and of the risks of relying on such areas as reservoirs for nature (*5*). Recent research suggests that habitat protection reduces extinction rates but also that extinctions occur regularly in protected areas of both developing and developed nations and at rates faster than predicted by conservative models (*6*, *7*). Alarmingly, there appear to be few obvious patterns to these extinctions that might allow conservationists to predict and protect those species most likely to be at risk (*7*–*10*).

At first glance, the causes of wildlife declines in a protected area may seem obvious. Excessive hunting, for instance, effectively extirpated wolves, mountain lions, and other large carnivores from Yellowstone National Park (*2*). Modern extinctions in protected areas, however, are seldom so easily attributed to one cause. Recent studies link them to an array of threats that vary, often unpredictably, across time and space (*7*–*10*). They range from global phenomena such as climate change and atmospheric pollution, to regional issues such as shifts in fire regimes, disease dynamics, or invasive species, to more localized threats such as overharvest, habitat conversion, and the effects of isolation. These threats can interact both additively and synergistically to create syndromes of extinction that confound diagnosis and remedy (*7*–*11*). A final layer of complexity is that each threat can have a unique impact that depends on an animal's vulnerability, as determined by life history and other traits (*8*).



Filtered out. Wildlife in protected areas (**top**) face a range of threats that can be envisioned as "extinction filters" (colored disks) passing through an ecological community. Species most vulnerable to a given threat, or to the combined or synergistic impacts of multiple threats, face local extinction (**bottom**).

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"Extinction filters" provide a useful, though static, tool for visualizing these complex threats, and predicting wildlife declines in protected areas. In this approach, each threat is envisioned as a filter that passes repeatedly through a wildlife community, selectively removing species most vulnerable to that threat and leaving less susceptible species (*12*). This framework assumes that (i) each filter selects on different traits of species and at varying strengths over time and space; and (ii) filters may act in conjunction or synergistically to heighten species' vulnerability. Characterizing any threat as a single filter, however, can be misleading. Climate change, for example, often is envisioned as an extinction filter, but realistically may be viewed as a phenomenon that creates or exacerbates myriad other filters (e.g., disease, fire, drought, and habitat change). As with other threats, and shown elegantly in new work by Gilman *et al.* (*11*) and discussed elsewhere (*8*–*10*), the direct impacts of climate change, fire, disease, and other factors may be dwarfed over time by their indirect effects on species interactions.

In light of this complexity, it is not surprising that even the most informed macro-scale reviews of threats to species and systems fail to identify a "smoking gun" responsible for declines. For example, recent studies of wildlife declines across India (*7*) and the extinction risk of mammals globally (*8*, *10*) reveal multiple, often overlapping pathways to extinction. Similarly, in a review of declines of marine species and ecosystems, Jackson (*9*) reasonably devotes equal attention to exploitation, pollution, habitat destruction,

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climate change, and the indirect and synergistic impacts of these threats. What might be more surprising is that even micro-level case studies struggle to attribute wildlife declines to a specific cause. Three new studies of wildlife declines in Australia's protected areas demonstrate this point.

In a detailed multiyear study in Kakadu National Park, Woinarski *et al*. (*13*) systematically surveyed small mammals and observed a 65% decline in species richness and a 75% decline in abundance from 1996 to 2009. Importantly, the researchers suggested that causes of the declines were species-specific and may have involved the individual or combined effects of changes in fire frequency and habitat structure, increases in invasive predators (feral cats and cane toads), and other factors that were not easy to measure. Fire and invasive predators also feature as likely culprits in new research by Firth *et al*. (*14*) on the extinction of the brush-tailed rabbit-rat in Australia's Garig Gunak Barlu National Park. Here, the authors experimentally determined that dry-season fires significantly reduced wildlife survival, but they also observed population declines in their unburned control areas and concluded that additional threats were at work. In contrast to these studies, Ford *et al*. (*15*) found that invasive species and fire played no major role in the decline of the brown treecreeper and hooded robin in New South Wales, Australia, but did observe powerful, lagged effects of isolation due to habitat loss and fragmentation over the past 100 years. Together, these studies emphasize the site- and species-specific drivers of wildlife declines. They also emphasize that the factors responsible for endangering a species may be distinct from the challenges experienced by dwindling populations of survivors. This point is illustrated tragically by the recent extinction of mountain caribou in Canada's Banff National Park; years of population decline from habitat loss, isolation, and apparent competition with moose ended with the death of the last known individual in an avalanche (*16*).

Research over the past 20 years shows that wildlife persistence is often positively associated with the size, connectedness, and remoteness of protected areas and the intactness of surrounding ecosystems (*17*). Beyond this, though, there are few obvious patterns or golden rules for predicting wildlife declines in protected areas. The lesson from this research, however, is not that we must surrender to the indecipherable complexity of modern declines and resign ourselves to inaction. Instead, we need to move away from broad generalizations and toward species- and community-specific approaches to conservation. A critical first step is a renewed commitment to wildlife monitoring in protected areas. The nearly exponential growth rate of protected areas since 1903 has greatly outpaced the allocation of resources for monitoring. Governments have used debt relief, foreign aid, direct payments, and other methods to incentivize the creation of protected areas in developing regions. Yet, there exist strikingly few incentives or resources for monitoring the fate of biodiversity in protected areas of the developing or developed world. While conservation science has made headway in quantifying the effectiveness of protected areas, our heavy reliance on habitat cover trends, expert opinion, and questionnaires does not allow us to fully understand or affect the dynamics of wildlife decline. Intensive, long-term monitoring is essential to gaining empirical knowledge of synergies among threats, the role of indirect effects, and other questions critical to minimizing species loss in protected areas.

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NEUROSCIENCE

Seeing the Light of Day

Constance Cepko

A potential gene therapy approach could restore some vision to patients with retinitis pigmentosa.

Human beings are highly dependent on vision. It is our most well-developed and cherished sense, giving us color vision with high acuity during the day as well as excellent sensitivity at night. Vision begins with light reception by specialized cells in the retina, a thin sheet of neural tissue that lines the inside of the eyeball (*1*). Rod photoreceptors provide for sensitivity in dim light, whereas cone photoreceptors provide for color vision in bright light. Unfortunately, photoreceptors are very sensitive to genetic insults. Mutations in more than 200 genes can lead to blindness, more than 40 of which lead to the disease retinitis pigmentosa (*2*, *3*). This disorder typically is due to a mutation in a gene expressed only in rods, and thus individuals with retinitis pigmentosa mutations are often born night-blind. Between ages 20 and 60, cone-mediated vision deteriorates (*4*), leading to total blindness. The poorly functioning cones in retinitis pigmentosa are the target of a potential gene therapy approach reported by Busskamp *et al*. on page 413 of this issue (*5*).

When stimulated, most neurons are depolarized and release more neurotransmitter. Photoreceptors are unusual, becoming hyperpolarized when stimulated (by light). Thus, for a signal to mimic light, the signal must hyperpolarize a photoreceptor. Halorhodopsin, a light-activated chloride pump of archaebacteria (*6*), does just that. Busskamp *et al*. delivered halorhodopsin [using an adeno-associated vector (AAV)] to cone photoreceptors in two mouse models of retinitis pigmentosa, hoping to bypass the need for the normal light sensor (opsin) in cones and the normal phototransduction process. Indeed, the authors detected light-induced electrical currents in the vector-infected photoreceptor cells, not unlike those measured in normal cones in which light stimulates cone opsin. In a normal retina, neurons that receive signals from photoreceptors extract patterns of interest, such as those that convey the direction of motion

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