Ungulate herbivory: Indirect effects cascade into the treetops

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Changes in population numbers of top (apex) predators are increasingly acknowledged to promote major shifts in ecosystem organization. The early evidence was both experimental and observationally based: for instance, predatory starfish can influence the ability of species to coexist on marine rocky shores (1); bass, by consuming grazing minnows, alter primary production in freshwater streams (2); and sea otters, by eating sea urchins, themselves major consumers of marine benthic algae, indirectly exert a major influence on the biological performance of these primary producers (3). The initial impression was that such potent top-down effects were "all wet" (4) and that terrestrial ecosystems might be fundamentally different from aquatic ones; in this issue of PNAS, Pringle *et al.* (5) add to a growing body of evidence suggesting the contrary. Some reasons for this initial impression seem obvious: many terrestrial apex predators have been hunted to near or local extinction; many of the more charismatic species now enjoy stringent legal protection, which hampers or denies any manipulation; and terrestrial ecosystems themselves are less experimentally tractable than their aquatic counterparts, in part because of extreme longevity of the plant community and because of the great spatial scale required to retain a semblance of natural reality. Nonetheless, an important role for apex predators is increasingly recognized as these predators persist in fragmented habitats (e.g., coyotes; ref. 6), are introduced to islands (e.g., fox–seabird–vegetation linkages in the Aleutian Islands; ref. 7), are reintroduced to historic habitats (e.g., wolves into Yellowstone; ref. 8), when comparable habitats with and without a massive human presence are examined (e.g., the mountain lion–amphibian connection in Zion National Park; ref. 9), and in the rare cases in which sufficient time series data exist to develop tri-trophic models (10). One conclusion is that sites with a fuller complement of apex predators often support a greater number of species, may be more productive, and deliver higher-quality ecosystem services (e.g., water). The structural differences are sufficiently clear to have led to a proposed "rewilding" of large tracts of land (11), that is, a repopulating by megafauna including apex predators.

Pringle *et al.* (5) examine an African savanna system in which three pairs of megaherbivore exclusions and their controls (sites with normal grazer access) were established on productive volcanic clays and compared with a second set within 12 km on less productive sandy loams. The ungulate herbivore exclusion, that is, all grazing mammals >15 kg, included a nine-species guild of such favorites as elephants and zebras but also domestic cattle and was enforced by a 2.4-m high electrified fence obviously entirely permeable by insects, snakes, lizards, birds, and smaller mammals.

Ecosystems with a low intrinsic primary production capacity will be more susceptible to anthropogenic modifications.

The exclosure treatment reduced ungulate density to zero over the manipulation's duration: this is analogous to an experimental system in which "predation" on these large ungulates was 100% efficient.

Pringle *et al.* (5) found greater productivity at all six ungrazed sites relative to controls. Plants, i.e., trees and more conventional forage, might be expected to grow better when not consumed by a phalanx of large-bodied consumers, but grazing is also known to stimulate growth (12). The research "gold" comes from the well documented but certainly incomplete cascade of related indirect effects. Associated with the increase in tree density and profile complexity was a 61% increase in lizard density. Their major prey, beetles (22% of diet), marched to the same drummer: greater production yields more beetles. One subtlety is the dual mechanisms by which ungulate exclusion increased lizard densities: density of beetles, a major lizard prey item, increased, as did arboreal habitat available for lizards to colonize. Multiple mechanisms linking ungulate herbivory to lizard density certainly support the idea that ungulates initiate rampant indirect effects.

Perhaps the most significant finding of Pringle *et al.* (5) is that the strength of the indirect influences was negatively correlated with site productivity; that is, at less-productive sites, exclusion of megaherbivores generated a greater effect. The environmental message seems clear: ecosystems with a low intrinsic primary production capacity, generated, for instance, by low annual rainfall or relatively reduced soil nutrients, will be both more susceptible to and less capable of responding to anthropogenic modifications than more productive sites. However, the relationship between effect strength and productivity carries with it other implications. Namely, Pringle *et al.* show how the nature of interspecific interactions in putatively similar communities changes in response to forcing by a "global" variable, in this case productivity. By documenting varying strengths of indirect effects of herbivores along a productivity gradient, Pringle *et al.* introduce a new twist to questions about community organization in terrestrial habitats (albeit one that has been explored in intertidal communities; ref. 13): how do species interactions within a given community vary along an environmental gradient? This added detail foreshadows a type of investigation, and a conceptual framework, that may help transition community ecology from a "science of place" to a science that subsumes place. Studies that look for general trends across widely dispersed sites (14) approach this challenge from one direction; the method used in the present case (5), characterizing variation in species interactions within a community in response to environmental heterogeneity, ap-

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proaches the problem from a different, yet informative, perspective.

Pringle *et al.* (5) barely discuss the species composition of what must be a complex and interactive community. Ants are mentioned and help defend the dominant *Acacia* trees, much as in Janzen's early neotropical studies (15). But what role do arachnid predators play? In an old-field ecosystem (16), spider-specific identity and abundance determined how herbivorous grasshoppers, plant nutrient level, and therefore primary production interacted: spiders in abundance reduced herbivore activity and thus facilitated plant performance. Could the "herbaceous species" studied by Pringle *et al.* (5) have benefited from such influences? The answer depends on effect magnitude. Similar relationships should be sought in two other trophic groups. Insectivorous birds could have been major players in the indirectly enhanced food web. Their exclusion has been shown experimentally to diminish plant production (17). In a neotropical forest, bird presence reduced insect damage to canopy foliage, although not in the less-productive understory (18). Finally there is the issue of snakes, apparently with numbers increased in the absence of ungulates (5). Did these eat small mammals and birds? By temperate-zone standards, the question is not trivial because small rodents can determine the survival of tree seeds and seedlings (19). The above questions are not criticisms: no ecological field study yet, and possibly ever, can be trophically complete. The question about indirect effects is always not whether they occur but rather, what is their magnitude and, therefore, significance.

Lastly, we turn to the problem of experimental intractability due to long-lived, slow-growing plants in terrestrial ecosystems. Suppose comparisons of exclosure and control sites had been conducted after 20 years, 50 years, or more. How different would the results have been? Fig. 1 illustrates an example of ecological change wrought by denying Roosevelt elk access to a portion of the Olympic rainforest. In this instance, grass biomass plummeted, herbaceous understory plant diversity declined, woody shrubs aggressively filled the site, and seedling and sapling density of the tree western hemlock (*Tsuga heterophylla*) increased (20, 21). In both the Olympic rainforest and the African savanna, it would be fascinating to know the long-term consequence of a maintained herbivore-free treatment. Structural development in the Olympic rainforest proceeds over several centuries (22), indicating, as we have alluded for the African savanna, that the transition to an herbivore-free equilibrium will be protracted. Obviously, a temperate rainforest is conspicuously distinct from an African savanna. However, both ecosystems share one feature in common: exclusion of ungulate herbivores increases the density of long-lived, habitat-forming trees. In the African savanna, this mediated an indirect effect of ungulates on arboreal lizards. Similarly, indirect effects of ungulate herbivory on epiphytic plants, for which the Olympic rainforest is famous, as well as other canopy biota will likely propagate through the trees. How will the species assemblage and the strength of interspecific interactions change as populations of trees fully respond (i.e., reach maximum size and structural complexity) to release from herbivory? Do the indirect effects of ungulate herbivory follow an independent "successional" trajectory themselves? Only long-term manipulative ecological studies can provide definitive answers to these questions.

Fig. 1. Vegetation response after 26 years of continuous exclusion of Roosevelt elk herbivory from a site in the Olympic rainforest of western Washington. Within the protected area, the shrub salmonberry (*Rubus spectabilis*) has formed a near-monodominant stand. Densities of the tree western hemlock increased with the exclusion of elk, suggesting that further changes to vegetation structure and composition will occur with the continued absence of herbivory.

1. Paine RT (1966) *Am Nat* 100:65–75.
2. Power ME, Stewart AJ, Matthews WJ (1988) *Ecology* 69:1894–1898.
3. Estes JA, Palmisano JF (1974) *Science* 185:1058–1060.
4. Strong DR (1992) *Ecology* 73:747–754.
5. Pringle RM, Young TP, Rubenstein DI, McCauley DJ (2007) *Proc Natl Acad Sci USA* 104:193–197.
6. Crooks KR, Soulé ME (1999) *Nature* 400:563–566.
7. Croll DA, Maron JL, Estes JA, Danner EM, Byrd GV (2005) *Science* 307:1959–1961.
8. Ripple WJ, Beschta RL (2006) *For Ecol Manage* 230:96–106.
9. Ripple WJ, Beschta RL (2006) *Biol Cons* 133:397–408.
10. McLaren BE, Peterson RO (1994) *Science* 266:1555–1558.
11. Donlan J, Greene HW, Berger J, Bock CE, Bock JH, Burney DA, Estes JA, Foreman D, Martin PS, Roemer GW, *et al.* (2005) *Nature* 436:913–914.
12. McNaughton SJ, Banyikwa FF, McNaughton MM (1997) *Science* 278:1798–1800.
13. Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) *Ecol Monogr* 64:249–286.
14. Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, *et al.* (2002) *Nature* 417:844–848.
15. Janzen DH (1967) *Univ Kans Sci Bull* 47:315–558.
16. Schmitz OJ (1994) *Proc Natl Acad Sci USA* 91:5364–5367.
17. Marquis RJ, Whelan CJ (1994) *Ecology* 75:2007–2014.
18. Van Bael SA, Brawn JD, Robinson SK (2003) *Proc Natl Acad Sci USA* 100:8304–8307.
19. Ostfeld RS, Manson RH, Canham CD (1997) *Ecology* 78:1531–1542.
20. Schreiner EG, Krueger KA, Happe PJ, Houston DB (1996) *Can J For Res* 26:255–265.
21. Woodward A, Schreiner EG, Houston DB, Moorhead BB (1994) *Northwest Sci* 68:97–110.
22. Van Pelt R, O'Keefe TC, Latterell JJ, Naiman RJ (2006) *Ecol Monogr* 76:277–298.