

Dominance, Diversity and Grazing in Tallgrass Restoration

Ecology has much to contribute to debates over the role of grazing in restoration—and much to learn from the results of experiments in restorative grazing.

by Henry F. Howe

In a recent article in this journal, Andrew Williams (1998) expressed surprise that moderate grazing benefited some rare species, while his critics worried about the role of large grazers in immediate precontact history, arguing, for instance, that early explorers did not report large numbers of bison in tallgrass habitat east of the Mississippi (Harrington, 1998; Henderson, 1998). While bison may have been scarce in the Prairie Peninsula just before Europeans arrived (Semken, 1983), this controversy and other attempts to bring ecological theory and practice into the mainstream of restoration ecology (see, for example, the special section edited by Allen and colleagues, *Restoration Ecology* vol. 5, December 1997), have given insufficient attention to three key issues relevant to the grazing/tallgrass debate:

(1) Reduction of dominant vegetation in productive habitats almost always increases the abundance of rare and infrequent species, which typically comprise 60-90 percent of all species in ecological communities.

(2) A substantial literature documents the inverse relationship between dominance and diversity in productive grass-

lands. The best tests have been with generalist ungulate grazers, such as bison (*Bison bison*), domestic cattle (*Bos taurus*), and wildebeest (*Connochaetes gnou*), which increase plant species diversity by preferentially foraging on dominant plant species. Failure to permit some grazing in productive grasslands typically results in dramatic decreases in plant species diversity.

(3) Historical anecdotes about tallgrass prairies immediately prior to European settlement are only marginally relevant to the long history of the evolution of grasslands and grassland taxa in North America, which spans at least 35 million years.

A general point is that tests of community hypotheses can best be controlled and interpreted safely with restored habitats before subjecting scarce remnants to risks of unintended consequences (see for example Jordan et al., 1987; Howe, 1994a,b, 1999). Habitats created by people are neither sacred or irreplaceable; they are the ideal medium for testing fundamental hypotheses concerning complex communities. This is especially true when their creation has been carried out in such a way as to test specific, clearly defined hypotheses.

Dominance, Diversity, and Species Abundance Distributions

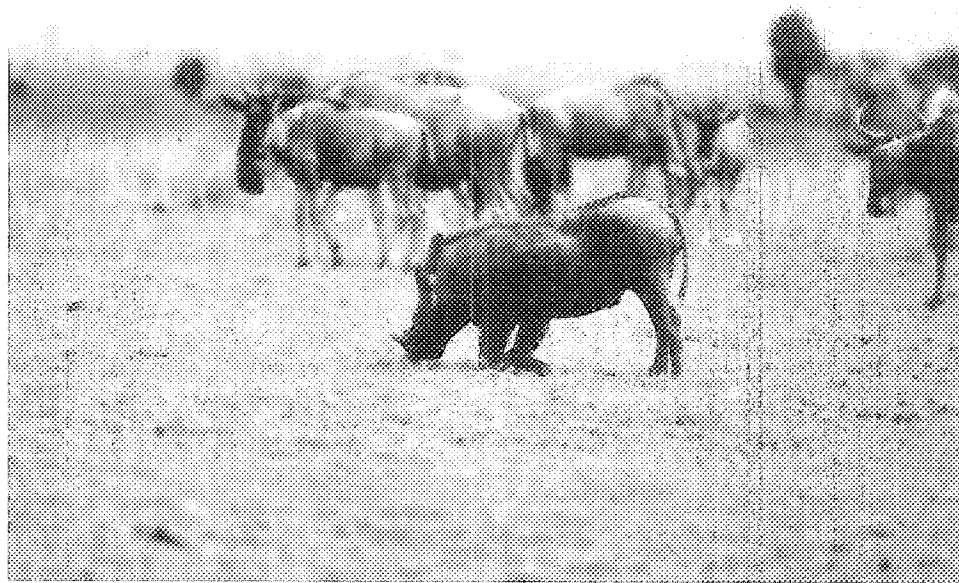
Dominant plant species co-opt a disproportionate share of resources, as indicated by numbers, cover, or biomass, while particular subdominant species use far fewer resources. In any collection of species from nature, subdominant species far outnumber dominants. The inverse relationship between the degree of dominance and various measures of diversity has proved a robust generalization, based on research in many kinds of ecological communities, and certainly applicable to productive grasslands, if not to ecological systems of all kinds. Integral to this inverse relationship is the widely observed fact that in any community a few species are always far more common than others; most species are infrequent or rare.

Dominance increases with time in the course of undisturbed succession, so that one or a few species that are especially well adapted to local conditions of soil, water, light, and climatic extremes even-

tually exclude most competitors from most suitable microsites (Huston, 1979). Under nitrogen deficiency in grasslands, for instance, large C4 grasses such as big bluestem (*Andropogon gerardi*) which are capable of efficiently using low concentrations of nitrogen, typically dominate other species, excluding them from most suitable microsites and thereby reducing subdominant populations (Tilman, 1987). Where nitrogen is less limiting, one or a few C3 species have a growth advantage over efficient nitrogen users and may dominate (Wedin, 1996; Wedin and Tilman, 1996). Huston (1979, 1994) makes the generally well supported prediction that where resources are abundant, the approach to dominance during succession is rapid and overwhelming. In contrast, floristically similar communities with impoverished water or nutrient resources approach dominance very slowly. Hence graminoid and forb communities on fertile, wet sites often proceed to low species richness and high dominance, sometimes resulting in virtual monocultures of very aggressive species best able to monopolize abundant resources (see for example

Howe, 1995, 1999; Galatowitsch and van der Valk, 1996). Where resources are more limiting, on dry sites, for example, or on nutrient-poor soils, the approach to dominance still occurs, but results in much higher species richness or other measures of diversity (e.g up to 28 species/m², in dry prairies; Peet and others, 1983) maintained over much longer periods of time. Over centuries or millennia, unimpeded succession on dry sites would theoretically result in dominance of one or a few species and exclusion or suppression of others. In many places, however, that end point is never reached because grazing, fire, incremental climate change, or even glacial episodes intervene and reset the successional clock, or change the course of succession. In a wet prairie restoration, for instance, an aggressive dominant might exclude most competitors within a decade. In a dry prairie restoration on poor soils, a comparable process could take centuries. Mesic sites are likely to fall in between.

The relationship between dominance and diversity obviously has important implications for ecological restoration. Where any resource such as light, nitrogen, or water is permanently limiting, and some species are especially well adapted for securing it, occupation is a zero-sum game in which one or a few species eventually exclude most others from most microsites. Random factors influence both the abundance and the survival of diminishing populations that are in the process of being deterministically excluded from a site, which probably accounts for the roughly lognormal species abundance distributions characteristic of both plant and animal communities (Preston, 1948, Hubbell, 1979; Magurran, 1988). In exceedingly diverse tropical forests on Barro Colorado Island, Panama, for instance, dominant trees may account for only 15-20 percent of the individual trees, but most other species are represented by only one to 16 individuals in a topographically homogenous 50-hectare (124-acre) plot (Fig. 1; see Hubbell and Foster, 1983). In this and most other tropical forests the approach to exclusive dominance is slowed by nutrient-poor soils, a vast pool of species to be excluded, minimal differentiation in resource use, and large and small



A warthog (*Phacochoerus aethiopicus*) foraging on a small grazing lawn in Kenya with wildebeest (*Connochaetes gnou*) in the background. Note the uneven cropping of grasses and forbs in the background, creating highly variable conditions for plants. Plots fenced from ungulates in East Africa and on tallgrass prairies in North America typically lose plant diversity as a few grass species gain dominance. Photo by the author

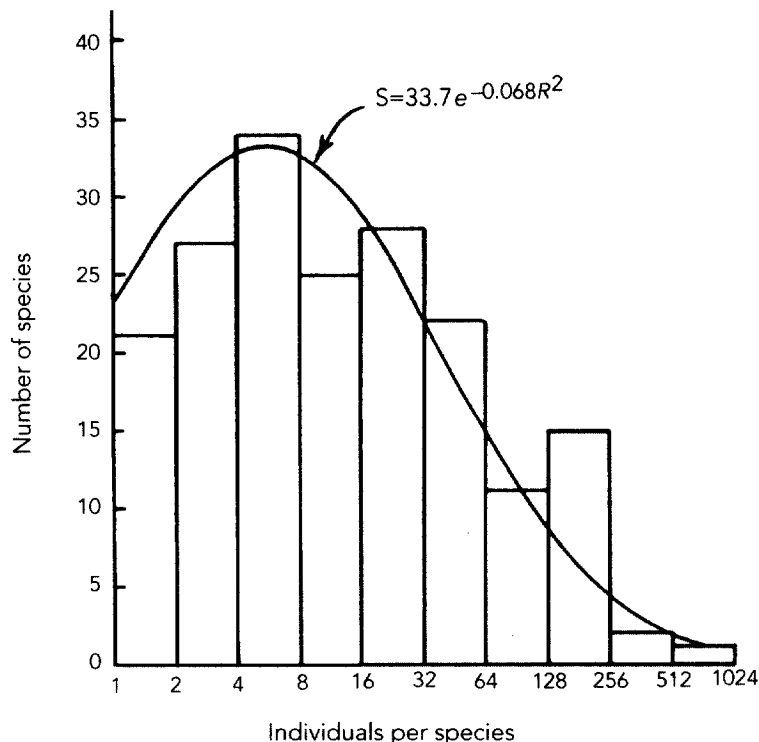


Figure 1. Lognormal distribution fitted to data on relative species abundance for all trees > 20 cm dbh in a 50-ha plot on flat ground on Barro Colorado Island, Panama. Species have been grouped into octaves of abundance. This truncated lognormal distribution has a typically small number of abundant species (more than 60 individuals); most species are infrequent or rare, and 82 are represented by fewer than eight individuals. From Hubbell and Foster (1983).

disturbances that maintain subdominant populations.

Woody or herbaceous communities of the temperate zone show higher dominance than in the tropics. In little-disturbed stretches of the Colorado/Mojave Desert, for instance, more than 60 percent of the stems of perennial shrubs and cacti may be bur sage (*Ambrosia dumosa*), while 24 other species are infrequent or rare (Miriti and others, 1998). It is not uncommon in ungrazed wet or mesic tallgrass prairie for one or two species to account for 40 to 80 percent of the cover (Weaver, 1968; references in Risser and others, 1981; Howe, 1994b). The point is that the shapes of species-abundance distribution curves are similar, regardless of geographical location or ecological system.

The take-home lesson for the restorationist is that if dominance is permitted to increase in a circumscribed area, subdominant species inexorably disappear. The inverse relationship between dominance and diversity exists regardless of the stan-

dard of diversity used or the community described (Magurran, 1988). For Simpson's Index of Diversity this is true by definition, where diversity (D) is defined as:

$$D = 1/\sum p_i^2$$

where p_i is the proportion of species i in a sample, and numerical dominance is:

$$C = 1/D$$

Diversity increases as the evenness of the distribution increases (that is, as the variance of the lognormal increases and the shape of the bell or truncated bell curve flattens). The Shannon Weaver index H' ($\sum \ln p_i$) behaves similarly (Pielou, 1977; Magurran, 1988). Species richness, a count of species that does not take abundance into account, inflates the importance of rare and very rare species too scarce to reproduce effectively, which may include most of the species in species-rich sites (for example, see Fig. 1). Reliance on species counts is a limitation of the work reported in John Curtis's classic, *The Vegetation of Wisconsin* (1959), which relies heavily on species "presence" with-

out reference to abundance. The key point is that where dominance is pronounced, many or most species in a community exist well below the effective population size required for long-term persistence. This is a central assumption of theories accounting for the loss of species accompanying a decrease in the size of islands or habitat patches (MacArthur, 1972, Appendix). As a colleague and I have argued (Maina and Howe, in review), the relationship between dominance and diversity is also a central factor in the prognosis for persistence of historical and anthropogenic metapopulations of plants and animals.

It is not surprising that rare species prosper when dominants are suppressed. In contemporary terminology, suppression or removal of dominants transforms competitively saturated communities into at least temporarily unsaturated communities, which admit additional species by immigration, release of suppressed individuals, or germination from the seed bank (see Cornell and Lawton, 1992). For those species that are infrequent or rare because they are excluded from preferred resources by competitors, light to moderate grazing should offer competitive opportunities that increase their visibility, and with it their diversity.

Finally, it is important to note that grazing may have different implications for different kinds of rarity. In any given lognormal species abundance distribution, the large number of species in low frequencies near and to the left of the mode of the distribution (Fig. 1) may be rare everywhere, or only locally rare. Deborah Rabinowitz and her colleagues (1986) defined several kinds of rarity based on geographic range, habitat specificity, and local population size (Table 1). In their analysis of the flora of the British Isles, these authors found that 105 species could be assigned to one of the "somewhere large" population categories, while only eight fall in one of several "everywhere small" population categories. If, as seems likely, similar patterns exist in other floras, two points need emphasis: (1) the vast majority of rare or infrequent species in a lognormal species abundance distribution are probably originally derived from a "somewhere large population" species, and

Table 1. Forms of commonness and rarity, based on geographic distribution, habitat specificity, local population size, and their likely relationships to species abundance distributions.

Geographic distributions	Wide		Restricted	
	Broad	Narrow	Broad	Narrow
Habitat specificity				
Populations large somewhere	Often dominant	Usually subdominant	Sometimes dominant	Usually subdominant
Populations small everywhere	Always subdominant	Always subdominant	Always subdominant	Always subdominant

Inspired by Rabinowitz, Cairns, and Dillon (1986).

(2) in central North America, where more than 99 percent of tallgrass prairie has been converted to intensive agriculture (Noss and others, 1995) most of the "somewheres" no longer exist. Most species, as Michael Huston (1994) put it, were once common somewhere, but in most places and times that we see them they are excluded from limiting resources by dominants and are therefore infrequent or rare. If few plants are "naturally" chronically rare, it is quite likely that most infrequent and rare species are not particularly well adapted to rarity, and persist largely at the whim of conservationists, managers, and restorationists who suppress or fail to suppress aggressive dominant vegetation by grazing, mowing, varied timing of burns, or other active measures.

Grassland Grazing

The effects of mammalian herbivores on plant diversity depend on what they eat, and what else they do (Huntly, 1991; Knapp and others, 1999). In theory, grazers may affect plant communities by eating species until they are rare, then switching to alternate foods, or by consistently suppressing strong competitors (see Pacala and Crawley, 1992). But the positive effects of grazing on plant diversity usually reflect the fact that large mammals preferentially eat large, common, and dominant plant species (McNaughton, 1976, 1983, 1984, 1985; Knapp and colleagues, 1999). On wet or mesic sites, light to moderate grazing by large generalist ungulates such as wildebeest or bison usually increases plant diversity by reducing dominant vegetation (for examples, see McNaughton and Knapp references above and Dykster-

hais, 1958; Ellison, 1960; Milchunas and others, 1988; Belsky, 1992; Milchunas and Laurenroth, 1993; Proulx and Mazumder, 1998). Cattle have the same general effect (see Senft, 1987; Howe, 1994a; Bailey and colleagues, 1996). Increases in plant diversity due to dominance-reduction can be further enhanced by patchy habitat alteration, as occurs when bison trample some areas more than others or create novel habitats in wallows (Collins, 1987; Vinton and others, 1993; Hartnett and others, 1996), or when bison or elk produce variable patterns of nitrogen enrichment by depositing urine or dung, which strongly affect plant establishment, growth, and competitive dynamics (Hobbs and others, 1991; Frank and McNaughton, 1993; Frank and others, 1994; Hobbs, 1996; McNaughton and others, 1997). Generally, any moderate grazing in productive habitats will tend to increase species richness, as will mowing for that matter. This effect is likely to be even more pronounced if, like bison (Knapp and others, 1999), large ungulates generally prefer to forage on large, dominant C_4 grasses. Most of the relevant data at this point come from short-grass and mixed-grass prairies of the Great Plains, where grazing occurs and is studied (Proulx and Mazumder, 1998). Much less information exists for tallgrass habitats further east, where surviving remnants are rare and are generally protected from grazing. What evidence exists, however, strongly suggests that the principles are general.

On the other hand, mammalian herbivory decreases plant diversity if subdominant species are eaten selectively (Huntly, 1991). Because smaller herbivores are in general more selective than larger ones (e.g.

McNaughton, 1979, 1984; Howe and Westley, 1988), one would expect that foraging by smaller mammals would generally decrease plant diversity. If the effect of grazing by large generalist herbivores like bison (350-450 kilograms) is often to increase plant diversity, smaller (35-112 kilograms) white-tailed deer (*Odocoileus virginianus*) are selective browsers of woody or herbaceous dicots and graminoids (McCullough, 1985), and often decrease plant species richness (McCaffery and others, 1974; Tighman, 1989; Miller and others, 1992; Strole and Anderson, 1992; Bowles and others, 1996, 1997). Yet smaller pikas (100-200 grams), rabbits (1 kilogram) and hares (1-7 kilograms) have long been known to reduce plant diversity (Farrow, 1917; Huntly, 1987; see Huntly, 1991), and in synthetic tallgrass plantings in Illinois, voles (*Microtus pennsylvanicus*; 30-50 grams) sharply decrease plant diversity, not by decreasing species number, but by skewing the species-abundance distribution in favor of dominant taxa (Howe and Brown, 1999). Cattle are not unselective feeders. Contrary to what one might suppose, different breeds of domestic cattle on the same range may have different food preferences (Winder and others, 1996). But the irony of the debate over grazing on tallgrass remnants and restorations is that managers of wet or mesic sites who are concerned with plant diversity probably have far more to fear from ubiquitous deer, rabbits, and rodents than from light-to-moderate grazing from large ungulates, domestic or otherwise.

Both community theory and extensive observations indicate that heavy grazing or severe or frequent disturbance of other kinds typically reduce plant diversity (see Connell, 1978; Huston, 1979, 1994). Heavy grazing may be a problem for restoration and conservation, particularly of fenced remnants or restorations on dry or nutrient-poor sites. While in unfenced nature animals choose to forage in productive rather than unproductive sites, but may choose to ignore some productive sites if water scarcity or risk of disease or predation decrease their marginal value, constrained livestock are often forced to forage where they otherwise would not (Senft and others, 1987; Bailey and others, 1996; McNaughton, 1984, 1985; for

conceptual underpinning, also see Schmidt and Brown, 1996; Brown and Morgan, 1995; Morgan and others, 1997). It is unlikely that "light or intermittent" grazing by free-ranging livestock would irreparably harm dry prairies, if only because large ungulates are unlikely to forage long in such places if they have choices. Harrington (1998) and Henderson (1998) are justified in worrying that substantial forced grazing on fenced dry prairie could result in severe degradation (Proulx and Mazumder, 1998). Heavy grazing in such situations would be anomalous in nature, and might easily have serious consequences if imposed by humans.

This caveat does not mean, however, that light to moderate grazing in mesic and moist restorations would necessarily result in degradation. In fact, the absence of grazing or other measures such as seasonal burns or mowing that reduce dominance can result in "vegetation stagnation" (McNaughton 1993), a range manager's term for loss of many species and a drop in productivity through increasing dominance of one or a few species in a mature vegetation. The combined effects of dominance reduction and repeated foraging, wallowing or trampling, and avoidance of inconvenient or productive sites by large ungulates creates mosaics of microsite diversity for plants, and generally enhances plant diversity. However, high grazing intensity forced on dry or nutrient-poor sites may be expected to eliminate many of the less common indigenous species, and to open habitats to invasion by exotic weeds and other opportunistic plants.

Floral History and the North American Megafauna

The suspicion that grazing by large mammals is inherently inimical to tallgrass prairie is scientifically doubtful, and perhaps preposterous. North America once harbored a variety of large ungulates that rivaled or even surpassed that of Africa today (Kurten, 1971; Kurten and Anderson, 1980). Over the last 30 million years, the abundance and diversity of grazing and browsing mammals more or less paralleled the expansion and contraction of grassland and savanna habitats (Webb,

1983, 1984). Five to 10 million years ago, as extensive forests were broken up by grassland/forest mosaics and savannas and ultimately by steppe, as many as 16 genera of horses shared the continent with the last oreodonts (two genera), rhinos (three genera), and tapirs (two genera), an increasing variety of elephant-like creatures (eight genera), camels (13 genera), antelopes (11 genera), pigs (four genera), and the first North American deer (three genera, including *Odocoileus*) and cattle (Bovidae; three genera). Most cattle (including *Bison*) did not migrate from Asia to North America until the last quarter of the Pleistocene. Before these latecomers appeared, the continent had already contended with 30 million years of oreodont grazing (at least 16 genera), along with the camels, rhinos, pigs, and horses. It is true that most of this vast assemblage of large mammals had become extinct by three million years ago (Webb, 1983), but far more than newly arrived bison and elk occupied the continent prior to the last glaciation (Kurten and Anderson, 1980: 407 ff). Most plant families, genera and even species of contemporary tallgrass prairies coexisted with, and in fact evolved because of or in spite of, a huge fauna of large browsing and grazing mammals.

Grasslands, grassland/forest mosaics, savannas, and steppes have occupied much of North America for at least 35 million years (Elias, 1942; Webb, 1983). While tallgrass prairie as we know it is a recent (6,000–10,000 years) assemblage of botanical elements from disparate geographical and ecological origins (Axelrod, 1985), many familiar genera found in it date back tens of millions of years (examples include *Aristida*, *Panicum*, *Phragmites*, *Setaria*, *Stipa*; see Elias, 1942). Enormous changes in climate, plant distributions, biome identities and characteristics, and grazing pressures obviously characterize this enormous span of grassland history. But even in relatively recent times there has been impressive ecological change, much of it driven by climate (Davis, 1986). Environmental change is inherent in the natural world, whether the time scale is a century (Fig. 2a), a millennium (Fig. 2b), an interglacial (Fig. 2c), a glacial cycle (Fig. 2d), or seven glacial cycles (Fig. 2e). Changes in mean tempera-

ture, plant ranges, community types, fire frequencies and intensities, precipitation, and changing summer and winter temperature extremes were overlaid with changing abundances and distributions of many taxa of large mammalian herbivores. It is not productive to think of the past as fixed.

Environmental dynamism has been the rule rather than the exception in recent history as well (Fig. 2c). As Richard Baker and his colleagues (1996) have shown, over the span of an interglacial, the vegetation in any one spot may well have shifted from subarctic vegetation to

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boreal forest to deciduous forest to prairie (of various types), and back to forest again. Because tallgrass prairie lacks true endemics (Axelrod, 1985), there is every reason to believe that representatives of this recent amalgam of species picked up and lost taxa throughout its long and varied history. Undoubtedly herds of mammalian herbivores changed in both abundance and composition within and between glacial periods, and this must have had a major impact on the composition and variability of plant communities (see Davis, 1986; Graham, 1986). Stasis was not the rule in the recent past, either.

Consideration of evolutionary history rather than anecdotes from European travelers presents a dilemma for nostalgists

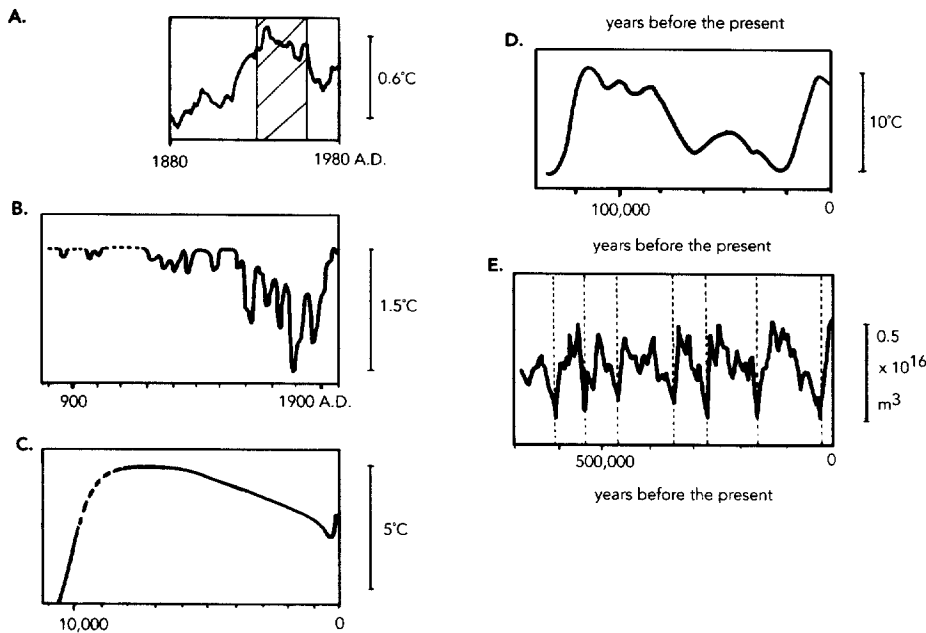


Figure 2. Temperature changes in the Northern Hemisphere at different time scales. (A) Instrumental record of mean annual temperature over 100 years between latitudes 23.6° N to 90° N. Hatched area is the 30-period 1931-1960 conventionally used to calculate climatic means (from Hansen and others, 1981). (B) Air temperature reconstructed from sea ice over 1,000 years in the North Atlantic (modified from Lamb, 1977). (C) Mean annual temperature over 10,000 years in northeastern United States, based on fossil vegetation (modified from Davis and others, 1980). (D) Reconstructed air temperature over 100,000 years in Europe, based on vegetation records, eustatic sea level, and fossil and geochemical records in deep-sea cores (modified from Mitchell, 1977). (E) Global ice volume during the last seven glacial interglacial cycles (500,000 years), based on oxygen isotopes in deep-sea cores (modified from Mitchell, 1977; Johnson, 1982). Composite figure from Davis (1986). Figure used with permission of Margaret Davis

fixated on a particular romantic image of pre-contact nature. There is no point at which one could identify a static, "pristine" state on scientific grounds—only an enormous variety of "pristine" states. As Margaret Davis (1986) points out, unsubstantiated "snapshots" framed in 1800 or 1700 are hardly representative of either the past, the present, or a plausible future. Restoration objectives framed in this way may be appealing in certain respects, but they are no more legitimate than any other time frame as models for the past or future. As I have argued elsewhere (Howe, 1994a), the best recourse is probably to define restoration objectives in terms of ecological or biocultural processes, rather than as arbitrarily chosen and illusory static communities. One may wish to preserve diversity as a key to the past and an offering to the future, but the particular composition of plant

communities in any single place or time, as far as anyone can determine, is ephemeral.

Learning About Grazing from Tallgrass Restorations

A key point here is that ecological restoration provides a medium for both learning about dominance-diversity relationships driven by grazing, and applying what we learn to community and ecosystem management. Both individual species and community responses to grazing may be quite different in contemporary fragments than in any particular historical context, because historical contexts varied too much with topography, climate, composition of herbivore communities, and the competitive environment in which plants lived. But feasible imposition of grazing regimes or their surrogates on restorations can be a

way to explore the ways in which large mammals increase or decrease diversity in different kinds of grassland contexts, many of which may no longer exist. In smaller remnants or restorations grazing may not be feasible, but management that fails to take into account the necessity of reducing dominance is out of step with much of what is known about processes that determine the composition of grassland communities.

Management, including plausible variation in plausible processes, is mandatory if diversity is to be preserved for decades or centuries (see Steuter and others, 1990; Howe, 1994a). If grazing is not feasible, growing-season mowing (Howe, 1999; see Anderson and Briske, 1995) or growing-season burns (Higgins, 1984; Steuter, 1987; Howe, 1994b, 1995) may suppress dominance enough to maintain species diversity. The first step in restoration planting may be to favor a more-even mix of species than is customary (see for example Howe and Brown, 1999), rather than species abundances skewed in favor of aggressive dominants like large C_4 grasses that quickly suppress subdominants (for instance Howe, 1995, 1999). In fact, given our state of ignorance about the particular consequences of grazing for species or communities of special interest, experimental restoration may be the best avenue for testing dominance-diversity relationships without risking destruction of the remnants that now comprise less than 1 percent of pre-contact tallgrass habitats east of the Mississippi (Noss and others, 1995). Experimental restoration may be the only feasible avenue for testing these relationships on arable land, and ultimately re-creating tallgrass systems on rich mesic or wet sites where this ecosystem has been virtually eliminated by intensive agriculture.

Graeme Caughley (1992) has argued that conservation biology is usually hamstrung by either a naive reliance on elegant and logically coherent theory with virtually no validation in nature (the "small population paradigm," including minimum viable population size), or by obsessive reliance on after-the-fact and inherently anecdotal explanations of habitat change. The first criticism speaks to unwarranted reliance on untested theory; the second speaks to an unwillingness to acknowledge that particu-

lar ecological circumstances reflect general principles or processes. He calls for integration of empirical knowledge, practice, and relevant theory, which he views as largely absent from conservation biology. An admirer of Caughley's critique, and the scientifically realistic approach to management championed by Al Steuter and his colleagues (1990), would be baffled by most of the restoration being carried out on tallgrass systems. Most of this work apparently has no clear relation to even well-established ecological theory, reflects little interest in relevant empirical patterns, processes or history, and is not designed in such a way that much can be learned from the effort. This is too bad.

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Henry F. Howe is at the Department of Biological Sciences (M/C 066), University of Illinois at Chicago, 845 W. Taylor Street, Chicago, IL 60607. Telephone 312-996-0666, fax 312-413-2435, email henry.f.howe@uic.edu.
