

REPORT

A rodent plague on prairie diversity

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Abstract

Selective vole (*Microtus pennsylvanicus*) suppression of prairie grasses and forbs in experimental restorations suggests why many of the plants are likely to be uncommon in nature. Vole herbivory reduced densities of legumes and grasses and increased unpalatable forbs in replicated plantings in Illinois: six otherwise common species (*Dalea purpurea*, *Desmanthus illinoensis*, *Elymus canadensis*, *Panicum virgatum*, *Phalaris arundinacea*, *Sorghastrum nutans*) declined 27–89% in abundance, whereas two species (*Echinacea purpurea* and *Rudbeckia hirta*) increased by 61% and 1023%. Species number dropped by 19% and plant diversity (Simpson's D) by 37% in one treatment to which voles had access. Plots were planted with 18 prairie species of the region, but in even distributions of 35 or 350 seeds species⁻¹ m⁻², rather than skewed in favour of large C₄ grasses common in native remnants. Manipulation of plant composition and vole access revealed what are likely to be formative effects of rodent herbivory on vegetative composition. These experimental tallgrass communities appear to be assembling from plant species that voles prefer not to eat.

Keywords

Diversity, experimental restoration, herbivory, *Microtus*, tallgrass prairie, vole.

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INTRODUCTION

Climate and soil determine the vegetative structure of biomes (Holdridge 1947), but animals often shape the composition of species in them at any given place and time (Huntly 1991). Best understood are effects of grazing, trampling, wallowing and nitrogenous waste redistribution by large ungulates (McNaughton 1985; Collins 1987; Milchunas & Laurenroth 1993; Frank *et al.* 1994; Hartnett *et al.* 1996; Hobbs 1996; Proulx & Mazumder 1998; Knapp *et al.* 1999), which as free-ranging foragers use and alter favoured feeding areas, streamsides and seasonal retreats, leading to spatially idiosyncratic impacts (Senft *et al.* 1987; Bailey *et al.* 1996). There is little doubt that long-term ungulate use leaves clear historical legacies in vegetation (Mack & Thompson 1982). Less appreciated are the influences of ubiquitous rodents (Hulme 1996; Keesing 2001). Turnover of earth by gophers (Huntly & Inouye 1987), selective herbivory on tree seedlings by voles (Ostfeld *et al.* 1997) and size-selective seed predation by kangaroo rats (Brown & Heske 1990) alter species composition and diversity of grasslands, forests and deserts. Unlike free-ranging ungulates, which may only use and alter a small fraction of available habitat (e.g. Senft *et al.* 1987), smaller mammalian herbivores are likely to be at least

periodically abundant wherever forage and cover exists. We use experimental restorations to address the additional questions: do small rodents eat enough native vegetation to have important impacts on tallgrass prairie richness and diversity?

Less than 1% remains of the tallgrass prairie that once covered more than 570 000 km² of Central North America (Noss *et al.* 1995). Understanding this biome, once one of the most important on the continent, is both a priority and a challenge. Scattered remnants probably represent a small fraction of the variety of plant assemblages that once comprised the ecosystem (Howe 1999). Paradoxically, well-conceived, quantitative tests of herbivorous rodent influences on native tallgrass vegetation show few effects in Kansas (Gibson *et al.* 1990). Lower vole densities in native than anthropogenic grasslands and lower palatabilities of many plants of native prairie as compared with pasture and forage plants may hold a key to the paradox (Lindroth & Batzli 1984); existing prairies may represent the leftovers of at least centuries of periodic rodent suppressions of palatable food species.

If this hypothesis is true, it can be approached through experimental restorations that manipulate plant and mammal densities, rather than through attempts to monitor rodent effects on extant remnants where both the rodents

and palatable plant species are likely to be scarce. An assumption is that rodents, by virtue of universal presence and a capacity for rapid increase (e.g. Taitt & Krebs 1985), have potentially profound impacts on grassland community structure and composition. In the first season of the Illinois experiment discussed here, voles (*Microtus pennsylvanicus*) decreased plant diversity in emerging tallgrass assemblages (Howe & Brown 1999), an effect that disappeared in two subsequent seasons when vole densities dropped by up to 96%. In a Wisconsin experiment, initial effects of seed depletion by voles that prefer large-seeded ($> 15 \text{ mg seed}^{-1}$) over small-seeded ($\leq 1.5 \text{ mg seed}^{-1}$) species had persistent effects of increased plant diversity through suppression of aggressive large-seeded dicots and release of small-seeded species (Howe & Brown 2000, 2001). Because voles are primarily herbivores, not granivores (Batzli & Cole 1979; Lindroth & Batzli 1984), an effect of more general interest would be a substantial decrease in the diversity of mature vegetation. Our Illinois experiment presents this possibility because voles and their effects vanished from the plots following the 1997 planting season, but returned in force with a spike in rodent numbers in the year 2000.

Here we report dramatic effects of vole herbivory on plant richness and diversity in experimental tallgrass restorations in Illinois. Whereas most tallgrass systems are dominated with up to 85–98% by cover of two or three species of late-flowering C_4 grasses and tough perennial forbs (Weaver 1968; Anderson & Adams 1981; Howe 1994), we planted equal numbers of 18 species at two densities, resulting in unusually high proportions of infrequent dicots and C_3 grasses. Here we ask the question: “Do ambient rodents influence richness, abundance and diversity through selective herbivory?” The result is a clue to tallgrass

dominance by C_4 grasses and tough forbs. Native prairies reflect, we believe, the “ghost of herbivory past”.

METHODS

The experiment consisted of a 4×6 grid of $24 \times 14 \times 14 \text{ m}$ enclosures on initially ploughed and disced oldfield in the Morton Arboretum, Lisle, Illinois. Each enclosure was separated by 3 m of oldfield vegetation. Experimental treatments among plots and subplots included planting date (June vs. December), planting density (10-fold difference between high and low seeding density), presence and absence of birds and/or rodents. Eighteen species of herbaceous perennials were broadcast seeded at 35 seeds m^{-2} in six plots, and 350 seeds m^{-2} in six plots in June 1997, with another set similarly seeded in December 1997 (Table 1; also see Table 1 of Howe & Brown 1999). Species were selected to test explicit hypotheses concerning seed-size selection following planting (Howe & Brown 1999). No attempt was made to emulate remnants already culled by small rodents; what is reported here is the serendipitous consequence of vole herbivory on local tallgrass species planted in atypical abundances.

Each $14 \times 14 \text{ m}$ enclosure was divided into four $7 \times 7 \text{ m}$ subplots, one of which admitted neither birds nor rodents, one both birds and rodents, one birds but not rodents, and the fourth rodents but not birds. Treatment levels nested within a $14 \times 14 \text{ m}$ plot were assigned randomly. Rodents were excluded with 1.23 m high hardware cloth fences sunk 0.6 m into the ground, with aluminium flashing bent over the top. Rodents were admitted with similar fences perforated by four ground-level $5 \times 5 \text{ cm}$ gates. Birds were excluded for 12 months after planting with 1.8 cm mesh

Table 1 Effects of vole access to 36-month-old tallgrass vegetation in an enclosure experiment in northern Illinois. F-statistics from a multivariate analysis of variance (MANOVA) and mean plants m^{-2} are shown for eight species that were significantly affected by vole access during the growing season of 2000. Significant density and planting season and non-significant bird effects are discussed in the text.¹

Species (family)	$F_{1,85}$	Voles absent (Mean \pm SE)	Voles present (Mean \pm SE)
Decreasers			
<i>Dalea purpurea</i> (Fabaceae)	6.972**	0.38 \pm 0.14	0.02 \pm 0.01
<i>Desmanthus illinoensis</i> (Fabaceae)	7.950**	2.44 \pm 0.38	1.10 \pm 0.29
<i>Elymus canadensis</i> (Poaceae)	10.751***	0.84 \pm 0.16	0.28 \pm 0.11
<i>Panicum virgatum</i> (Poaceae)	47.077****	2.90 \pm 0.45	0.33 \pm 0.12
<i>Phalaris arundinacea</i> (Poaceae)	3.939*	6.34 \pm 0.82	4.60 \pm 0.81
<i>Sorghastrum nutans</i> (Poaceae)	20.312****	0.72 \pm 0.12	0.12 \pm 0.04
Increasers			
<i>Echinacea purpurea</i> (Asteraceae)	7.717**	8.60 \pm 1.00	13.86 \pm 1.82
<i>Rudbeckia hirta</i> (Asteraceae)	26.312****	0.83 \pm 0.34	8.49 \pm 1.76

¹Species common enough for statistical analysis but showing no statistically significant response in 2000 included *Echinacea pallida* (overall mean 1.42), *Heliopsis helianthoides* (8.44; both Asteraceae), *Penstemon digitalis* (1.88; Scrophulariaceae), *Pycnanthemum virginianum* (0.56; Labiatae) and *Solidago rigida* (2.26; Asteraceae). Nomenclature follows Mohlenbrock (1986). * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.005$, **** $P \leq 0.001$.

Bird-X netting over the top of each enclosure; these nets were removed in June 1998 when vegetation reached a height (1.23 m) that pressed against them. Details of design, planting, species planted and of selective herbivory on vegetation in the first season (for the June 1997 planting) are given in Howe & Brown (1999). Because this was a test of small vertebrate effects, deer (*Odocoileus virginianus*) were excluded with a 2-m fence surrounding the 24 plots.

Plant analyses are from October counts of all perennial stems in five randomly placed permanent 1 m² sampling plots \geq 1 m from the fence within each of the 96 subplots. Bunches of grasses were counted as one plant each. Rodents were censused for two days and three nights on a grid of 130 Sherman live traps baited with rolled oats in October 1997, April, June and August 1998, February, July and November 1999, and May and October 2000. Voles (*Microtus pennsylvanicus*) and mice (*Peromyscus leucopus*) were captured, ear-tagged and released.

Our analytical tool for species effects was a multivariate analysis of variance (MANOVA). Richness is the number of experimental species m⁻². Calculations were for each of the five 1 m² sampling plots per subplot for species richness and for Simpson's diversity (D),

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

where p is the frequency of species i among all individuals of a given sample (in each of 5 m² per 7 × 7 m subplot). We used a partially hierarchical MANOVA to test for the effects of experimental factors on the eight plant species sufficiently common for analysis. As the eight dependent variables, we used the mean number m⁻² (calculated from the five 1 m² samples) of each species from each subplot ($n = 96$ for each species). The independent variables included mammals (present or absent), birds (present or absent), planting density (high or low), planting season (June or December) and plot (nested within the four combinations of planting density and planting season). We tested for main effects and for all six two-way interactions. Complete results are presented for mammal effects on species, and are summarized for bird, density and planting date effects on species. Parallel single factor analysis were done for diversity (D).

RESULTS

Vole effects on individual tallgrass species were not subtle. Of the 13 planted species common enough for analysis, eight were clearly affected by vole activity (Table 1), which largely eliminated legumes (Fabaceae) and common grasses (Poaceae). Of the 'decreasers', five of six were two to 10 times more common when voles were absent than when they were present (Table 1). The legumes purple prairie clover (*Dalea purpurea*) and Illinois bundleflower (*Desmanthus illinoensis*) and the cool-season grass Canada rye (*Elymus*

canadensis) were eliminated from some subplots, and reduced in others. For switchgrass (*Panicum virgatum*), canary reed grass (*Phalaris arundinacea*) and Indiangrass (*Sorghastrum nutans*), reduction in numbers appeared to be accompanied by reduction in clump size, which probably reduces competitive ability. A common sunflower (*Heliopsis belianthoides*) appeared unaffected. Of the two 'increasers', the biennial *Rudbeckia hirta* was 10 times more common when voles were present than when they were absent, whereas the long-lived perennial *Echinacea purpurea* increased in abundance by 61%. Other species may prove to be increasers with time. Stiff goldenrod (*Solidago rigida*) appeared to compensate but counts were too variable to constitute a statistically significant response. Foxglove rosettes (*Penstemon digitalis*) and mountain mint (*Pycnanthemum virginianum*) were exceptionally common in some December plantings to which voles had access, but were not widespread enough by the year 2000 to approach statistical significance. Overall, the MANOVA was highly significant (Wilk's lambda = 0.445, $F_{8,78} = 12.183$, $P < 0.001$).

Effects of other factors were less compelling. The MANOVA yielded no significant bird effects (presence or absence) left over from 1997 to 1998 manipulations for any species in 2000, and the overall MANOVA was unimpressive (Wilk's lambda = 0.967, $F_{8,78} = 0.329$, $P > 0.95$). In 2000, ongoing vole effects overwhelmed bird effects, which had been clear in 1998 and 1999 (unpublished). Planting density (35 or 350 seeds m⁻²) was significant for *E. canadensis* (positive; $F_{1,85} = 5.033$, $P < 0.05$), *P. arundinacea* (positive; $F_{1,85} = 18.818$, $P < 0.001$), *E. purpurea* (positive; $F_{1,85} = 15.664$, $P < 0.001$) and *R. hirta* (negative; $F_{1,85} = 9.555$, $P < 0.005$). Overall, the MANOVA was highly significant (Wilk's lambda = 0.558, $F_{8,78} = 7.709$, $P < 0.001$). Sowing time in 1997 (June or December) influenced *D. illinoensis* (more common in the June planting; $F_{1,85} = 4.199$, $P < 0.05$), *E. canadensis* (December; $F_{1,85} = 19.474$, $P < 0.001$), *P. virgatum* (June; $F_{1,85} = 32.756$, $P < 0.001$), *P. arundinacea* (December; $F_{1,85} = 42.526$, $P < 0.001$) and *R. hirta* (December; $F_{1,85} = 12.359$, $P = 0.001$). Overall, the MANOVA was highly significant (Wilk's lambda = 0.406, $F_{8,78} = 14.237$, $P < 0.001$). None of the two-way interactions involving birds was significant. There was a significant mammal by planting date (reflecting plant maturity) interaction for *P. virgatum* (high in June without voles; $F_{1,85} = 26.913$, $P < 0.001$) and *R. hirta* (high in December with voles; $F_{1,85} = 13.157$, $P < 0.001$). The MANOVA was highly significant (Wilk's lambda = 0.592, $F_{8,78} = 6.717$, $P < 0.001$).

Vole-driven changes in plant species richness and diversity (Simpson's D) were not subtle either (Fig. 1). Overall, richness dropped an average of 19%, or one species m⁻², where voles had access (6.20 ± 0.25 SE to 5.04 ± 0.28 ; $F_{1,92} = 16.791$, $P < 0.001$). Reduction was greatest at 37%, or 2 species m⁻², in June plantings. Diversity, a surrogate for

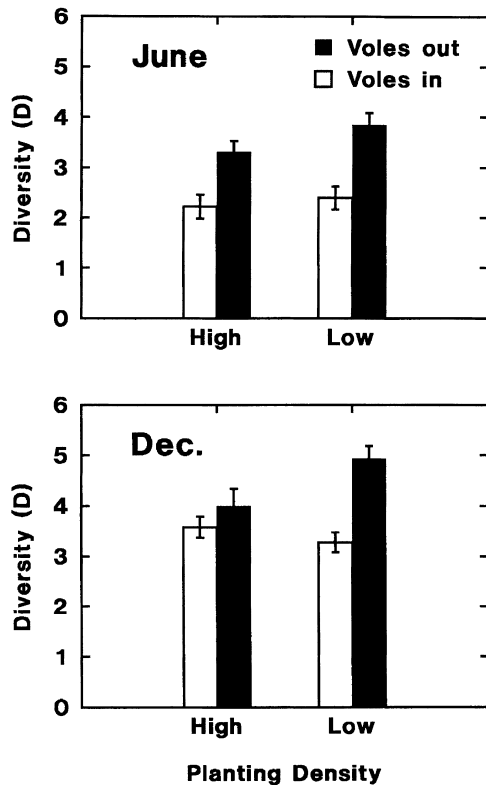


Figure 1 Plant diversity (Simpson's D) as a function of planting density and vole (*Microtus pennsylvanicus*) access. Top: diversities assessed in autumn 2000 of plots planted with 18 tallgrass species in June 1997. Bottom: diversities assessed at the same time for plots planted with the same species in December 1997. Low planting density (35 seeds species⁻¹ m⁻²) had higher diversities ($F_{1,88} = 4.046$, $P < 0.05$) than high planting density (350 seeds species⁻¹ m⁻²), but higher diversities are more strongly associated with December sowing ($F_{1,88} = 34.094$, $P \ll 0.001$) and exclusion of voles ($F_{1,88} = 44.781$, $P \ll 0.001$). A significant density by mammal interaction ($F_{1,88} = 5.115$, $P < 0.05$) reflected greater vole depression of diversity at low planting densities, where vole-driven changes involved loss of 1–2 species m⁻² and a sharp increase in the skew of species-abundance distributions.

community structure, reflects both richness and the species-abundance distribution of a community (Magurran 1988). MANOVA suggested that mammal access explained 18% of the variation in species number m⁻², and sowing date and density explained none (Table 1). Overall, access by voles reduced diversity 28%, from 4.02 ± 0.15 to 2.88 ± 0.14 ($t = -5.617$, d.f. = 92, $P < 0.001$).

The connection between species counts and diversity was indicated by skewness, or the degree of asymmetry in the species-abundance distribution. Here species-abundance distributions were four times as skewed in replicates where voles had access (0.618 ± 0.114) than where they did not (0.140 ± 0.101 ; $F_{1,46} = 9.851$,

$P < 0.005$), indicating vole-driven changes in community structure.

Voles decreased plant diversity in the season of planting (Howe & Brown 1999), but no vole effects were evident in years of low vole numbers in 1998 and 1999 (linear repeated measures, $P > 0.15$). Much more severe cropping of plants, reductions in richness and diversity, and positive numerical responses of other species (e.g. *E. purpurea* and *R. hirta*) are new in 2000.

The minimum number of *M. pennsylvanicus* known to be alive ha⁻¹ at the site from live trap censuses varied widely: (month and year 10/97) 85, (4/98) 4, (6/98) 19, (9/98) 61, (2/99) 43, (7/99) 51, (11/99) 96, (5/00) 155 and (10/00) 35. Runways, nests and clippings were ubiquitous in vole-access plots in years of moderate or high abundance. *Peromyscus leucopus*, a seed-eater, was scarce, one *Spermophilus tridecemlineatus* ground squirrel occupied a subplot briefly but did not survive a winter, and no *Sylvilagus floridanus* cottontails or *Marmota monax* woodchucks were observed.

DISCUSSION

Our experiment shows that in grassland vegetation herbivory by voles, like ungulates (Milchunas & Laurenroth 1993; Proulx & Mazumder 1998; Knapp *et al.* 1999), insects and molluscs (Fraser & Grime 1999), has the capacity to shape plant composition. Questions that remain are how can the effects of rodent herbivory on synthetic communities be interpreted, and what might they imply for prairie ecology?

Specific effects on species have general implications for diversity. Reduction in numbers by voles of otherwise common plant species by up to 89% leaves room for subdominant species (Howe & Brown 1999, 2000, 2001; see Cornell & Lawton 1992). The extent to which "decreasers" rebound when voles become scarce will depend on the degree to which competitors compensate and occupy space over the short and long term (Belsky 1987, 1992). We found immediate compensation by black-eyed Susan (*Rudbeckia hirta*) and purple coneflower (*Echinacea purpurea*) in subplots to which voles had access, and we expect that other species tolerant of or distasteful to voles may do the same over the long term. In a more general sense, voles shaped plant diversity and therefore community structure (Fig. 1). Partitioned by planting season and density, low planting density had higher diversities, but higher diversities are much more strongly associated with December sowing and exclusion of voles. A significant density by mammal interaction indicates a greater effect of mammals at low density, with reductions in diversity at high and low planting densities of 10% and 33% in the December plantings and 33% and 37% in the June plantings.

Our use of experimental restoration ecology (*sensu* Jordan *et al.* 1987) bears three notable implications:

First, ambient populations of *Microtus pennsylvanicus* are capable of altering the relative abundances of tallgrass plant species, either by direct suppression of vegetation or by indirect release of less palatable competitors. Two successful “compensators”, *E. purpurea* and *R. birta*, remained as vigorous rosettes in vole-decimated plots, a growth stage associated in other species with high levels of chemical defence (Ohnmeiss & Baldwin 2000). These rosettes, 3–6 cm high, offered low stature and poor cover for rodents, which then could be expected to reduce foraging activities (Brown 1992, 1999). As in successional hardwood forests in New York, voles removed some otherwise common species and created conditions conducive for proliferation of others (Ostfeld & Canham 1993; Ostfeld *et al.* 1997). There *M. pennsylvanicus* eliminated seedlings of some otherwise common hardwood species during oldfield succession, and reduced others up to 80%, thereby changing the course of succession. In prairies, voles could impose a periodic forcing function in which high vole populations reduce or eliminate some plant species every few years, allowing a partial recovery when the animals become scarce. Microtines show 10-fold pulses of abundance with a periodicity of 3–6 years (Taitt & Krebs 1985), whether predation, resource depletion, chaos, or some dynamic mix of factors drives rodent fluctuations (Turchin & Ellner 2000; Turchin & Batzli 2001). If voles eliminate plant species that play key roles in the community, such as legumes that fix soil nitrogen (Sirotnak & Huntly 2000), their effects may extend beyond simple repression and release.

Second, voles alter the templates for tallgrass community change. What they leave as seeds, seedlings, repressed juveniles, damaged and stunted adults, or vigorous rosettes “in waiting” influences the potential response to future change (Howe & Miriti 2000). Eliminated species may re-colonize, but at a disadvantage in competition with established survivors that are tolerant of or are released by vole herbivory on competitors (e.g. Belsky 1987). One can expect different species, or the same species in different spatial and competitive circumstances, to have different demographic trajectories, and therefore different contributions to community change (Miriti *et al.* 2001). For instance, the numerical surge of *R. birta*, an opportunistic biennial that was especially prominent in the December plantings, will disappear as longer-lived tolerant species displace it (Howe 1995). A 10-fold increase in the numbers of this species in a year is less consequential than what will replace it in 2–3 years. For *E. purpurea*, a long-lived perennial, the vole-driven increase of 61% in abundance will be much more persistent as a direct species-specific effect. Other species relegated to small numbers of scattered individuals are unlikely to anchor viable populations over time (Maina & Howe 2000). One expects small populations to disappear, thereby limiting the template for change.

An open question is whether vole-driven succession will ultimately produce apparently natural communities or stable alternatives. These assemblages could become communities of less palatable dominants that superficially resemble more diverse native prairies (e.g. Peet *et al.* 1983), or vole herbivory might produce alternative stable states from a smaller species pool, such as a *R. birta*–*E. purpurea* oscillation around less volatile *E. pallida* and *H. belianthoides* populations, with *P. digitalis*, *P. virginianum* and *S. rigida* populations playing dynamic but indeterminate roles (Table 1). Alternatively, space now occupied by *R. birta* might be usurped by less palatable but aggressive perennials such as *P. aurindinacea* (reduced by 27%) rather than other grasses (reduced by 67–89%; Table 1), ultimately reducing food available to voles. Explorations of such effects could begin with models that predict balancing plant resource competition (R^*) and predator density affecting plants (P^* ; Holt *et al.* 1994), where the predators are voles feeding on and killing alternative competing plant species.

Third, the controlled manipulations employed here yield insights that remnant prairie vegetation or close mimics cannot give. Voles prosper better in fields of forage crops, pastures or oldfield successions than in native prairies because pasture legumes and grasses cultivated for livestock are more palatable than native prairie plants (Batzli & Cole 1979; Lindroth & Batzli 1984). We hypothesize that native prairies, or artificial restorations that mimic them, show little obvious evidence of vole depredations because extensive stands of large C_4 grasses (e.g. *Andropogon*) or tough unpalatable forbs (*Echinacea*, *Heliopsis*, *Silphium*) have been favoured by millennia of rodent suppression of palatable competitors, a result confirmed by the absence of detectable rodent herbivory in plantings with a predominance of such species (Howe & Brown 2000, 2001). It may be that in North American tallgrass where large ungulates and small rodents coexist, one guild partially compensates for temporary absence of the other in effects on vegetation, as in the Serengeti of Africa (Young *et al.* 1998; Keesing 2001). This is not an issue over most North American tallgrass habitats, where important large native ungulates are extinct.

In native vegetation long since culled by voles, effects may be subtle. Contemporary rodent herbivory is likely to be of infrequent or rare subdominants that are often too uncommon to register positive numerical responses when voles are temporarily absent, or even to allow easy detection of reduced numbers when voles are common. One consequence of selective vole herbivory, as for that of molluscs and insects in grasslands, might be to accelerate succession of inedible late-successional species (Fraser & Grime 1999). In tallgrass communities continually sorted by ubiquitous rodent and invertebrate herbivores, common plants are probably assembled, randomly or not, from

species with seeds and foliage that small herbivores do not care to eat.

Connell (1980) explored a “ghost of competition past”, reflected by existing plant associations shaped by much earlier competitive partitioning of resources. A recent experiment has demonstrated the potential for a “ghost of granivory past”, reflecting changes in species composition that resulted from early rodent seed predation on aggressive large-seeded species, resulting in persistent release of small-seeded but physically large perennial competitors (Howe & Brown 2001). In remnant prairies of tough vegetation we see the more general “ghost of herbivory past”, reflected by community-wide responses to conditions that no longer exist because voles and other herbivores have long since eaten the evidence.

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