All assays were performed in triplicate and the data expressed as the fraction of total cells appearing on the bottom of the filter.

17. Migration of low passage (1 to 3) human saphenous vein smooth muscle cells was assessed as described (*16*). Cellular spreading was assessed by phase-contrast microscopy of cells after 15 to 30 min at 37°C in microtiter wells coated with fibronectin or BSA. At least 200 cells were counted and the fraction remaining rounded was expressed as a percentage of the total.
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30. Abbreviations for the amino acid residues are as follows: A, Ala; E, Glu; F, Phe; G, Gly; H, His; I, Ile; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; S, Ser; T, Thr; and Y, Tyr.
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Ecological Determinants of Species Loss in Remnant Prairies

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Recensuses of 54 Wisconsin prairie remnants showed that 8 to 60 percent of the original plant species were lost from individual remnants over a 32- to 52-year period. The pattern of species loss was consistent with the proposed effects of fire suppression caused by landscape fragmentation. Short, small-seeded, or nitrogen-fixing plants showed the heaviest losses, as did species growing in the wettest, most productive environments. The interruption of landscape-scale processes (such as wildfire) by fragmentation is an often overlooked mechanism that may be eroding biodiversity in many habitats around the world.

Prairies covered 800,000 ha in Wisconsin before European settlement, but today they occupy less than 0.1% of their former extent and are mainly restricted to small, isolated remnants in a fire-suppressed landscape (*1*, *2*). Current theory predicts that each remnant should lose several plant species by habitat fragmentation. Because it alters the size, spacing, and context of individual habitat patches, fragmentation may increase the local rate of extinction by reducing population sizes or colonization from similar habitats (*3*–*5*), by eliminating keystone predators or mutualists (*6*, *7*), by exacerbating stochastic phenomena and genetic bottlenecks (*8*), or by changing the physical or biological environment through edge effects (*9*). The highest extinction rates are expected in species that are initially rare (*3*, *4*, *10*), that are geographically restricted (*10*, *11*), that require large unbroken patches of habitat or short distances between such patches (*5*, *9*), that rely on specialized pollinators or other mutualists (*6*, *7*, *10*), or that are competitive dominants with limited dispersal ability (*12*). However, such predictions ignore the effects of fragmentation on landscape-scale processes, such as wildfire, that affect the disturbance regime within individual patches (*13*). We propose that such effects are a dominant source of plant species loss in prairie remnants in the central United States; that they lead to disproportionate losses in short-statured, N-fixing, and small-seeded species; and that such losses are greatest in the most productive environments. We support these predictions by using a unique data set on species occurrences in prairie remnants, which display a remarkable rate of local plant extinction of 0.5 to 1.0% per annum over a 32- to 52-year period.

In the upper midwestern United States, frequent fire was the primary disturbance maintaining the open nature of prairies and oak savannas before European settlement, selecting against woody plants and favoring fire-adapted grasses and forbs (*1*, *2*). Once ignited by Amerindians or lightning (*1*, *2*), such fires were able to burn for many kilometers before being stopped by natural barriers (such as streams, swamps, and topographic breaks) or quenched by rain. For a given climate and soil, the area and local frequency of fires should increase with the area and contiguity of flammable terrain; the greater the area devoid of fire barriers, the more extensive each fire should be, increasing the average fire frequency at each point (*13*). After European settlement, we believe that local fire frequencies were reduced (*14*) not only by overt suppression, but also by fragmentation of a fire-prone landscape by nonflammable barriers such as roads and agricultural fields. By the 1940s and 1950s, most prairies in Wisconsin had disappeared except in certain fire-prone refugia (*1*, *2*, *15*), including railroad rights-of-way (where, before the 1950s, sparks cast by steam locomotives frequently started fires) and steep slopes with thin soils (where tilling was precluded and farmers had often grazed livestock and set fires in spring to encourage a new flush of growth). A few prairie remnants also persisted in country cemeteries, where infrequent mowing may have substituted for fire or grazing by native ungulates. Plant species lists of some 200 prairie remnants were compiled by Curtis and his colleagues (*1*) during the 1940s and early 1950s.

During and after the 1950s, the frequency of fire in railroad and hillside prairie remnants declined abruptly as human sources of ignition (steam locomotives and grazing of livestock on low-productivity slopes) were withdrawn in the context of a highly fragmented prairie landscape. We predict that, as a consequence, several

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groups of plant species would have become especially prone to local extirpation within remnants, especially those with short stature, N-fixing symbioses, or small seeds. Herbs with leaves close to the ground gain an advantage on sparsely vegetated sites by allocating less energy to supportive tissue, but can be excluded by taller competitors on more productive, densely covered sites (*16*). Frequent fire, by reducing cover from live and standing dead plants, fosters the persistence of short species. By suppressing fire, fragmentation should thus increase local loss of short species; tall or woody species should rise in abundance. Frequent fires should favor plants with N-fixing symbioses, because fire opens sites and volatilizes N stocks (*17*) and because such symbioses should provide a net advantage only on open, sunny, N-poor sites (*18*). Fragmentation and consequent fire suppression should thus select against plants with N-fixing symbioses. Fragmentation may also select against plants with small seeds, which are favored in sparsely vegetated or frequently disturbed microsites, or both, where local competition is reduced and small seed size yields an advantage in dispersal and fecundity (*19*). Finally, loss of short-statured or N-fixing species should be greatest on the most productive remnants, where fire suppression by fragmentation would lead most rapidly to dense coverage.

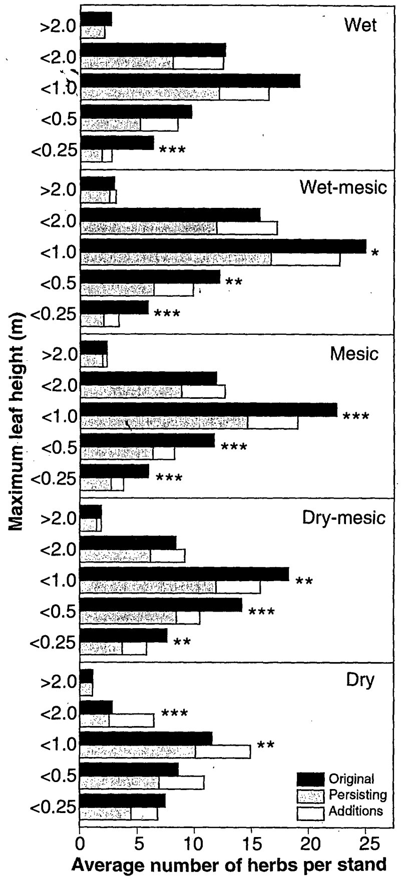

Fig. 1. Average number of herbaceous species per site. Shown are species originally present (black bars), species persisting until 1987–88 (gray bars), or species recruited between censuses (white bars), as a function of maximum leaf height and site moisture status [based on initial species composition (*1*)]. The difference between black and gray bars at a given leaf height indicates absolute species loss over the study period; the difference between black and combined gray and white bars indicates net loss. Total area of black bars gives the average number of herbaceous species initially found on sites at a given position on Curtis' moisture gradient (*1*); note the broad peak in species number in the middle of the gradient. Asterisks indicate significance of net change in total number of species occurrences for species with a given leaf height, based on the McNemar change test (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Total occurrences are products of average species number (shown) and number of sites per position on moisture gradient (6 wet sites, 12 wet-mesic, 17 mesic, 14 dry-mesic, and 5 dry).

We tested these hypotheses by resampling 54 prairie remnants studied by Curtis and his colleagues (*1*). The remnants studied met three criteria. First, each was extant, on the basis of the presence of a high proportion of native species, prairie physiognomy, and lack of overt destruction (such as plowing or paving); second, each had remained roughly constant in area; and third, at least five remnants were included for each community type (dry, dry-mesic, mesic, wet-mesic, and wet). Remnants ranged from 0.2 to 6.0 ha in area and were scattered in 14 counties on a wide range of soils and topographies; 74% were on railroad rights-of-way.

We based the presence or absence of 273 indigenous prairie species in each remnant on three to five censuses at different seasons, using the same techniques employed by the original investigators. Most of the original surveys were completed between 1948 and 1954; one was completed in 1936, and another in 1942. Resampling was conducted in 1987–88. Temporal shifts in species occurrence (number of stands occupied by each species) and species richness (number of species in a remnant) were related by multiple regression to remnant area, position on Curtis' moisture gradient (*1*), and time between surveys. Species loss and new species occurrence (recruitment) were related to leaf height, N-fixation, and seed weight by the McNemar change test, χ^2, and Kruskal-Wallis test.

As expected from the theory of island biogeography (*3*, *4*), the number of species lost decreased with an increase in remnant area and increased with an increase in the number of species originally present:

$$\ln \text{No. of spp. lost} = -0.184 \ln \text{area} + 1.65 \ln (\text{No. of original spp.}) - 3.97 \quad (1)$$

($r^2 = 0.67$, $P < 0.001$ for 51 df). Backward-elimination regression failed to identify a significant effect for time between surveys (raw or log-transformed), raw area or original number of species, or position on Curtis' moisture gradient when other factors were excluded (see below). Remnant area and time between surveys showed little correlation with each other or with position on the moisture gradient ($r < 0.14$, $P > 0.4$). The

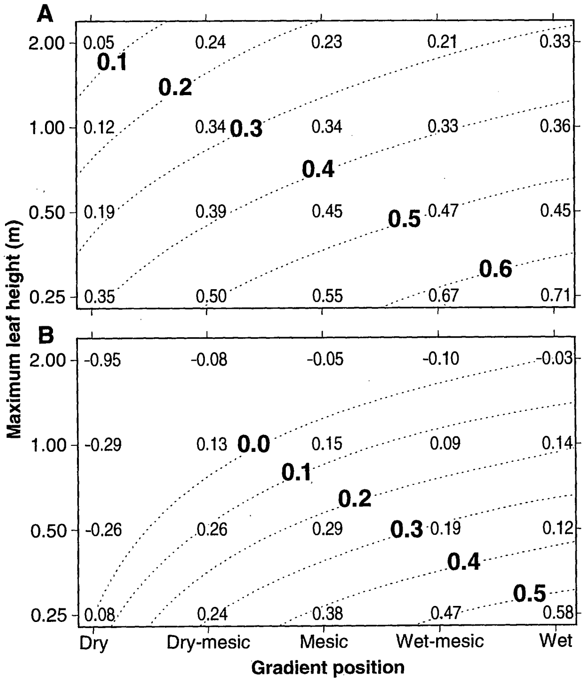

Fig. 2. Absolute (**A**) and net (**B**) species loss, expressed as a fraction of the initial species pool, plotted as a function of maximum leaf height and site moisture status. Contours (labeled in bold) indicate best-fit multiple regressions relating loss rates to maximum height [0.25 m (0 to 0.25 m), 0.5 m (0.26 to 0.50 m), 1.0 m (0.51 to 1.00 m), and 2.0 m (1.01 to 4.00 m)] and site moisture status; numbers indicate actual average rates of loss for each height- and site-class combination. Note that absolute and net species loss both increase with decreasing leaf height and increasing site moisture and productivity. Absolute loss equals $-0.162 \ln$ leaf height $+ 0.167 \ln$ gradient position $+ 0.148$ ($r^2 = 0.92$, $P < 0.0001$ for 17 df; $P < 0.0001$ for individual effects of both variables). Net loss equals $-0.252 \ln$ leaf height $+ 0.574 \ln(1 + \ln$ gradient position$) - 0.367$ ($r^2 = 0.77$, $P < 0.0001$ for 17 df; $P < 0.0001$ for individual effects of both variables).

Table 1. Local extinction and recruitment in species with and without N-fixing symbioses, based on total numbers of species occurrences across 54 sites in the 1940s and 1950s versus the late 1980s.

Guild	Original	Persisting	Recruitment	Absolute extinction (%)	R/P* recruitment (%)	Net extinction (%)
N-fixers	278	171	41	38.4	23.9	23.7†‡
Non-fixers	2913	1926	830	33.9	43.1	5.4†

*R, number of species recruited; P, number of species persisting. †Net loss differs significantly from zero ($P < 0.001$, McNemar change test), ‡Net loss among N-fixers is significantly higher than among non-fixers ($P < 0.03$, $\chi^2 = 5.20$ for 1 df).

number of species originally present peaked in the middle of the moisture gradient, although only dry remnants had a mean species richness (34.0 ± 9.9) significantly lower than that of remnants at any other position on the moisture gradient ($P < 0.05$, Kruskal-Wallis test).

As predicted, the historical decline in herb occurrence was greatest in species that had leaves closest to the ground, with the magnitude of the absolute decline increasing along the moisture and productivity gradients from dry to wet prairies (Figs. 1 and 2A). The net decline, which included recruitment, of occurrence in each leaf-height class showed a similar pattern, with the greatest decline in the shortest species and only the tallest species (leaf height >1 m) showing a net increase in all but the dry remnants (Figs. 1 and 2B). When recruitment between surveys was excluded, the decline in the number of the shortest species (<0.25 m) ranged from 35.1% in dry remnants to 70.5% in wet remnants. When recruitment was included, the net decline of the shortest species varied from 8.1% in dry remnants to 57.9% in wet remnants (*20*). Overall, there was a significant net decline in the number of herb species in dry-mesic, mesic, and wet remnants. Woody species (trees, shrubs, and vines) showed a small but significant increase ($P < 0.05$, McNemar change test) in richness across the moisture gradient, with average species number per site increasing from 5.3 ± 2.9 to 7.2 ± 2.7, and 4.3 ± 2.4 of the original 5.3 species persisting at least into the late 1980s.

Herb species richness increased significantly in dry prairies, owing to the invasion of tall herbs, as well as a few woody plants. These taller species are favored by dense coverage (*16*) and are typical of more mesic prairies, which had a larger overall species pool and more species per remnant than the unusually species-poor dry prairies (Fig. 1). The unexpected net increase in species number in dry prairies may be due to the loss of a small number of short species offset by recruitment from a much larger pool of tall species.

As predicted, the summed occurrences of plants with N-fixing symbioses [legumes and *Ceanothus americana* (Rhamnaceae)] showed a marked net decline, which averaged 23.7% across remnants (Table 1). Such species are too few to test whether their decline varies with moisture availability. However, most of their net decline is related not to low persistence (61.6% in N-fixers compared with 66.1% in non-fixers) but to low recruitment (41 new occurrences of N-fixers compared to 830 for non-fixers) (Table 1). Low recruitment might reflect a competitive disadvantage of N-fixers during seedling establishment, a low capacity for dispersal between remnants, the small number of species ($n = 17$) available for recruitment, or the number of sites available for invasion. Fire suppression would indicate the importance of the first of these factors; lack of long-distance dispersal in many prairie legumes suggests the second may also be important. When the number of new species occurrences (recruitment) was divided by the number of species in the potential pool of recruits for remnants in each of the five prairie community types, the difference in recruitment rate between N-fixers (7.9 ± 1.3%) and non-fixers (6.4% ± 3.6%) was not significant ($P > 0.3$, two-tailed t-test with 8 df). However, when recruitment rates ($\Delta p/\Delta t$) were instead normalized—in accord with a standard metapopulation model [$\Delta p/\Delta t = mp(1 - p)$]—by both the relative occurrence (p equals average fraction of sites occupied) of species in the landscape and the proportion of sites unoccupied by those species ($1 - p$), the relative recruitment rate (m) over the study period was 0.27 for N-fixers and 0.37 for non-fixers. When all factors were taken into account, N-fixers thus showed a recruitment rate 27% lower than that of non-fixers.

Species with small seeds (<1 mg) showed significantly higher rates of decline than those with larger seeds (Table 2), which is consistent with our hypothesis that small-seeded species would have lower competitive ability in a fire-suppressed landscape. The overall pattern of species loss agreed with predicted effects of fire suppression and seemed inexplicable in terms of other systemic changes since 1950, such as increases in white-tailed deer (*Odocoileus virginianus*) or N deposition. High deer density can adversely affect N-fixers (*21*), but would favor short or small-seeded species by exposing tall plants to more damage. Increased N deposition might adversely affect short, N-fixing, and small-seeded species, in effectively the same ways as fire suppression. However, current rates of dry deposition in southern Wisconsin (about 6 tons/ha) (*22*) are far lower than the threshold of 42 to 55 tons/ha needed to decrease plant diversity in calcareous European grasslands (*23*). Species loss can occur in prairies on dry, infertile sands at such rates of N addition (*24*), but on such sites we observed the only net gain of plant species (Fig. 2). Few data exist on the effects of experimental fire suppression on prairies, but they are consistent with our predictions and the observed pattern of species loss. In Nebraska (where invasion by woody plants was not an issue), Weaver and Rowland (*25*) found that a prairie that had not been burned, mowed, or grazed in 15 years lost most of its forb understory and almost all short- or medium-height grasses. At Konza prairie in Kansas, overall plant diversity declined with intervals greater than 6 years between fires (*26*); annual burning more than doubled legume density and share of total forb biomass (*27*). Fire may thus play a key role in making legumes a leading component of prairies.

In Wisconsin, the average absolute loss of species per site per year (a minimal estimate of local extinction rate, excluding re-

Table 2. Local extinction and recruitment as a function of seed mass, based on total numbers of species occurrences across 54 sites in the 1940s and 1950s versus the late 1980s. A total of 37 species were excluded from analysis because of a lack of data on seed mass.

Seed mass (mg)	Original	Persisting	Recruitment	Absolute extinction (%)	R/P* recruitment (%)	Net extinction (%)
<0.1	136	54	43	60.3	79.6	28.7†
<1	1087	665	302	38.8	45.4	11.0†
<10	1316	947	290	28.0	30.6	6.0†
<20	290	187	94	35.5	50.3	3.1
>20	238	176	66	26.1	37.5	−1.7

*R, number of species recruited; P, number of species persisting. †Net loss differs significantly from zero ($P < 0.01$, McNemar change test).

colonization between censuses) was 0.45% for dry prairies, 0.77% for mesic prairies, and 1.03% for wet prairies. These values imply that half the plant species present in a remnant wet prairie would disappear in less than a half-century, whereas, in the best case, half the botanical diversity of a remnant dry prairie would disappear in slightly more than a century. Much of this loss involves short plants; species <0.5 m tall account for 52, 42, and 41% of the absolute loss in dry, mesic, and wet prairies, respectively. N-fixers account for 11% of the absolute loss and have 45% less recruitment than non-fixers. Losses among regionally rare species were especially severe; the 13 state-listed endangered or state-listed threatened species in our remnants lost 28 of 38 total occurrences, an absolute loss of 74%, more than twice the average of 34% for all species.

The implications of our findings for conservation are clear. First, it is essential to burn existing prairie remnants to help offset loss of ignition sources due to disruption of landscape context and human cultural practices. Prescribed burns should be conducted over a small portion of each remnant in any single year so that fire-sensitive organisms (for example, certain insects and lizards) are not extirpated. Second, conservation efforts should focus on species that are short, small-seeded, N-fixing, regionally rare, or possess a combination of these traits, especially on mesic to wet sites. Third, local plant extinctions are proceeding at such a high rate (0.5 to 1.0% per annum) that several taxa are in danger of being lost from the landscape. Of 266 species originally found across 54 sites in the 1940s and 1950s, only 228 persisted until the late 1980s, which represents an absolute loss of 14.3% of all native plant species. Although such species are not restricted to prairie remnants, often they are most common there, which suggests that the observed losses reflect a broad regional process.

The interruption of the landscape-scale process of wildfire may be eroding biodiversity in many habitats worldwide. The composition, structure, dynamics, and productivity of several ecosystems—taiga, temperate forests and grasslands, Mediterranean scrub, savannas, and even some wet tropical forests—are strongly affected by fire; many of their species require fire to persist or reproduce (*1, 13–15, 28*). The mechanism underlying local plant extinction we propose for prairies may operate in many other fragmented communities and thus have broad ramifications for conservation and ecosystem management.

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Effects of Disturbance on River Food Webs

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A multitrophic model integrating the effects of flooding disturbance and food web interactions in rivers predicted that removing floods would cause increases of predator-resistant grazing insects, which would divert energy away from the food chain leading to predatory fish. Experimental manipulations of predator-resistant grazers and top predators, and large-scale comparisons of regulated and unregulated rivers, verified the model predictions. Thus, multitrophic models can successfully synthesize a variety of ecological processes, and conservation programs may benefit by taking a food web perspective instead of concentrating on a single species.

Although conservation programs typically concentrate on the direct impacts of environmental change on a single species, ecological experiments and theory demonstrate that species are affected in complex ways by other species, ecosystem productivity, and disturbance regimes (*1–4*). Therefore, to understand and predict the consequences of impacts on the environment, ecologists must shift from an autecological perspective to consideration of the interaction of multiple causal factors. For example, changes in climate, land use, and water regulation or diversion all may alter the flooding regime