QUADRATIC VARIATION IN OLD-FIELD SPECIES RICHNESS ALONG GRADIENTS OF DISTURBANCE AND NITROGEN

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Abstract. We followed species richness, colonizations, extirpations, and turnover for eight years in 16 combinations of disturbance and nitrogen addition applied to a 30-yr-old Minnesota field. Four levels each of disturbance and nitrogen were applied in a completely factorial design, producing 16 treatments. There were four replicates of most treatments and 14 replicates of the four extreme treatments (lowest and highest disturbance and nitrogen). After 5–6 yr, species richness varied quadratically and significantly with disturbance in plots receiving no nitrogen or the lowest level of added nitrogen. Richness increased over time at intermediate disturbance as annuals colonized plots otherwise dominated by perennials. The number of growth forms also varied quadratically with richness, whereas the number of species belonging to each growth form did not, suggesting that high richness was due to coexistence of species with different life histories. The strongest quadratic variation in species richness was associated with significant quadratic variation in colonization with increasing disturbance, and no significant variation in extirpation, suggesting that increased richness at intermediate disturbance was attributable to colonization at the middle of the disturbance gradient, and not to extirpation at either end of the gradient. Richness decreased with increasing nitrogen at all levels of disturbance. Colonization also decreased and extirpation increased with increasing nitrogen availability, suggesting that decreases in richness with increasing nitrogen reflect accelerated extirpation, and not colonization of nitrogen-poor soils. Simultaneous competition experiments showed colonizations in disturbed plots to be related to reduced root competition, and extirpations in fertilized plots to be related to increased shoot competition. Surprisingly, untreated control plots had higher rates of colonization, extirpation, and species turnover than disturbed or fertilized plots. Turnover in control plots was caused mostly by uncommon species, and control plots were always dominated by the perennial grass *Schizachyrium scoparium*. In contrast, the dominant species of the extreme environmental treatments varied over time in spite of their low levels of richness. The array of responses generated by our factorial experiment helps explain why richness varies with disturbance and fertility in different ways along different natural gradients: patterns and dynamics of richness clearly depend on location within the fertility–disturbance matrix.

Key words: colonization; disturbance; diversity; extirpation; nitrogen; old field; species richness.

INTRODUCTION

Models predicting maximum diversity at intermediate levels of disturbance and productivity (Grime 1973, Connell 1978, Huston 1979, Tilman 1988, Ritchie and Olff 1999) help explain the variety of ways in which plant species richness varies along local environmental gradients (see reviews in Ricklefs and Schluter 1993, Huston 1994, Rosenzweig 1995). Disturbance, such as burning, grazing, or drought, can both increase and decrease richness, depending on whether common or uncommon species are most affected (Huntly 1991, Belsky 1992, Tilman 1993, Wilson 1994*a,* Halpern and Spies 1995, Steinauer and Collins 1995, Collins et al. 1998, Gough and Grace 1999, Keddy and Fraser 1999). Environmental gradients in wetlands often incorporate both productivity and disturbance, and these typically show quadratic variation in richness with community biomass (Wilson and Keddy 1988, Moore and Keddy 1989, Shipley et al. 1991, Pollock et al. 1998). Richness also varies quadratically along some terrestrial productivity gradients (Vermeer and Berendse 1983, Nilsson and Wilson 1991, Ritchie and Olff 1999, Waide et al. 1999), and decreases with productivity along others (Lundqvist 1968, Wheeler and Shaw 1991, Gough et al. 1994), possibly because these cases reflect the descending part of the proposed quadratic relationship. Richness generally decreases with increasing productivity along experimental gradients (reviewed by Gough et al. 2000). Although both disturbance and productivity are thought to control richness, there are few simultaneous manipulations of both factors.

Several lines of evidence highlight the importance of multiple controls. A review found that univariate analyses typically explained one quarter of the variation in richness, whereas multivariate analyses explained about one half (Grace 1999). The experimental fertilization of Louisiana marshes decreased richness only in plots from which herbivores were excluded (Gough and Grace 1998). Another review found that grazing decreased plant richness in nutrient-poor terrestrial systems and increased it in nutrient-rich systems (Proulx and Mazumder 1998). All of these studies suggest that disturbance and productivity have interactive effects on richness.

Richness is controlled ultimately by disturbance and productivity, but proximately by colonization and extirpation (Rydin and Borgegård 1988, Grace and Pugasek 1997). In species-rich Minnesota old fields, colonization is decreased and extirpation is increased by nitrogen addition, resulting in lower richness (Tilman 1993). In recently abandoned Michigan fields, however, colonization and extirpation were unaffected by nitrogen (Huberty et al. 1998). Disturbance increases both colonization and extirpation (Belsky 1992, Montalvo et al. 1993, McIntyre and Lavorel 1994), and these contribute to the turnover of species through time. Turnover is high in natural vegetation (Rydin and Borgegård 1988, O'Connor 1991, van der Maarel and Sykes 1993, Robinson et al. 1995, Collins 2000) and contributes to diversity because patches undergoing different stages of turnover differ in species composition. The responses of colonization, extirpation, and turnover to fertility and disturbance also need examination.

Quadratic variation in richness has been attributed to the coexistence of contrasting growth forms (Denslow 1980, Shipley et al. 1991, Wilson 1994b) in some cases but not in others (Wilson and Keddy 1988), and there is no consensus on which is the general mechanism, or whether this differs between disturbance and productivity gradients.

Here we describe an experiment in which disturbance and resource availability were manipulated in an old field for eight years. We tested for quadratic variation in richness, colonization, extirpation, and turnover. We also tested whether variation in richness was caused by changes in the number of growth forms present, or by the number of species belonging to each growth form. We relate our results to simultaneous measurements of root and shoot competition conducted within the experiment (Wilson and Tilman 1993, 1995, Wilson 1994c).

METHODS

An experimental gradient of nitrogen availability and disturbance was established in 1988 in a then 31-yr-old field on a nitrogen-poor sand plain (Field B at Cedar Creek Natural History Area; 45°24′ N, 93°12′ W; 50 km north of Minneapolis, Minnesota, USA). The field has fine sand soil, was last farmed in 1957, and is characterized by *Schizachyrium scoparium,* a perennial C_4 grass, and cryptogamic soil (a dark surface crust of cyanobacteria and moss protonema). Nitrogen is the limiting soil nutrient in the field (Tilman 1988).

Four levels of nitrogen (N1–N4) and four of disturbance (D1–D4) were applied annually (1988–1995) in a factorial design, producing 16 treatment combinations (Wilson and Tilman 1991). Treatments were applied in a completely randomized design to 5 × 5 m plots separated by 2 m wide corridors. There were four replicates of each treatment except for the four extreme treatments (N1D1, N1D4, N4D1, N4D4), which had ten additional replicates used in competition experiments (Wilson and Tilman 1993, 1995, Wilson 1994b).

Nitrogen was applied as commercial solid NH_4NO_3 at 0, 2.0, 9.5, and 17 $g \cdot N \cdot m^{-2} \cdot yr^{-1}$ in early May and late June each year. P, K, and trace elements were also added to all plots in all treatments to ensure that only nitrogen was limiting (see Wilson and Tilman 1991).

D1 plots received no disturbance. Other plots were tilled annually in late April or early May, before N application, to a depth of 10 cm with a rear-tined, self-propelled rototiller (Wilson and Tilman 1991). This machine spread the disturbance evenly across the plots in a repeatable manner. Disturbance was applied uniformly to avoid the introduction of spatial effects (Miller 1982, Coffin et al. 1996). Disturbance intensities varied according to the amount of bare ground produced (D1: 0%; D2: 25%; D3: 50%; D4: 100%). These disturbance regimes were not designed to reproduce any particular natural disturbance. Rather, they incorporate the common definition of ecological disturbance, i.e., biomass removal (Grime 1979, Tilman 1988), using a method which can be applied consistently across space and time.

The experiment was surrounded by a 2 m tall fence to exclude large mammals and hardware cloth buried to a depth of 50 cm to exclude pocket gophers, the most important natural agent of disturbance at the study site (Inouye et al. 1987). Seasonal dynamics of standing crop, litter, root mass, available nitrogen, and light in the plots are described by Wilson and Tilman (1991, 1993). The experiment was accidentally burned in early spring 1994, but this had no detectable effect on richness, species composition, standing crop, or resources measured in August 1994 (S. D. Wilson and D. Tilman, *unpublished data*).

Species covers were measured in mid-August (1988–1995) along a transect that ran diagonally across each plot. Two quadrats (0.5 × 1 m) were placed along the transect, each 1.5 m towards the center of the plot from the ends of the transect. The cover of each species was recorded in each quadrat using Daubenmire's (1959) scale. The mean cover of each species in each plot was determined. Appropriate species covers were summed to find the covers of growth forms (C_4 perennial grasses, C_3 perennial grasses, perennial forbs, annual grasses, annual forbs, cryptogams [lichens, mosses, and
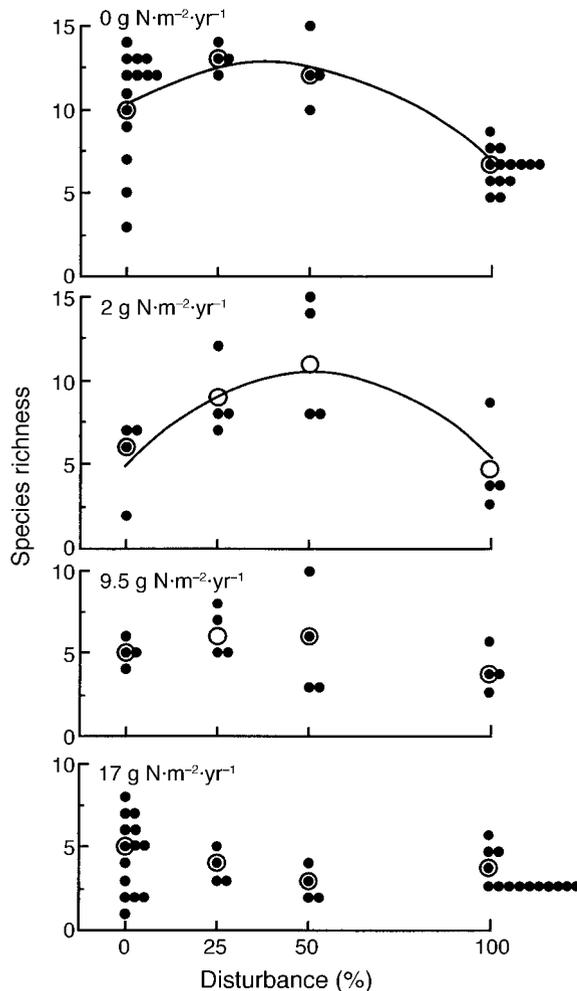
FIG. 1. Species richness after eight years across four levels of disturbance at four levels of nitrogen addition. Dots are values from replicate plots (1 m²). Open circles are means. Lines are shown only for significant relationships ($P < 0.05$; Table 1). The top and bottom panels also appear in Wilson (2000).

as the number of species lost from each plot in each year. Species turnover in each plot in each year was determined by adding colonization and extirpation. We did not address the proportions of species lost or gained because variation in richness among treatments is determined by changes in absolute numbers, not proportions. We examined whether colonization, extirpation, and turnover averaged across all years varied quadratically with disturbance at each level of nitrogen. These three response variables were also examined for variation with nitrogen addition at each level of disturbance.

In order to examine whether richness, colonization, and extirpation varied with time, we used repeated-measures analysis of variance (ANOVA) to examine each variable with respect to disturbance, nitrogen supply, and time (year sampled). We present data from all treatments but only the four extreme treatments (N1D1, N1D4, N4D1, N4D4) were analyzed because there were 14 replicates of these and only 4 replicates of the other treatments. 1993 data were excluded from the analysis because 10 replicates of the extreme treatments may have been disturbed by harvesting a competition experiment in 1992 (Wilson and Tilman 1995). Proportional variables were arcsine-square root transformed, and other variables were log transformed in order to improve normality and reduce heteroscedasticity.

RESULTS

Species richness and disturbance

In plots receiving no nitrogen or the lowest level of added nitrogen, richness in 1995 varied quadratically and significantly with disturbance (Fig. 1). Richness did not vary significantly with disturbance at the two highest levels of nitrogen addition.

Richness in 1995 was highest at intermediate disturbance at the two lowest level of N addition because the number of growth forms varied quadratically and significantly with disturbance (Table 1). As in the case of richness, the number of growth forms did not vary

cryptogamic soil], and woody plants) in each plot in each year. The number of species belonging to each growth form was also noted.

Species richness was determined for each plot in each year as the total richness in the two quadrats. We examined whether richness varied quadratically with disturbance at each level of nitrogen in each year by testing whether a second-order polynomial regression equation accounted for a significant proportion of variation in richness. We examined the number of growth forms and the number of species in each growth from in the same way. We also examined whether species richness, the number of growth forms, and the number of species in each growth form varied with nitrogen addition at each level of disturbance.

We calculated colonization as the total number of species gained in each plot in each year, and extirpation

TABLE 1. Summary of variation in species richness (R), the richness of growth forms (R_{GF}), and the number of species in each growth form (R/R_{GF}) across four levels of disturbance for four levels of nitrogen addition, at the end of the experiment.

N added (g·m⁻²·yr⁻¹)	R	R_{GF}	R/R_{GF}
0	0.44***†	0.32**†	0.24**‡
2	0.49*†	0.66***†	...
9.5	...	...	...
17	...	...	...

Notes: Values are regression coefficients (r^2). Ellipses denote no significant variation in richness.

† Richness varied quadratically and significantly with disturbance.

‡ Richness decreased significantly with disturbance.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 2. Summary of variation in colonization, extirpation, and turnover (colonization plus extirpation) across four levels of disturbance for four levels of nitrogen addition (averaged across all years).

N added ($g \cdot m^{-2} \cdot yr^{-1}$)	Colonization (species/yr)	Extirpation (species/yr)	Turnover (species/yr)
0	0.35***‡	0.25**§	0.33***‡
2	0.61**†	...	0.52**†
9.5	0.41**†	...	0.42**†
17	...	...	...

Notes: Values are regression coefficients (r^2). Ellipses denote no significant variation.
† Varied quadratically and significantly with disturbance.
‡ Decreased significantly with disturbance.
§ Increased significantly with disturbance.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

significantly with disturbance at the two highest levels of nitrogen addition.

The number of species belonging to each growth form did not vary quadratically with disturbance at any level of N (Table 1), suggesting that this variable did not contribute to quadratic variation in species richness with disturbance.

Peak richness at intermediate disturbance at low rates of N addition was associated with high numbers of species colonizing these plots: colonization (averaged across all years) varied quadratically and significantly with disturbance in N2 and N3 plots (Table 2). Species turnover also varied quadratically and significantly with disturbance in N2 and N3 plots (Table 2), suggesting that plots with intermediate disturbance were diverse through time, as well as in space. In contrast, extirpation did not vary with disturbance in a manner consistent with high richness at intermediate disturbance (Table 2).

Species richness and nitrogen

Richness in 1995 decreased significantly with increasing nitrogen availability at every level of disturbance (Fig. 1; $r^2 = 0.42$–0.76, $P < 0.001$). This was associated with significant decreases in the number of species belonging to each growth form at all levels of disturbance (*data not shown*; $r^2 = 0.29$–0.69, $P < 0.001$), as well as decreases in the numbers of growth forms ($r^2 = 0.08$–0.69, $P < 0.05$ at D2, D3, and D4).

Decreasing richness with increasing N was associated with significant decreases in colonization, increases in extirpation, and decreases in turnover (all averaged over all years) with increasing N at every level of disturbance (*data not shown*; $r^2 = 0.24$–0.81, $P < 0.05$).

Temporal dynamics

On a year by year basis, richness varied quadratically ($P < 0.05$) with disturbance at low N only after several years: quadratic variation occurred in both 1994 and 1995 in N1 plots, and in 1993–1995 in N2 plots (*data not shown*). Richness decreased montonically with disturbance in N1 plots for the first 5 yr of the experiment. Richness generally did not vary with disturbance in N3 or N4 plots in any year.

Repeated-measures ANOVA confirmed regression analyses (Tables 1 and 2) by showing that richness, colonization, extirpation, and turnover all varied significantly with both disturbance and nitrogen, but in this section we focus on interannual variation in these variables.

Repeated-measures ANOVA showed that richness varied significantly with time (Fig. 2, $F_{7, 354} = 4.0$, $P < 0.05$) and the interaction between time and nitrogen ($F_{7, 354} = 6.5$), because richness decreased among years in plots with added nitrogen (N4D1 and N4D4) but was constant in plots without (N1D1 and N1D4). Richness increased over time at intermediate levels of disturbance and low levels of nitrogen addition (N1D2, N1D3, N2D2, N2D3).

Colonization (Fig. 3) varied significantly with time ($F_{4, 252} = 4.8$) and with the three-way interaction involving time, nitrogen, and disturbance ($F_{4, 252} = 4.3$). Colonization was constant with time in undisturbed plots (D1), higher in undisturbed and unfertilized plots (N1D1) than in undisturbed and fertilized plots (N4D1), and decreased with time in disturbed plots (N1D4 and N4D4).

Extirpation decreased significantly over time (Fig. 3, $F_{4, 252} = 6.6$), and was greatest at the start of the experiment, especially in the extreme treatments N1D4, N4D1, and N4D4. As a result, there were significant interactions between both time and nitrogen ($F_{4, 252} = 5.9$), and time and disturbance ($F_{4, 252} = 4.5$). Extirpation in disturbed or nitrogen-enriched plots (e.g., N4D4) was almost 0 after three years and for most of the experiment, whereas extirpation in control plots (N1D1) was variable throughout the experiment. The low extirpation in older nitrogen-enriched and disturbed plots occurred after high initial loss rates, and reflects the fact that all the species that were going to be lost from these treatments were lost early in the experiment.

Species turnover (colonization plus extirpation, Fig. 4) varied significantly with time ($F_{4, 252} = 4.4$), as well as with the interactions between time and nitrogen ($F_{4, 252} = 3.4$), and time and disturbance ($F_{4, 252} = 4.0$). Turnover was consistently high in control plots (N1D1) but decreased over time in both fertilized and disturbed plots (N4D1, N1D4, N4D3).

Species composition

Control plots (Fig. 5, N1D1) were dominated by the C_4 perennial grass *Schizachyrium scoparium. Poa pratensis,* a C_3 perennial grass, was the second most common taxon in control plots at the end of the experiment. Cryptogams had 15–30% cover in the first four years but declined after that.

Intermediate levels of disturbance in unfertilized plots allowed most common perennials to persist, but
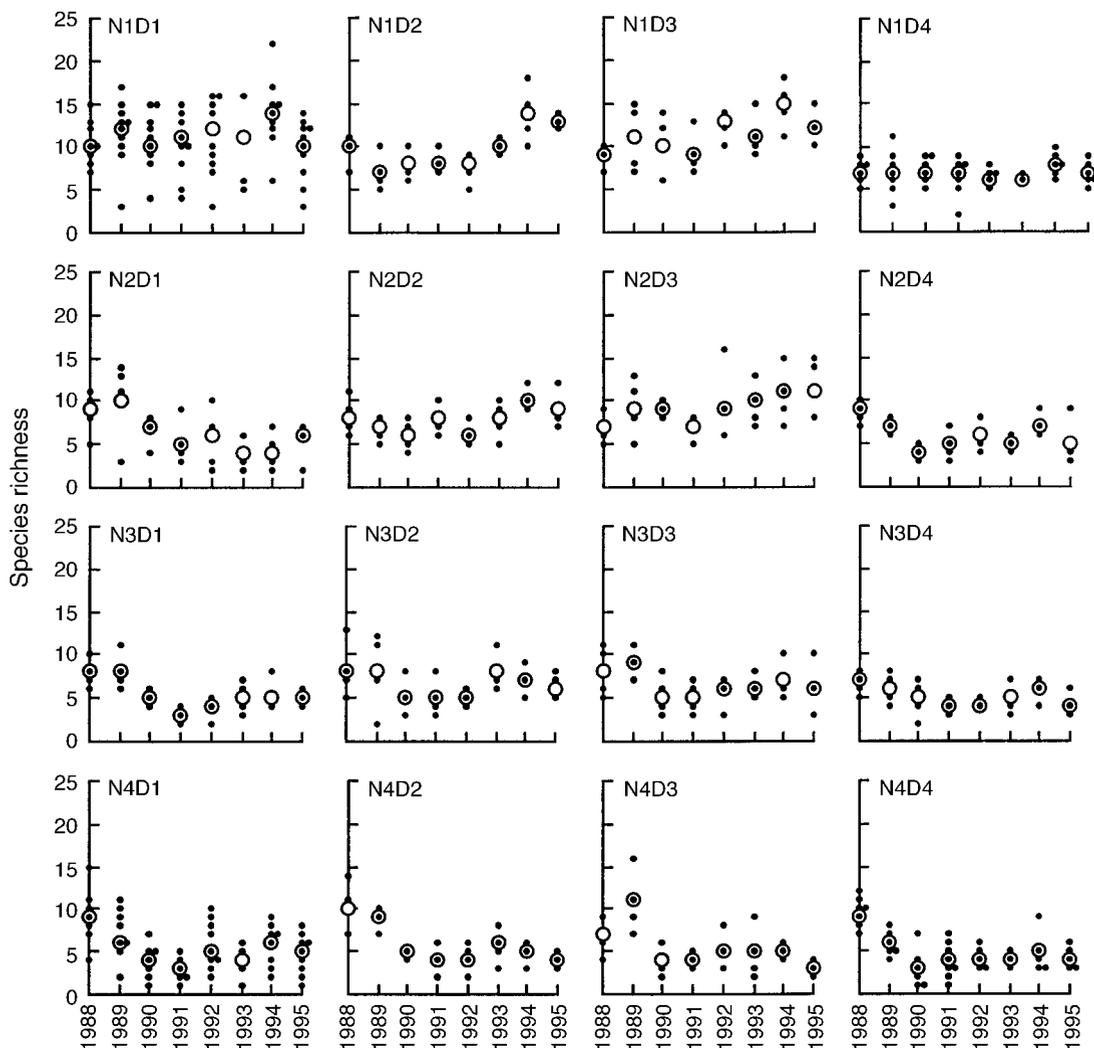
FIG. 2.   Species richness over time in 16 combinations of nitrogen addition and disturbance in an old field. Dots are values from replicate plots. Open circles are annual means.

also introduced annuals such as *Panicum capillare* and *Setaria viridis* (Fig. 5, N1D2, N1D3). Highly disturbed plots were dominated by *Setaria viridis* and the annual forbs *Polygonum convolvulus* and *Chenopodium album* (Fig. 5, N1D4). Thus, maximum richness at intermediate disturbance in unfertilized plots (Fig. 1) reflected the coexistence of annuals and perennials.

In plots receiving high rates of nitrogen, perennials were replaced by annuals as disturbance increased (Fig. 5, N4D1. . . N4D4), but without the coexistence of contrasting growth forms that occurred in unfertilized plots (Table 1).

Adding nitrogen to undisturbed plots led to progressively greater dominance by *Poa* (Fig. 5, N2D1 and N3D1). At the highest rate of nitrogen, however, plots were dominated the perennial C_3 grass *Agropyron repens*. Two annuals, the vine *Polygonum convolvulus*

and the forb *Chenopodium album,* appeared in high-nitrogen, undisturbed plots (Fig. 5, N4D1).

Adding nitrogen to plots with intermediate levels of disturbance (D2 and D3) accelerated the replacement of *Schizachyrium* by *Agropyron*: *Schizachyrium* persisted in plots with little added nitrogen (N1–N3) but disappeared from heavily fertilized plots (Fig. 5, N4D2, N4D3). Adding nitrogen to the most disturbed plots (D4) resulted in dominance by *Chenopodium* by the end of the experiment.

DISCUSSION

Disturbance and its interaction with nitrogen

Our experiment produced quadratic variation in richness with disturbance in infertile plots due to the persistence of perennials and colonization by annuals. This was reflected by significant quadratic variation in both
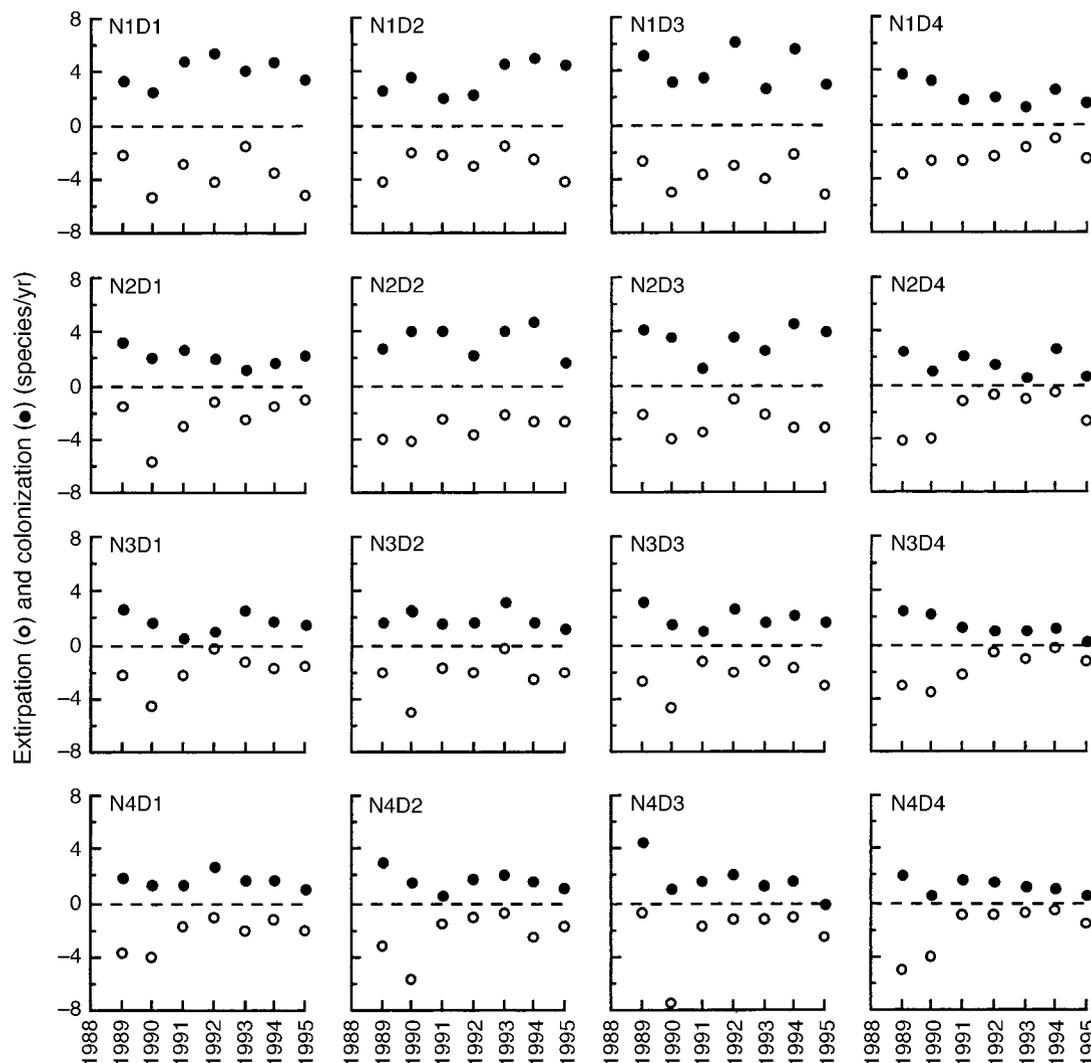
FIG. 3. Colonization (closed circles) and extirpation (open circles) over time in 16 combinations of nitrogen addition and disturbance in an old field. Note the direction of the axis for extirpation. Means for each treatment combination are shown.

colonization and in the number of growth forms along the disturbance gradient at low nitrogen (Tables 1, 2). High richness has also been linked to the coexistence of different life forms along successional (Denslow 1980), wetland (Shipley et al. 1991), and mountainside gradients (Wilson 1994b).

Our manipulations support observations from natural vegetation that attribute peaks in richness to intermediate levels of disturbance (Connell 1978, Coppock et al. 1983, Wilson and Keddy 1988, Pollock et al. 1998). The intermediate disturbance hypothesis predicts that richness is enhanced by reduced competition (Grime 1973, Connell 1978, Huston 1979), and competition intensity was indeed reduced by disturbance in our experiment (Wilson and Tilman 1993, 1995). Our intermediate disturbance treatments also increased soil resource heterogeneity by creating patches of bare soil within a matrix of perennial species (Paine and Levin

1981). Increased heterogeneity may increase diversity by creating establishment sites (Grime 1979), variation in resource ratios (Tilman 1988), or variation in the relative importance of root and shoot competition (Wilson 2000): different experiments are required to determine the relative contributions of these mechanisms.

The emergence of quadratic variation in richness with disturbance after 5–6 yr emphasizes the need for long-term studies for understanding controls of diversity (Likens 1989), and suggests that the relationship between diversity and disturbance may continue to vary through time.

Disturbance of plots without added nitrogen (N1D4) reduced biomass, increased soil available nitrogen (Wilson and Tilman 1991), and reduced root competition (Wilson and Tilman 1993). Competition still caused a considerable (30%: Wilson and Tilman 1993) reduction in transplant growth in these plots, however,
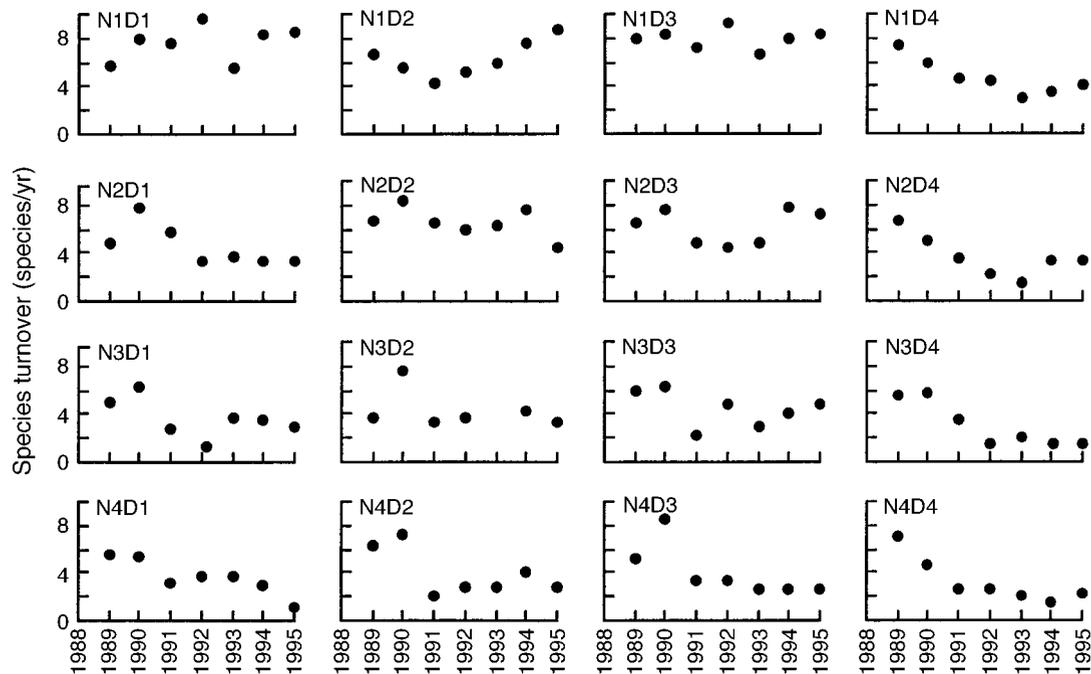
FIG. 4.   Species turnover (colonization plus extirpation) over time in 16 combinations of nitrogen addition and disturbance in an old field. Means for each treatment combination are shown.

and a combination of low nutrient availability and constant disturbance may allow certain grasses to outcompete others (e.g., Berendse et al. 1992).

In contrast to the constant dominance of undisturbed and unfertilized plots by *Schizachyrium* (Fig. 5, N1D1), the dominant annuals of disturbed plots changed nearly every year (N1D4). Annuals also showed great interannual variation in dominance in a 13-yr experiment in a wheat field (Firbank 1993), and annually burned Kansas prairie was more variable than infrequently burned prairie (Collins 2000). Competition may continue to influence the structure and diversity of disturbed communities (Wilson 1999), but the factors determining the identity of dominant species are clearly more variable in disturbed vegetation.

Applying the most intense level of disturbance to unfertilized plots caused both colonization and extirpation to decrease steadily with time (Fig. 3: N1D4). This contrasts with undisturbed plots (N1D1), where colonization and extirpation remained at high levels throughout the experiment. Thus, by the end of the experiment, disturbed plots had low rates of turnover (Fig. 4) in spite of nearly annual changes in the identity of the dominant species (Fig. 5). Because the balance between colonization and extirpation was near 0 (Fig. 3, N1D4), species richness in highly disturbed plots was fairly constant over the course of the experiment (Fig. 2), and low relative to undisturbed plots. Grassland species richness is also reduced by plowing (Montalvo et al. 1993), frequent burning (Collins et al.

1995), and intense grazing (Coppock et al. 1983, Huntly 1991).

In contrast to our finding of quadratic variation of richness with disturbance at low nitrogen, richness was unaffected by disturbance if nitrogen availability was high (Fig. 1). Differences between nutrient levels in the response of richness to disturbance may be related to differences between nutrient levels in the intensity of root competition, the dominant form of competition in grasslands (Wilson 1998). Removal experiments showed that disturbance decreased root competition in unfertilized plots but not in fertilized plots (Wilson and Tilman 1993). Root competition in unfertilized plots was reduced because tilling killed roots and decreased nutrient demand. Root competition was unaffected by disturbance in fertilized plots because nutrients were highly available regardless of disturbance regime. Thus, quadratic variation in richness with disturbance in unfertilized vegetation was consistent with a significant decrease in the intensity of root competition, and the lack of variation in richness with disturbance in fertilized vegetation was consistent with the absence of a decrease in root competition.

Nitrogen and its interaction with disturbance

Richness decreased with nitrogen addition regardless of disturbance regime (Fig. 1), as typically occurs in fertilization experiments (Gough et al. 2000). Simultaneous competition measurements within our experimental gradient showed that light competition in-

creased with increasing nitrogen, regardless of disturbance (Wilson and Tilman 1993). Intense light competition with increasing nitrogen would also account for significant decreases in the numbers of growth forms and the number of species in each growth form. Significant decreases in richness with increasing fertility in Michigan old fields were also attributed to aboveground effects, specifically litter (Foster and Gross 1998).

Nitrogen addition caused the native grass *Schizachyrium* to be replaced by the aliens *Poa* and *Agropyron* (Fig. 5), as occurred in earlier experiments at Cedar Creek (Wilson and Tilman 1991). The replacement of native species by aliens is typical of fertilized herbaceous vegetation (Lauenroth et al. 1978, Hobbs and Atkins 1988, Huenneke et al. 1990, Burke and Grime 1996). Native grasses, including *Schizachyrium,* are relatively effective competitors at low levels of nitrogen, but may not be as effective in high-nitrogen, low-light environments (Wedin and Tilman 1993).

Nitrogen addition significantly decreased colonization (Fig. 3), as occurred in other undisturbed nitrogen gradients nearby (Tilman 1993). Colonization was consistently low throughout the experiment (Fig. 3, N4D1), resulting in a net loss of species in the first few years. Fertilization of Colorado shortgrass prairie, in contrast, resulted in the addition of annuals without a loss of perennials (Milchunas et al. 1990). The few species that did colonize our nitrogen-enriched but undisturbed plots included the annuals *Polygonum convolvulus* and *Chenopodium album* (Fig. 5: N4D1). These annuals may appear in nitrogen-enriched plots because early successional species use increased nitrogen supply rates as germination cues (Bazzaz 1979). *Polygonum* may have persisted because it was able to forage for light due to its climbing ability. *Chenopodium* first colonized disturbed plots but, by the end of experiment, had become common in all fertilized plots regardless of disturbance regime (Fig. 5). *Chenopodium* is noteworthy for being facilitated by neighbors in fertilized plots (Wilson and Tilman 1995), and this may contribute to its success. It is possible that *Chenopodium* in undisturbed, fertilized plots simply represented a sink population established from seeds from disturbed plots, but colonization of undisturbed but fertilized soils by annuals has also been found in Ohio (Carson and Barrett 1988), Colorado (Lauenroth et al. 1978), and western Australia (Hobbs and Atkins 1988), suggesting that this is a common result and is not restricted to our experiment.

Nitrogen-enriched plots lost about four species in each of the first two years (Fig. 3, N4D1). Species lost from our fertilized plots included short perennial forbs such as *Solidago nemoralis* and *Hieracium* spp. (S. Wilson, *unpublished data*) which were presumably unable to compete for light against taller species such as the grass *Agropyron repens* (Fig. 5). Forbs were also displaced by grasses in a fertilized annual grassland in California (Hobbs et al. 1988, Huenneke et al. 1990). Cryptogams on and in the soil also disappeared from our fertilized plots, as occurred in a fertilized arctic shrub community (Press et al. 1998), presumably due to a lack of light.

The dominant perennial grass *Schizachyrium,* like most perennials, disappeared from high-nitrogen, disturbed plots after one year (Fig. 5, N4D4), but persisted in low-nitrogen, disturbed plots for four years (N1D4). *Schizachyrium* may have disappeared quickly from high-nitrogen disturbed plots because, like high-nitrogen undisturbed plots, they were characterized by intense light competition (Wilson and Tilman 1993). Our results for *Schizachyrium* complement those obtained from a factorial fertility and disturbance gradient in a limestone grassland, where the highest rate of invasion by aliens occurred in plots that were both disturbed and fertilized (Burke and Grime 1996): indigenous species are replaced by invading species most rapidly in plots that are both fertilized and disturbed (Hobbs and Atkins 1988).

In spite of the fact that high-nitrogen undisturbed plots were dominated by perennials and high-nitrogen disturbed plots were dominated by a completely different set of annual species, there were very strong similarities between these treatments in terms of patterns of biomass, litter, resources (Wilson and Tilman 1991), competition (Wilson and Tilman 1993), species replacements, extirpation, colonization, and turnover, suggesting that perennial and annual communities have similar responses to nitrogen addition. The behavior of high-nitrogen disturbed plots (N4D4) was also similar to that of high-nitrogen undisturbed plots (N4D1) in that a clear dominant species emerged by the fifth year (1992), *Chenopodium* in disturbed plots and *Agropyron* in undisturbed plots (Fig. 5). This contrasted with the constant shift in dominants in disturbed plots without added N (N1D4). Taken together, the results suggest that the winner in competition for light in nitrogen-enriched plots is more predictable than the winners in competition for soil resources in nitrogen-poor plots, probably due to the directional nature of light (Givnish 1986).

Dynamics in control plots

Changes in species composition were not restricted to plots receiving experimental manipulation: control plots (N1D1) varied considerably through time in the absence of fertilization or tilling, as reflected by changes in species composition (Fig. 5) and relatively high rates of turnover (Fig. 4). Long-term fluctuations in grassland species composition are common (Tomanek and Hulett 1970, Tilman 1993, Dodd et al. 1995) and the most common species in our control plots, *Schizachyrium,* varied in cover from 30% to 50%, but without any trend. *Schizachyrium* has been described as a fairly constant "core" species in Kansas and Oklahoma, where it varies less among years than do
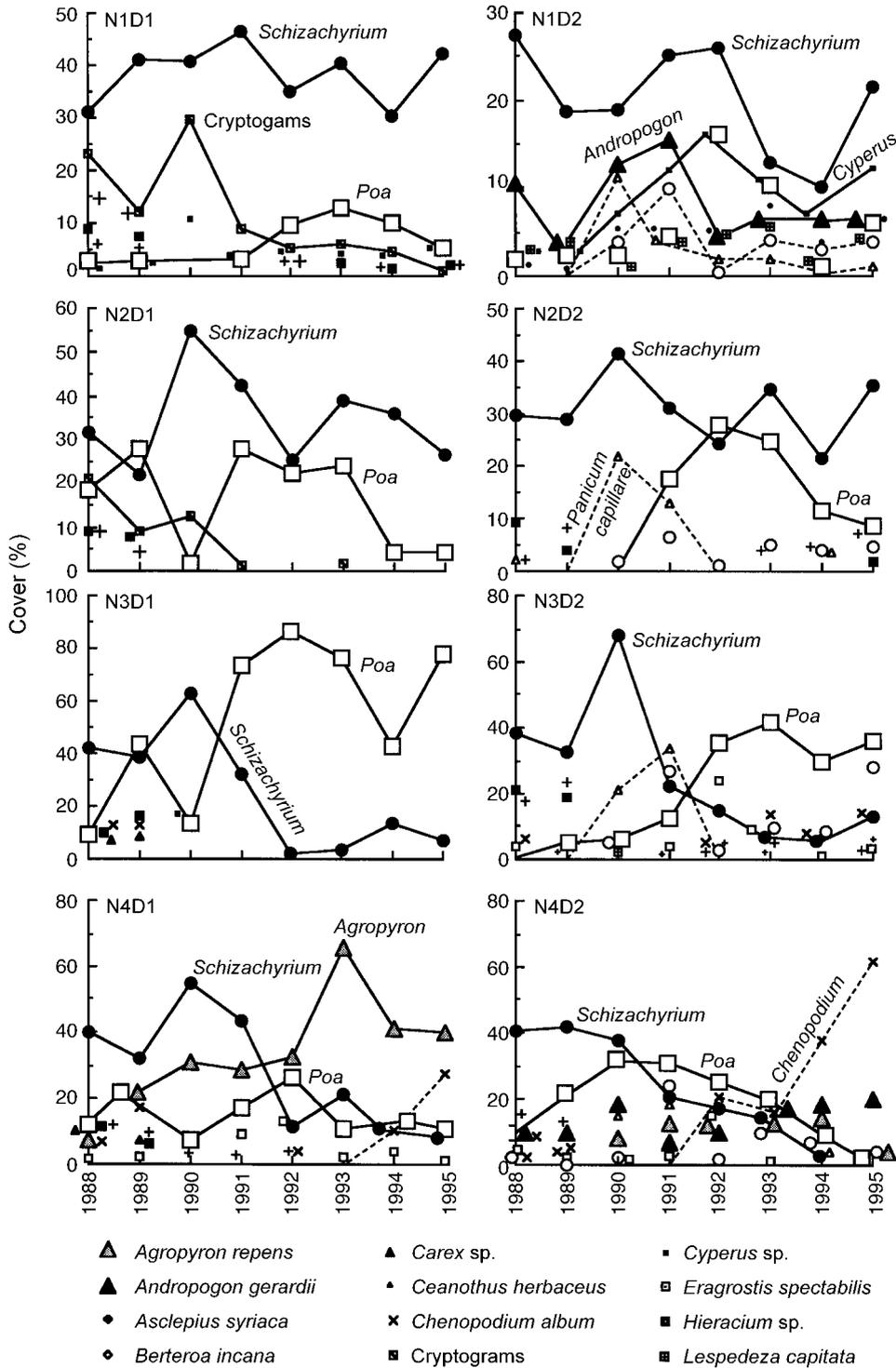
FIG. 5. Covers of common species (>5% cover in at least one treatment in at least one year) over time in 16 combinations of nitrogen addition and disturbance in an old field (solid lines, perennials; dashed lines, annuals). Some lines have been omitted for clarity.
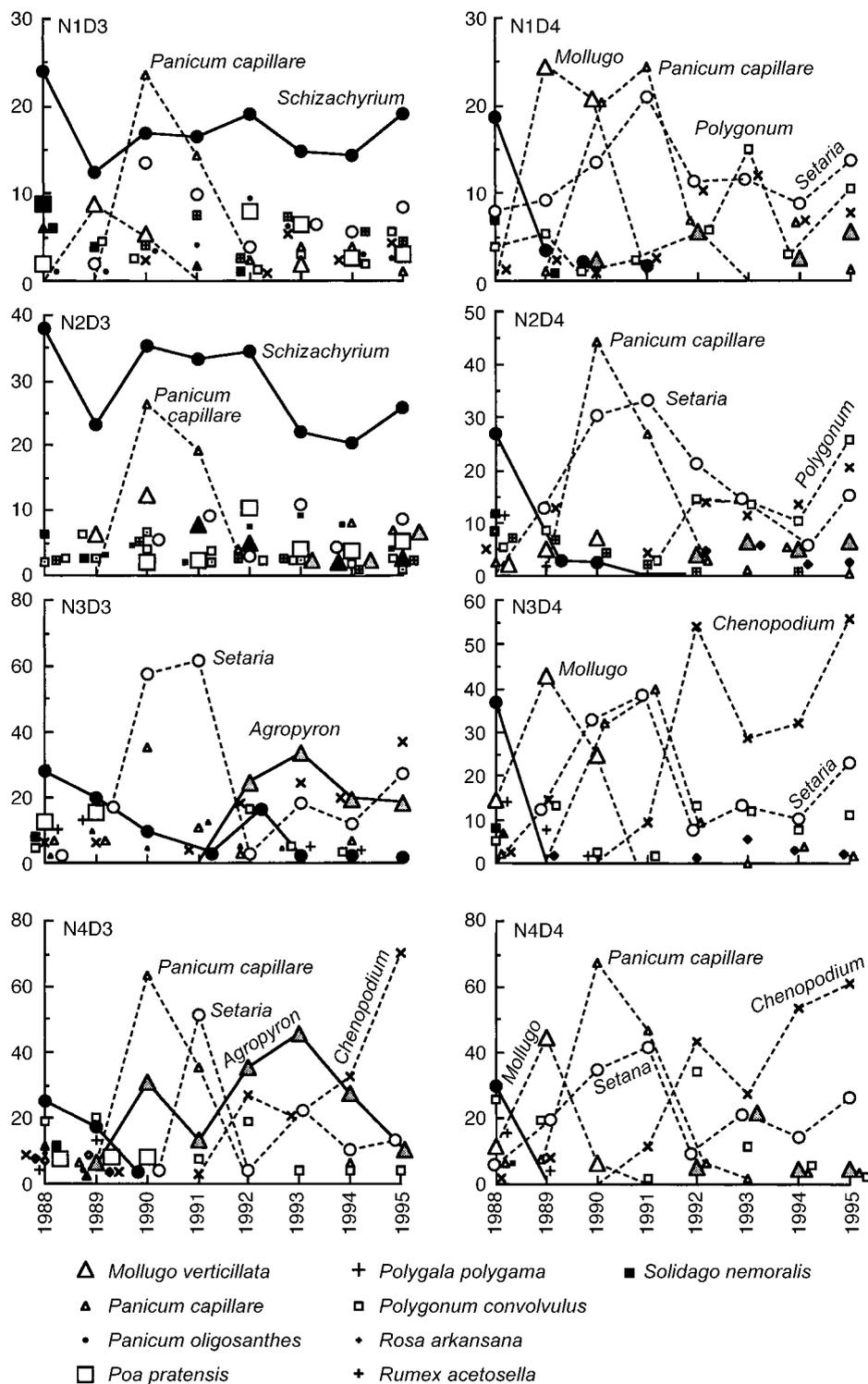
FIG. 5. Extended.

uncommon "satellite" species (Glenn and Collins 1993). *Schizachyrium* also varies less through time than do uncommon species in fertilization experiments at Cedar Creek (Tilman and El Haddi 1992, Tilman 1993). *Poa pratensis* increased during the experiment (Fig. 5), possibly because of drought recovery (Tilman and El Haddi 1992). Interestingly, the decline of N-fixing cryptogams in our control plots corresponded to the loss of N-fixing legumes from undisturbed prairie fragments (Leach and Givnish 1999): the accumulation of litter over time probably deprives these species of light needed for N fixation.

Relative to other treatments, control plots had consistently high rates of colonization and extirpation (Fig. 3), and the highest rates of turnover (Fig. 4). Because control plots were dominated by perennials (Fig. 5), this turnover probably resulted from perennials producing shoots in some years and remaining dormant in others. Many examples of local extirpation have been reported (e.g., Crawley 1990, Tilman and El Haddi 1992). In some cases, lost species are replaced by different species (McIntyre and Lavorel 1994, Tilman 1996), but in our control plots, lost species tended to reappear later (Fig. 5). High rates of turnover in natural diverse vegetation are common (Rydin and Borgegård 1988, O'Connor 1991, van der Maarel and Sykes 1993, Robinson et al. 1995, Collins 2000). In summary, richness was high in control plots, but this was associated with much extirpation, colonization, and turnover, so that control plots were relatively dynamic. The results support the suggestion that diverse vegetation is characterized by relatively variable population-level attributes, such as colonization and extirpation (Fig. 3), but less variable community-level attributes such as richness (Fig. 2; Chapin and Shaver 1985, Collins et al. 1987, Tilman 1996).

The accidental burning of the experiment in early spring in 1994 had little or no effect on species richness (Fig. 2), species composition (Fig. 5), or standing crop (S. D. Wilson and D. Tilman, *unpublished data*), probably because the perennials were dormant meristems and the annuals were ungerminated seeds, and most grassland biomass is belowground (Wilson 1993). *Chenopodium* appeared to increase following the fire (Fig. 5), but this increase was merely following the trend set in years before the fire.

The array of responses generated by our factorial gradient helps explain why richness varies with fertility and disturbance in different ways along different natural gradients (Waide et al. 1999): the pattern and dynamics of variation clearly depends on location within the fertility-disturbance matrix.

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