

# Spatial relationships between plant litter, gopher disturbance and vegetation at different stages of old-field succession

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**Abstract.** Fine-scale spatial patterns of small mammal disturbances and local accumulation of plant litter were studied together with the spatial pattern of vegetation in different stages of old-field succession at Cedar Creek Natural History Area, Minnesota, USA. Seven stands from one to 66 years old were sampled. Presence of living plant species, local soil disturbances by pocket gophers (*Geomys bursarius*) and plant litter accumulation were recorded in 10 cm × 10 cm contiguous microquadrats along elliptical transects. Spatial patterns and associations were analyzed using information theory models. Dominant grasses were spatially independent, while subordinate functional groups were strongly dependent on the existing patchwork of dominant species, plant litter and gopher disturbances. Litter had consistent negative associations with subordinate functional groups in all but the initial years. Gopher disturbances were abundant but had weak and variable associations with vegetation. These results suggest that gopher disturbance does not facilitate the colonization of native prairie species and that diversity can be improved by controlling litter accumulation in Minnesota old-fields.

**Keywords:** Functional group; Information theory; Minnesota old-field; Pairwise association; Patch dynamics; Randomization test; Spatial scaling.

**Nomenclature:** Anon. (1999).

## Introduction

Plant litter and small mammal disturbances are among the most important factors influencing organization and dynamics in plant communities. By altering the physical and chemical environments dead plant material affects the probability of germination and establishment as well as other demographic and community processes (Grime 1979; Facelli & Pickett 1991). The observed effects vary considerably among studies depending on latitude, community type, quality and quantity of litter (Xiong & Nilsson 1999). Disturbance affects community structure by removing dominant competitors and opening space for subordinate species. Soil disturbance also changes soil properties and biogeochemical processes

(Whitford & Kay 1999). Disturbances caused by different animals differ in size, frequency and turnover (Coffin & Lauenroth 1988). Detailed surveys of temporal and spatial patterns of disturbance are relatively rare (Goldberg & Gross 1988; Coffin & Lauenroth 1988; Milton et al. 1997). Field experiments with artificial designs (e.g. Armesto & Pickett 1985; Virágh 1987; Carson & Peterson 1990; Lavorel et al. 1994; Virágh & Bartha 1996; Foster & Gross 1997, 1998; Suding & Goldberg 1999) reveal potential effects but do not report on the contributions of these mechanisms under natural conditions. Despite the numerous (facilitative and inhibitory) effects and complex interactions of these variables, the net expression of the effects can be simple. Information about 'in situ' magnitude and relative contribution to community structure and dynamics at different stages of vegetation development is essential for the management of natural systems (Xiong & Nilsson 1999).

Old-field succession provides excellent opportunities for studying the relative roles and interactions of litter and disturbance in vegetation dynamics. The changing vegetation cover, composition and structure during succession (Pickett 1982; Osbornová et al. 1990; Tilman 1988) provide contrasting, but comparable, conditions for studying these mechanisms. Vegetation dynamics at Cedar Creek Natural History Area in Minnesota is one of the most closely studied cases of old-field succession (Inouye et al. 1987a; Tilman 1988, 1990). At Cedar Creek, previous field experiments have already documented the potential importance of certain mechanisms (colonization limitation, nitrogen competition, gopher disturbance and litter effect) in controlling diversity (Tilman 1983; Inouye et al. 1987a; Tilman 1988, 1990, 1993, 1997). My aim is not to provide additional evidence about the existence of these mechanisms but to describe the spatial organization of dominant and subordinate species, as well as the functional groups, together with the spatial patterns of gopher disturbance and litter accumulation. My intent is to explore the net effect and relative contribution of disturbance and litter on vegetation structure in various stages of succession. I examine the following questions: 1. How do the abundance and

spatial patterns of plant litter, gopher disturbance and the dominant and subordinate components of vegetation change with successional age? 2. Is there evidence of developing spatial associations between these characteristics? 3. Do these spatial associations reflect the same relationships that were detected in experimental studies? 4. Does the relative importance of litter and gopher disturbance change during succession?

## Methods

### Study sites

Seven old-fields of different ages were sampled at Cedar Creek Natural History Area (CCNHA) in east-central Minnesota, USA. The study site is located on a well-drained, sandy, glacial outwash plain in Anoka and Isanti counties. Mean July temperature is 22 °C, mean January temperature is -10 °C and mean annual precipitation is 660 mm. Plant growth is limited mainly by the shortage of nitrogen (Tilman 1988). Six old-fields were selected among the Lawrence Successional Strips (Inouye et al. 1994). This field is ca. 120 m × 650 m and cultivated with rye. Each year since 1974, a 120 m × 20 m strip has been left undisturbed following two years of repeated preparation disking. The strips were aban-

doned sequentially.

Six strips (1, 4, 6, 10, 14 and 18 yr old) were sampled by recording the presence of living plant species, local soil disturbance by pocket gophers (*Geomys bursarius*, *Rodentia*, gophers hereafter) and plant litter accumulation in 10 cm × 10 cm contiguous microquadrats along elliptical transects of 1200 units. The long axes of the ellipsoids was ca. 50 m and they were located in the centre of the strips with their long axes parallel to the longer sides of the strips. To avoid artefacts due to the potential spatial autocorrelations between strips, neighbouring strips were not chosen for sampling and analyses. Vascular plants (except sedges) were identified to species. Sedges, mosses and lichens were recorded by group. Litter accumulation was recorded if estimated cover exceeded 25% in a particular microquadrat. An additional 66-yr old-field (Field #72, abandoned since 1927, 3 ha in size, with potato as last crop) was also sampled to represent the late stage of succession which was dominated by native tall-grass species. In old-fields aged 18 and 66, which had closed vegetation, the presence of bare soil was also detected. In younger fields with low vegetation cover bare soil was present in almost all microquadrats and its spatial pattern was not detectable. *Conyza canadensis* and *Crepis tectorum* are the most abundant species in the first year of succession. Year 4 is dominated by *Agrostis scabra* and the next 10 years

**Table 1.** Some vegetation characteristics along the Minnesota old-field chronosequence.

Years since abandonment	1	4	6	10	14	18	66
Frequency%							
<i>Agrostis scabra</i>	0.25	50.17	41.33	12.74	16.08	2.08	0.00
<i>Elymus repens</i>	15.33	20.25	49.58	76.45	45.00	4.90	0.00
<i>Poa pratensis</i>	0.00	0.00	0.00	12.60	23.42	92.08	71.50
<i>Andropogon gerardii</i>	0.00	0.00	0.00	0.00	0.00	0.67	35.00
Cover							
<i>Agrostis scabra</i>	0.33	18.83	25.17	4.83	0.67	3.33	0.00
<i>Elymus repens</i>	4.25	13.08	25.83	31.67	23.33	0.50	0.00
<i>Poa pratensis</i>	0.00	0.00	0.00	4.17	26.67	45.83	11.33
<i>Andropogon gerardii</i>	0.00	0.00	0.00	0.00	0.00	0.00	40.00
Total cover	54.45	59.02	61.58	86.75	104.53	99.37	83.43
Cover of litter	0.00	0.00	15.83	8.33	9.17	17.50	20.50
Frequency%							
Annuals	96.33	88.70	77.42	85.24	78.00	25.67	21.00
Short-lived perennial forbs	2.00	0.00	1.75	9.19	56.42	10.67	0.33
Perennial forbs	0.83	0.25	2.00	4.92	20.25	10.42	31.75
Perennial grasses	0.00	0.17	0.50	1.21	20.42	28.83	22.67
Sedges	2.33	0.50	4.00	4.84	5.25	3.08	46.50
Mosses	0.00	0.00	3.17	9.52	27.67	1.67	0.83
Lichens	0.92	9.08	1.17	18.44	16.92	18.92	37.67
Woody perennials	0.00	0.00	0.00	0.00	0.00	0.00	5.58
Species richness	19.00	15.00	26.00	31.00	42.00	35.00	38.00
Species density	2.05	1.37	1.77	1.98	2.42	0.86	1.34
True prairie spp.%	15.79	20.00	19.23	16.13	21.43	40.00	68.42

by *Elymus repens*. *Poa pratensis* becomes dominant by year 18 and is still frequent in the late successional stage (year 66) dominated by *Andropogon gerardii*. Tables 1 and 3 present the changes of some vegetation characteristics and the abundance of litter and gopher disturbance along the studied chronosequence. Percentage cover of dominant species was estimated in six 2 m × 2 m sampling units in each site. The natural vegetation of the area is a mosaic of open oak woods and wetlands. Table 1 shows that the colonization rates of native species are relatively fast. On the basis of the transect samples of this study, 20% of the species are native prairie species in the 4th year of succession. This number increases to 40% in year 18 and to 68% in the late successional site. The space for time substitution (Pickett 1989) is reasonable here because the first six successional old-fields are close to each other (parts of the same Lawrence Successional Strips). Previous studies showed that these fields (Lawrence Strips and Field #72) have similar landscape context, history, and soil, and that they belong to the same successional pathway (Inouye et al. 1987b).

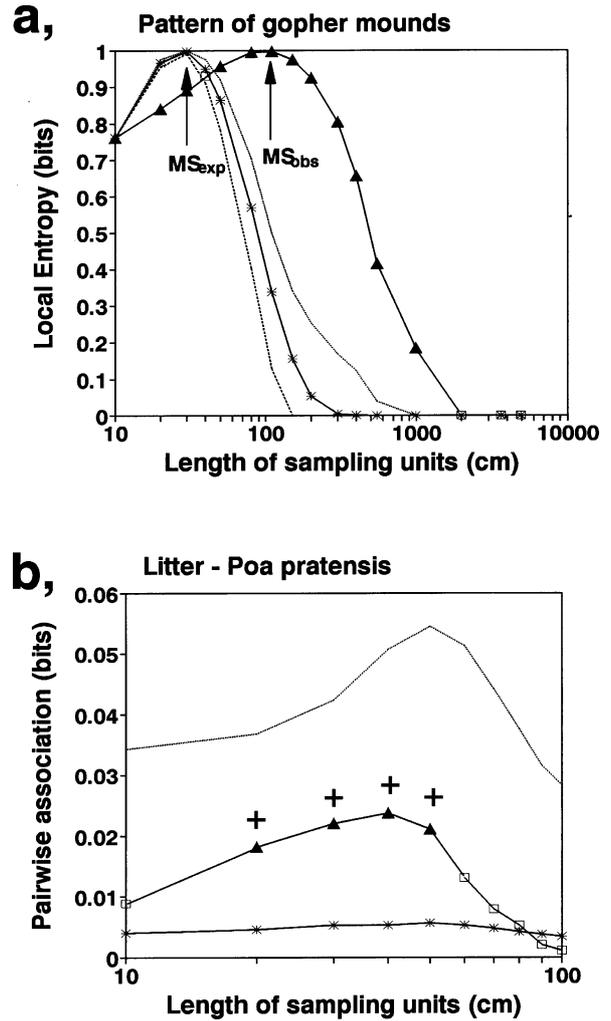
### Analyses

#### Characterizing univariate patterns by local entropy

Univariate spatial dependence was expressed by the local entropy, an information theory model of Juhász-Nagy (1984). Contrary to the traditional methods of spatial pattern analyses (Dale 1999), this model is particularly robust to departures from spatial stationarity of vegetation characteristics in the early stages of succession (Bartha 1993). Local entropy of a spatial variable  $i$  is defined by:

$$H_j(i) = -p_j(i) \cdot \log_2 p_j(i) - (1-p_j(i)) \cdot \log_2(1-p_j(i)) \quad (1)$$

where  $p_j(i)$  is the expected probability of presence,  $p_j(i) = e_j(i)/n_j$ ,  $e_j(i)$  the number of presence of the variable  $i$  in  $n$  sampling units and the term  $(1-p_j(i))$  refers to the expected probability of absence at sampling units of size  $j$ .  $H_j(i)$  changes with scale and follows a unimodal curve (Fig. 1a). It ranges between  $0 \leq H_j(i) \leq 1$ .  $H_j(i) = 1$  at  $p_j(i) = 0.5$ , i.e. at the scale where the variable is present in the half of the sampling units. The scale, where local entropy reaches its maximum, is characteristic to the pattern and is called maximum scale (MS). The maximum scale depends on the abundance and spatial distribution of a variable. In order to separate these effects a null model where the presences of a variable were randomly redistributed among the microquadrats by using Monte-Carlo simulation was used (Site model, Watkins & Wilson 1992), 2500 randomizations were applied in this



**Fig. 1. a.** Local entropy as a function of scale characterizing the spatial pattern of gopher mounds in the 14th year of old-field succession.  $MS_{obs}$  is the scale of maximum value for field data,  $MS_{exp}$  is the scale of the expected maximum value in case of random reference data.

**b.** Pairwise association as a function of scale. Association between plant litter and *Poa pratensis* in the 66th year of old-field succession.

(+) marks significant associations (filled triangle): field data different from random ( $p < 0.05$ ) (empty square): field data not different from random; (\*) mean of randomized patterns; (...) maximum of random data; (- - -) minimum of random data.

analysis. Plotting the values of local entropies against quadrat size, spatial aggregation causes a shift of the curve towards the larger scales and segregation makes a shift towards the smaller scales (Bartha & Horváth 1987; Podani et al. 1993). An index of aggregation (Campetella et al. 1999) was used:

$$I_{aggr}(i) = \log MS_{obs}(i) / \log MS_{exp}(i) \quad (2)$$



*Sampling and spatial scaling*

The field transects served as primary samples (cf. Horváth 1998) for the subsequent computerized sampling (Podani 1987). Information theory models were calculated at a series of increasing sampling unit lengths (space series, Podani 1992). Local entropy was calculated at scales between 0.1 m and 50 m. Pairwise associations were analysed between 0.1 m and 1 m. Complete sampling, i.e. sampling from all possible overlapping sampling units (Bartha et al. 1995; Horváth 1998) was performed at each scale. Previous studies (Podani et al. 1993; Bartha & Kertész 1998) have shown that the scaling behaviour of a particular association depends on three factors: (1) the absolute abundance, (2) the relative abundances and (3) the spatial autocorrelation of the variables. Using a series of sampling units at multiple resolutions, the probability of detecting a significant relationships can be increased. Fig. 1b and Table 2 present examples for the scale dependence of spatial associations. In this study the majority (ca. 80 - 90%) of significant relationships were found at the same fine scales, between 0.1 m and 0.3 m.

**Results**

*Patterns of plant litter and disturbances over space and time*

The frequencies of microquadrats with gopher disturbances vary between 0.58 and 22.08% (Table 3). Gopher mounds are present from the first year of succession. The highest frequency is in the 14 yr old strip, while gopher activity is lowest in the late stage of succession (year 66). The amount of litter is high in the 6th year of succession, with 30% frequency, while its

frequency is between 10% and 20% in years 10 and 14. The highest amount of litter is found in year 18 during the dominance of *Poa pratensis* (73%), after which abundance declines to (42%) by the late stage (dominated by *Andropogon gerardii*). Bare soil was only recorded in years 18 and 66, and its frequency remained below 10%.

These variables have remarkable spatial patterns, with high and varying degrees of aggregation (Table 3). The only exception is the random spatial distribution of plant litter in year 4. The scales of maximum heterogeneity of litter and gopher disturbance are over 10 m in the early stages of succession, indicating coarse-grain patterns. The maximum heterogeneity of gopher mounds is at fine scales during mid-succession (years 10 and 14), with a later increase (years 18 and 66); relating to the sampling design of this study, scales 2 m or less are ‘fine-grain’, and scales 20 m or larger are ‘coarse-grain’. There is a coarse to fine-grain trend in the changes of the patterns of plant litter, with a decrease of characteristic scales from 20 m (year 4) to 0.1 m (year 66). The spatial pattern of bare soil is coarse-grain in year 18, and becomes fine-grain by year 66.

*Spatial associations between plant litter, gopher disturbances and vegetation*

Dominant grasses are spatially independent in most cases (Table 4). The exception is *Agrostis scabra*, which is negatively related to *Elymus repens* in year 6 and to *Poa pratensis* in year 18. No significant associations were found between gopher mounds and bare soil, while litter shows consistent negative associations with both gopher mounds and bare soil. There are negative associations between *Agrostis scabra* and litter. *Elymus repens*, *Poa pratensis* and *Andropogon gerardii* have positive associations with plant litter which are restricted

**Table 3.** Abundances and spatial patterns of litter, gopher mounds and bare soil in different years of old-field chronosequence (\* = missing data; empty cells = non-detectable relationships.)

Years since abandonment	1	4	6	10	14	18	66
Frequency%							
Litter	.00	0.33	30.50	17.50	11.00	73.30	42.25
Gopher mounds	4.41	4.25	8.42	13.95	22.08	12.08	0.58
Bare soil	*	*	*	*	*	1.08	9.83
<b>Index of aggregation</b>							
Litter		1.000	2.306	1.436	1.410		1.176
Gopher mounds	1.517	1.379	1.367	1.281	1.382	1.532	1.187
Bare soil						1.300	1.343
<b>Maximum scale of heterogeneity (m)</b>							
Litter		20.0	10.0	2.0	4.0	0.1	0.15
Gopher mounds	20.0	10.0	4.0	1.5	1.1	4.0	36.50
Bare soil						36.5	3.00

**Table 4.** Spatial associations between litter, gopher mounds, bare soil and dominant species in different years of old-field chronosequence (0 = independence; + = positive; - = negative;  $p < 0.05$ ; empty cells = non-detectable relationships).

Years since abandonment	1	4	6	10	14	18	66
<i>Agrostis scabra</i> / <i>Elymus repens</i>		0	-	0	0	0	
<i>Agrostis scabra</i> / <i>Poa pratensis</i>				-	-	-	
<i>Agrostis scabra</i> / <i>Andropogon gerardii</i>						0	
<i>Elymus repens</i> / <i>Poa pratensis</i>				0	0	0	
<i>Elymus repens</i> / <i>Andropogon gerardii</i>						0	
<i>Poa pratensis</i> / <i>Andropogon gerardii</i>						0	0
Litter / Gopher mounds			-	-	-	-	0
Litter / Bare soil						-	-
Gopher mounds / Bare soil						0	0
Litter / <i>Agrostis scabra</i>			-	-	-	-	
Litter / <i>Elymus repens</i>			+	+	0	0	
Litter / <i>Poa pratensis</i>				0	+	+	+
Litter / <i>Andropogon gerardii</i>						0	+
Gopher mounds / <i>Agrostis scabra</i>		-	0	0	0	+	
Gopher mounds / <i>Elymus repens</i>	0	0	+	-	+	0	
Gopher mounds / <i>Poa pratensis</i>				0	0	-	0
Gopher mounds / <i>Andropogon gerardii</i>						0	0
Bare soil / <i>Agrostis scabra</i>						0	
Bare soil / <i>Elymus repens</i>						+	
Bare soil / <i>Poa pratensis</i>						0	-
Bare soil / <i>Andropogon gerardii</i>						0	-

**Table 5.** Spatial associations between litter, gopher mounds, bare soil and functional groups in different years of old-field chronosequence (0 independence, + positive, - negative,  $p < 0.05$ , empty cells = non-detectable relationships).

Years since abandonment	1	4	6	10	14	18	66
Litter / Annuals			-	-	-	-	-
Litter / Short-lived perennial forbs			0	0	-	-	
Litter / Perennial forbs			0	0	-	-	-
Litter / Perennial grasses			0	0	-	0	-
Litter / Sedges			0	-	-	-	-
Litter / Woody perennials							0
Litter / Mosses			0	0	-	-	0
Litter / Lichens			0	-	-	-	-
Gopher mounds / Annuals	-	0	0	0	0	+	0
Gopher mounds / Short-lived perennial forbs	0		0	0	0	+	
Gopher mounds / Perennial forbs	0		0	+	0	0	0
Gopher mounds / Perennial grasses			0	0	-	0	0
Gopher mounds / Sedges	0	0	0	0	-	+	0
Gopher mounds / Woody perennials							+
Gopher mounds / Mosses			0	0	-	+	0
Gopher mounds / Lichens	0	0	+	-	-	+	0
Bare soil / Annuals						0	+
Bare soil / Short-lived perennial forbs						0	
Bare soil / Perennial forbs						0	0
Bare soil / Perennial grasses						0	0
Bare soil / Sedges						0	0
Bare soil / Woody perennials							0
Bare soil / Mosses						0	0
Bare soil / Lichens						0	+

to the stage of their dominance. Dominant grasses have a particular year of dominance when they are negatively associated with gopher disturbances or bare soil. Before and after this stage, *Poa pratensis* and *Andropogon gerardii* are always independent, while the other two grasses have some positive associations with gopher mounds or bare soil (*Elymus repens* in years 6, 14 and 18, *Agrostis scabra* in year 18).

There are consistent negative associations between litter and the functional groups of subordinate species (Table 5). Significant associations were found between annuals and litter in each year between year 6 and 66. Lichens and sedges are not associated with litter in year 6, but are in other years. The spatial dependence of perennial forbs, perennial grasses and mosses appear in the next stage, from year 14. However, perennial grasses are spatially independent from litter in year 18, while mosses are independent in year 66. Woody plants are not present in the samples except year 66, where they are not associated with litter. The overall spatial dependence between litter and functional groups, measured by the number of significant associations, is lower in the earlier stages of succession (before year 14).

The overall dependence between the spatial patterns of functional groups and the spatial patterns of gopher mounds and bare soil is smaller than the overall spatial dependence with litter. There are only sporadic associations during the first 10 years. The maximum spatial dependence appears in year 14 when abundance of gopher mounds is highest, there are only negative associations in this year. In contrast, later stages are characterized by positive associations. On the *Poa pratensis* dominated old-field (year 18), annuals, short-lived perennials, sedges, mosses and lichens are positively associated with gopher mounds, while perennial forbs and grasses are independent. The spatial patterns of functional groups and gopher mounds are all independent in year 66, the only exception being the positive association with woody species. There are no spatial associations between bare soil and functional groups in year 18, although bare soil does have positive associations with annuals and lichens in year 66.

## Discussion

The spatial associations found between litter accumulation, gopher mounds and vegetation characteristics indicate the important role of litter and disturbance in succession. Together with dominant grass species, plant litter and gopher mounds are key variables structuring subordinate species and the pattern of functional groups.

### *Consistent negative effect of plant litter*

Comparison of the relative contributions of litter and gopher disturbance reveals that litter has stronger and more consistent effects during succession than expected. Positive associations switch between grass species, as they change dominance in subsequent successional stages. This suggests that litter is produced predominantly by a single species, the dominant grass species and that litter turnover is probably relatively fast in this system (Wedin et al. 1995). The changing litter composition (in terms of which species produced the litter) does not influence the consistent pattern of negative associations. However, the number of significant spatial associations between litter and functional groups increases over time, suggesting a stronger control in the later stages of succession. This is consistent with the general increase in the total amount of plant litter (cf. Table 1 and Table 3). Monk and Gabrielson (1985) found that pioneer species were more affected by litter than late successional species. The results also indicate slight differences between the responses of functional groups. The sample size analysed in this study was too small to generalize this tendency; however, the pattern of decreasing sensitivity is consistent with the differences in the life history traits of functional groups.

### *Context dependent variability of gopher effects*

Previous studies of the relationship between gopher disturbance and vegetation used a single, arbitrary scale (e.g. Tilman 1983; Inouye et al. 1987a). The methodology used in this study has a greater potential to find relationships with gopher disturbances. However, contrary to expectations and to the high frequency of gopher disturbances, relatively few spatial associations were found between gopher mounds and vegetation characteristics. Compared to plant litter, gopher disturbances have a less pronounced and more variable relationship with vegetation.

At a few of the disturbed microsites, only sporadic associations were found between gopher mounds and subordinate functional groups. At many of the disturbed microsites, mounds were negatively related to the perennial subordinate species. In closed homogeneous

vegetation with intermediate frequency of disturbed microsites annuals, short-lived perennials, sedges, mosses and lichens had positive associations with gopher mounds while perennial forbs and grasses were not associated.

Gophers are fossorial mammals that feed primarily while burrowing underground (Myers & Vaughan 1964). They create burrow systems that vary in size from less than 30 cm to more than 1000 cm in diameter (Inouye et al. 1987a). Field experiments performed on an 8 yr old field (Tilman 1983) showed that gophers prefer high productivity, nitrogen-rich plots dominated by perennial graminoids. Gophers also prefer patches of early successional grass species, as was indicated by the positive associations of gopher mounds with *Agrostis scabra* and *Elymus repens*. However, gophers probably do not prefer the closed turf of late successional *Poa pratensis* and *Andropogon gerardii*. Abundance of gopher mounds was low in late successional grassland and was not associated with subordinate functional groups. In the 66-yr old field most of the subordinate species are native perennial forbs and grasses adapted to closed canopy and fine-scale heterogeneity. These species are probably less dependent on larger scale openings created by gopher activity than subordinate species typical of earlier stages of succession.

#### *The role of litter and gopher disturbance on species coexistence*

Species coexistence and the temporal sequence of dominant species have been explained by the colonization – competition trade-off in the successional grasslands at Cedar Creek Natural History Area where species compete for a single limiting resource; nitrogen (Tilman 1988, 1990). Species dominant at the beginning of succession colonize faster but are weaker competitors than species dominating the later stages. Fertilizer experiments conducted at Cedar Creek found negative correlation between litter and diversity and it was suggested that plant litter reduced diversity by affecting local species turnover (Tilman 1993). A seed addition experiment demonstrated the importance of recruitment limitation in this system (Tilman 1997). The positive associations between litter and dominant species and the negative associations between litter and subordinate functional groups found in this study suggest that litter is produced mainly by the actual dominant species and its accumulation enhances local competitive extinctions of subordinate species. According to the theory based on the colonization-competition trade-off, subordinate species coexist at the field scale due to their greater mobility, enabling them to invade temporary open microsites. Gopher disturbances potentially increase di-

versity by increasing the number of such microsites. A previous field survey of an old-field chronosequence in Minnesota (Inouye et al. 1987a) found positive correlations between gopher mounds and species richness, particularly in older fields. This correlation was due to the increase of early successional species (annuals and short-lived perennials) on gopher mounds. In the present study similar positive associations of gopher mounds with annuals and short-lived perennials were found in a particular year only, in closed homogeneous vegetation with intermediate frequency of disturbed microsites. Annuals and short-lived perennials were independent of the disturbed microsites in other years, except the first year of succession when annuals had a negative association with gopher mounds. True prairie species appear early in this succession. In the vegetation of the 18-yr old field 40% of species are true prairie species (Table 1), mostly perennial forbs and grasses. Spatial analyses showed that these functional groups are independent of the pattern of gopher mounds and bare soils. This might indicate strong propagule limitation, even at late succession, but also suggests that other mechanisms (niche differentiation and selective herbivory) can explain species coexistence in these Minnesota old-fields.

#### *Implications for management*

Contrary to the complex effects of plant litter and gopher disturbances indicated by previous field and experimental studies, the present results suggest relatively simple, net effects in these Minnesota old-fields. Litter has consistent and strong negative effects on subordinate functional groups in all but the initial years. Gophers have negative effects on litter and dominant grass species, therefore having the potential to increase diversity by producing gaps for subordinate species. However, the realization of this potential effect depends on vegetation cover and pattern, dispersal limitation and disturbance regime. Gophers had positive associations with subordinate functional groups only in mid-successional stages. Even at this stage, perennial grasses and forbs remained spatially independent from gopher mounds, suggesting that gopher disturbance is probably not important in the colonization of native perennial species. Because of the consistent negative effect of plant litter and the inconsistent, temporal effect of gopher disturbances, management efforts aimed at increasing species diversity should focus on the control of litter accumulation in this system.

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