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Small-scale spatial dynamics of plant species in a grassland community over six years

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Abstract. In a species-rich mountain grassland in the Krkonoše Mts., Czechoslovakia, data from four permanent plots of 50 cm × 50 cm were recorded annually from 1985 to 1990 to study the spatial dynamics of the species. Plots were divided into 15 × 15 subplots and the number of vegetative units of all plants within each subplot was determined. There was not much net change at the plot level, but the subplots were very dynamic. Two aspects of the spatial dynamics of the species were followed: (1) persistence, i.e. the tendency of the species to remain in the same subplot, and (2) long-distance spreading, i.e. movement to subplots beyond the immediate neighbourhood. Species differed widely in their persistence and long-distance spreading and were classified into mobility types: long-range guerrilla, short-range guerrilla, phalanx and 'sitting'. The mobility types were, to a certain extent, correlated with the growth form of plants, but some species of one growth form showed different types of small-scale dynamics and some species with different growth forms had the same spatial dynamics.

Keywords: Growth form; Guerrilla strategy; Mountain grassland; Permanent plot; Phalanx strategy; Species richness.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Temperate grasslands can be very rich in species. Some investigators explain this diversity without taking into account spatio-temporal interactions. For example, Tilman (1982) suggested treating space as a resource in communities of sessile organisms; the resource supply rate would then be the rate of disturbance through which open space is formed. However, because of the sedentary life of plants, the accessibility of a given disturbed patch will be different for several species, which depends on complex spatial processes and on the space occupation strategies of plants. New light has been shed on this idea by the recent identification of active spatial dynamics of plants, especially those with runners, as a mechanism of foraging for space or nutrients (Slade & Hutchings 1987; Sutherland & Stillman 1988; van Groenendael & de Kroon 1990).

Other concepts of species diversity maintenance, though not directly applied to grasslands, are even more space-oriented. Field studies and models have shown the non-transitivity of interaction matrices and non-linear interactions between species to be responsible for species coexistence in communities of clonal organisms, such as marine invertebrates and terrestrial cryptogams (Buss & Jackson 1979; Buss 1986; Jahns 1982; Karlson & Jackson 1981). Different mobility characteristics may also facilitate the coexistence of species (Bell 1984) and maintain community diversity (Ljubarski 1988).

All these approaches require information about the spatial behaviour of the species in plant communities and about space-mediated dynamic relations between species. This information is crucial because the clonal nature of most plants (Harper 1985) implies a strong correlation between the occupation of a given patch and the occupation of neighbouring patches. Species coexistence and community diversity in turn depend on the particular parameter values of this correlation in competing species (Bell 1984).

The spatial dynamics of higher plants is well-documented. Much attention has been paid to the spatial dynamics of single species (e.g. Noble, Bell & Harper 1979; Lovett Doust 1981; Svensson & Callaghan 1988). This led Lovett Doust (1981, Lovett Doust & Lovett Doust 1985) to the concept of phalanx and guerrilla strategies. In contrast to previous descriptions of plant strategies (Gadgil & Solbrig 1972; Grime 1979), which primarily refer to plant adaptations to the abiotic environment, the phalanx/guerrilla distinction separates species as to their strategy of spatial dynamics within one community. Therefore, this approach can be used to study processes responsible for the coexistence of species (Schmid & Harper 1985). However, any strategy concept has a relative meaning: it makes sense only when species with different strategies are compared. In the case of the phalanx/guerrilla distinction, morphology and growth form are considered a sufficient basis for comparing species as to their strategy.

Comparative data on spatial behaviour within assemblages of coexisting plant species are scanty. Changes in quantitative relations between species in grasslands have been studied widely, but most of this research addresses the community level and does not take into account spatial structure and dynamics within plots (Grubb, Kelley & Mitchley 1982; Rabotnov 1984). The survey of permanent plot research in the British Isles (Hill & Radford 1986) does not report a single study including within-plot spatial changes of more than one species. Symonides (1979) described the change in a dune community after invasion by the clonal species *Carex arenaria*. Thórhalsdóttir (1990) studied temporal persistence of species in 1-cm diameter circular plots, but did not address the importance of the lateral spread of species. Van der Maarel & Sykes (1993) present data from alvar vegetation which addresses this question most directly. All these studies report great variability between species in their spatial mobility characteristics.

The aim of this paper is to present a community-centred view of species mobility in a grassland. Using small-scale recording of permanent plots, we attempt to (1) assess the variability of spatial dynamics among species growing together in one community, the strategy of space colonization and rate of spatial dynamics, and (2) relate the spatial dynamics to the growth form of these species.

Methods

Study site

The data were collected in a mountain meadow in the Krkonoše Mountains, N. Bohemia, ca. 4 km ESE of Pec pod Snezkou. The grasslands were mown once or twice a year, grazed in autumn, and manured once every few years. The studied plots are very rich in species. See Herben et al. (1993) for details. Table 1 lists common species in the plots. The meadows can be classified as *Sileno-Nardetum crepidetosum* (*Nardo-Agrostion* alliance, *Nardetalia* order, see Krahulec 1990). At the plot level, there was not much net change in species frequency or abundance during the observation period.

Data collection

Four permanent plots of 50 cm × 50 cm were established in 1985 and recorded once a year before mowing (ca. mid June) to1990. The plots were fixed with 20 cm long plastic tubes in the soil with 15-cm long matching oiled nails inside them. When partly pulled out, these nails fitted into the recording frame. This system of marking enabled recording precision of < 0.5 cm. To record, a grid of 15 × 15 subplots, 3.3 cm × 3.3 cm each, was established by fitting wires into the slots in a wooden recording frame. The number of plant units of all plants rooted within each subplot was determined. For all grasses and graminoids, the plant unit was a tiller; for large forbs, the plant unit was a leaf, and for small forbs it was a rosette. Flowering stems were counted as one plant unit in all plants. Seedlings with only juvenile leaves were not counted since a rather different time scale would be needed for their study. The plots were clipped after recording. Two plots, J1 and J2, were manured with horse dung in autumn 1985, $pH = 8.15$, which added 0.54 g/m^2 NO_3-N, 8.4 g/m^2 NH_4-N and 1.8 g/m^2 PO_4-P.

Data analysis

Only species with a frequency of > 20 subplots (out of 225) in at least two recordings of one plot were included in the study. The number of these more frequent species varied from 12 to 14 in one plot, with a total of 20 species (Table 1). Species within the genera *Alchemilla* and *Campanula* were combined since they were difficult to identify in the vegetative or sterile state.

The small-scale dynamics of individual species were expressed in two ways:

1. A qualitative measure of temporal autocorrelation, further called persistence, was based on a 2 × 2 contingency table comparing species presence/absence in subplots at two recording times. The association within this table is a measure of the tendency of a species to remain within the same subplots over the respective time inter-

Table 1. List of frequent species with species code (used in Figs. 1 and 3) and plots in which they occur.

Species	Code	Plots
Achillea millefolium	mi	1
Agrostis capillaris	a	1,2,3,4
Alchemilla spp. (*acutiloba, monticola*)	al	1,2,3,4
Anthoxanthum odoratum	x	1,2,3,4
Campanula spp. (*rotundifolia, bohemica*)	cn	1,2
Cardaminopsis halleri	h	1,2
Carex pilulifera	cx	1,4
Deschampsia flexuosa	d	1,2,3,4
Euphrasia rostkoviana	eu	3,4
Festuca rubra	f	1,2,3,4
Galium pumilum	g	3
Hypericum maculatum	hy	2,3,4
Luzula multiflora	l	2,3,4
Nardus stricta	n	1,2,3,4
Poa pratensis	p	1,2,3,4
Polygonum bistorta	b	3,4
Ranunculus acris	r	1
Rumex acetosa	rx	1
Veronica chamaedrys	vc	1,2,4
Veronica officinalis	vo	2,4

val. The point correlation coefficient (Pielou 1969) was used as a measure of association in this table. Two sets of point correlation coefficients were calculated for each species in each plot: (a) from all possible pairs of successive years (time lag = 1), and (b) from comparison of all years with the beginning of the observation (1985, time lag = 1 - 5). This technique was used to avoid difficulties of non-stationarity of the plots (Jongman, ter Braak & van Tongeren 1987). Plotting the point correlation coefficients against the time lag produced persistence decay curves for each species at the subplot level. Principal component analysis (PCA) was used to summarize the species persistence patterns. All species in all plots were included in one analysis as cases; values of persistence over different time intervals were variables.

2. Long-distance spreading of species was expressed by counting the number of subplots where the species newly appeared, without having been observed in the surrounding eight subplots in the previous year. Edge subplots were excluded for this analysis. This measure was expressed relative to the number of subplots which do not have the species in question in their neighbourhood. The number of newly occupied subplots depends on the frequency and spatial pattern of species and can be compared between species only with caution. Therefore a χ^2 test was used to assess whether the number of subplots occupied by long-distance spreading is significantly different than expected under a null hypothesis in the 2×2 table.

Growth form and life histories of species were based on Grime, Hodgson & Hunt (1988), specialized papers following the bibliography of Jäger & Müller-Uri (1981), and our own field observations.

Table 2. Small-scale spatial behaviour of species, based on (1) the absolute level of persistence; (2) change in persistence with increasing time lag: ≈ no decrease; < decrease; and (3) long-distance spreading. Species in parentheses do not show the same behaviour in all plots or/and all recording times.

		Long-distance spreading	
Persistence Level	Change	High	Low
High	≈		**Sitter**
		(*Cardaminopsis halleri*)	*Carex pilulifera* *Luzula multiflora* *Ranunculus acris* *Polygonum bistorta*
High	<		**Phalanx**
			Nardus stricta *Festuca rubra* *Alchemilla* spp.
Low	≈, <	**Long-range guerrilla and annual**	**Short-range guerrilla**
		Achillea millefolium *Agrostis capillaris* *Anthoxanthum odoratum* *Campanula* spp. (*Cardaminopsis halleri*) *Deschampsia flexuosa* *Euphrasia rostkoviana* *Galium pumilum* *Poa pratensis* *Rumex acetosa*	*Hypericum maculatum* *Veronica officinalis* *Veronica chamaedrys*

Results

Persistence varied between species. As regards persistence over a 1-yr interval, the difference within the set of species was significant, as found in a one-way ANOVA (species as effects, $F = 18.393$, d.f. = 20/234, $p < 0.001$). Species can be roughly divided into stable species, e.g. *Carex pilulifera*, *Luzula multiflora*, *Nardus stricta*, *Ranunculus acris*, and moving species, e.g. *Achillea millefolium*, *Anthoxanthum odoratum*, *Rumex acetosa* and *Veronica chamaedrys* (Table 2, Fig. 1). Using a two-way ANOVA for each species (with years and plots as effects), the difference between years was insignificant for all species; the difference between plots was significant at $p < 0.05$ for *Euphrasia rostkoviana*, *Festuca rubra*, *Cardaminopsis halleri* and *Poa pratensis*. None of these differences can be attributed to the manuring of the plots. When persistence curves for an increasing time lag (see Fig. 2 for examples) are com-

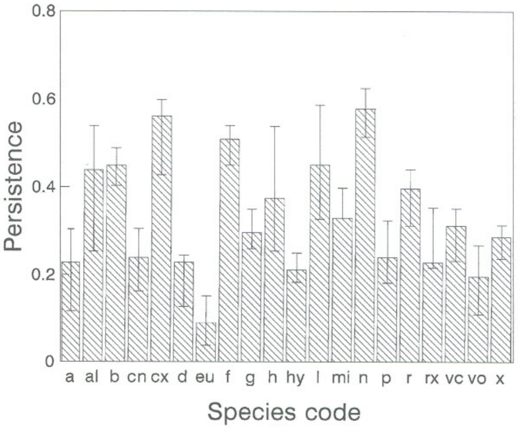

Fig. 1. Median persistence, time lag = 1 for all species (for codes, see Table 1). Bars indicate 25 % and 75 % quartiles.

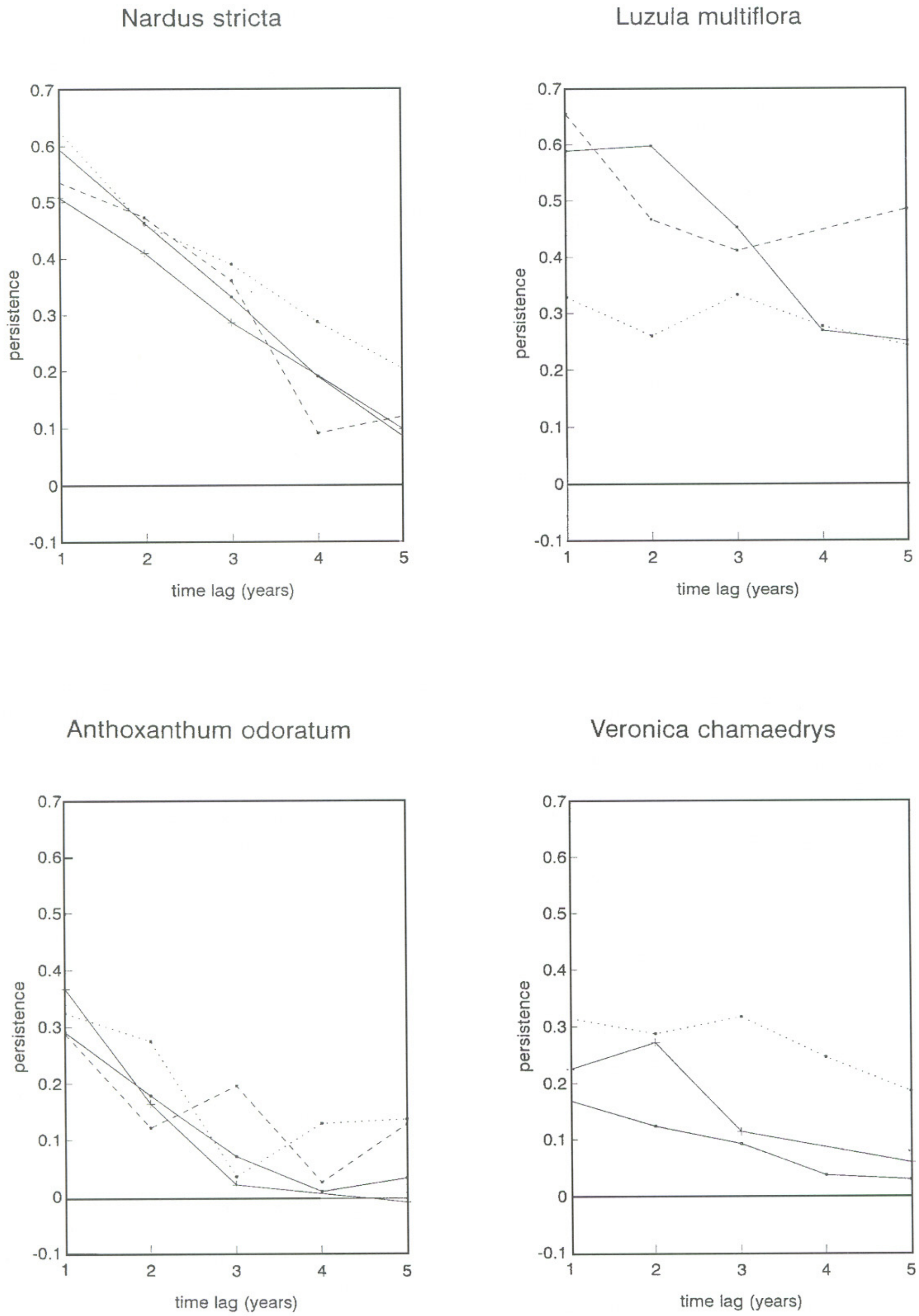

Fig. 2. Examples of persistence curves (plot of point correlation coefficient vs. time lag since 1985) for four species. Numbers indicate individual plots. *Nardus stricta* and *Luzula multiflora* are species with a high absolute level of persistence, *Anthoxanthum odoratum* and *Veronica chamaedrys* have a low level. *Nardus* and *Anthoxanthum* show a large decrease in persistence, *Luzula* and *Veronica* a small decrease. Full line (points) = plot 1; Dotted line = plot 2; Dashed line = plot 3; Full line (crosses) = plot 4.

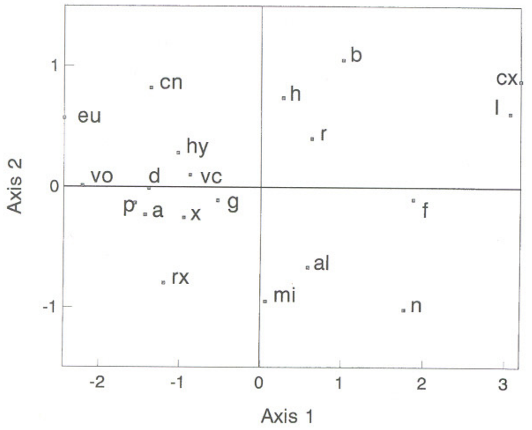

Fig. 3. Principal component scores for the Principal Component Analysis of the spatial persistence data (cf. also Table 1). Cases: species at one plot; variables: spatial persistence over different time intervals. For species codes, see Table 1.

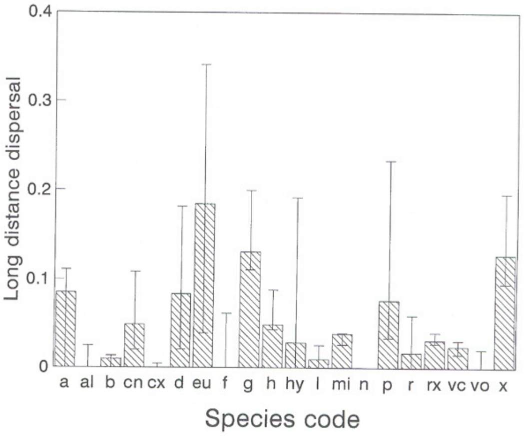

Fig. 4. Median long distance spreading over time lag = 1 for all species. The values are proportions of colonized subplots out of the total number of subplots available. For species code, see Table 1. Bars indicate 25 % and 75 % quartiles.

pared, two components of species behaviour can be distinguished:

(1) distance of the curve from the abscissa is a measure of the absolute magnitude of the species persistence;

(2) angle of the curve with the abscissa indicates the rate of decrease of persistence with increasing time lag.

In a PCA applied to the persistence data to summarize their variability, as much as 74.5 % and 14.2 % of the total variance was accounted for by the first two axes. In the PCA-graph species (points) are arranged according to the similarity of the shape of their persistence curves. The first axis (Fig. 3) separates species of high and low absolute level of persistence; axis 2 separates species with strongly decreasing and little - to not - decreasing persistence curves. Dicots tend to keep their persistence level over time, whereas grasses generally show a decreasing persistence (Fig. 3). This division is independent of the absolute level of persistence; in both groups there are species showing rapid changes, such as *Campanula* spp., *Hypericum maculatum*, *Deschampsia flexuosa* and *Poa pratensis*, as well as species with a high persistence, e.g. *Alchemilla* spp., *Ranunculus acris*, *Nardus stricta* and *Festuca rubra*.

Species also differ in their capacity for long distance spreading (Fig. 4); this difference was significant using one way ANCOVA (with species as effect, $F = 5.635$, d.f. = 20/232, $P < 0.001$; with available subplots as covariate: $F = 15.913$, d.f. = 1/232, $P < 0.001$). Most species able to move over longer distances do not have high spatial persistence, whereas those that move only short distances may or may not be spatially persistent. A two-way ANCOVA with plots and years as effects for each species separately, showed that the differences between plots are non-significant ($P = 0.05$) for all species; differences between years are significant only for *Polygonum bistorta*. On the basis of a combination of absolute level of persistence, change of persistence with increasing time lag, and long distance spreading, we can define four basic types of the species spatial dynamics within the community: Short-range guerrilla, long-range guerrilla, phalanx and sitting (Table 2).

Discussion

The absolute level of persistence expresses the tendency of a species not to leave its original position and not to colonize new subplots. Persistence defined in the way we did, is dependent on both subplot size and recording interval. A decreasing persistence curve with increasing time lag indicates that the spatial dynamics of the species is commensurable with the scale of sampling, i.e. in the order of 3 cm/yr. A non-decreasing persistence curve implies that the rate of change of the species is either greater than or smaller than the scale of sampling.

Long-distance spreading also expresses the relation between rate of spatial dynamics and the recording system. Species which show long-distance spreading, as defined here, are able to move much faster in a community than one subplot size per year (i.e. ca. 3 cm/yr).

Spatial persistence and long-distance spreading can be used to classify species according to their spatial dynamics (Table 2). In clonal species, which form the majority of the species assemblage, the difference in spatial persistence and long-distance spreading divides species into relative phalanx and guerrilla strategists. The guerrilla character of the species' spatial dynamics increases downwards and to the left in Table 2. The most stable species within the set are those with a high and non-decreasing persistence level; they are stationary on the time-scale of the observation and may be termed 'sitting'. They do not fit well in the phalanx/guerrilla dichotomy; in the framework of this military terminology, this strategy could be called fortress.

These parameters of spatial dynamics are related to species growth form and life history (Table 3). Grasses typically show decreasing persistence with increasing time lag, and hence are found in the lower part of the ordination diagram (Fig. 3). Grasses tend to move through the grid at a steady rate. A low proportion of seed establishment in grasses (Zhukova & Ermakova 1985) and the absence of long runners are also responsible for this persistence pattern. Some grasses, however, do spread over longer distances, either because of stolons (*Poa*, *Agrostis*, *Deschampsia*) or of seedling establishment (*Anthoxanthum)* (unpubl. data).

Dicots show a more variable behaviour. Plants with stolons or long rhizomes, and annuals have a low persistence level and often possess the ability to spread over long distances. Rosette plants are represented in all spatial-dynamical types; species without a rosette growth form usually have a low level of persistence. There are also fortress species among the dicots; those are clonal species with an extremely slow rhizome growth rate (0.5 - 1.5 mm/yr for *Alchemilla*, cf. Petukhova 1977).

At a smaller scale, the correlation between spatial behaviour and growth form is limited. Within one type of spatial dynamics we find species of several growth forms (Table 3). Low and non-decreasing persistence levels and long-distance dispersal may be shown both by clonal species with fast runners (*Cardaminopsis halleri* or *Poa pratensis*), and by non-clonal species with seed dispersal (*Euphrasia rostkoviana*). Rhizomatous plants also fall into several spatial behaviour types. This is due to differences in rhizome growth rate (fast growing rhizomes in e.g. *Achillea millefolium* or *Poa pratensis* vs. slower growing rhizomes in *Anthoxanthum* or *Agrostis*). The behaviour of species with slowly growing compact rhizomes may also vary according to differences in seedling recruitment (*Ranunculus acris*).

The spatial dynamics of a particular species varies with respect to the community and to abiotic conditions. Some species, notably *Festuca rubra*, show considerable plasticity. In the plots described in this study, *Festuca* behaves as a matrix-forming phalanx species; in contrast, in a poor high-mountain grassland with a large proportion of *Nardus stricta*, it behaves rather as a guerrilla species in the matrix of *Nardus* (Herben et al. 1990). *Cardaminopsis halleri*, *Poa pratensis* and *Luzula multiflora* also show variable behaviour.

The data presented here enable us to distinguish

Table 3. Growth form of species vs. types of small-scale dynamics (see Table 2). For full species names, see Table 1. T = tufted plants; R = rosette plants; I = plants with individual shoots.

	Long-range guerrilla	Short-range guerrilla	Phalanx	Sitting
Annuals	I: *Euphrasia*			
Long rhizomes	T: *Poa* R: *Campanula* *Achillea* *Rumex* I: *Galium*	I: *Hypericum* *Veronica ch.*		
Short rhizomes	T: *Deschampsia* *Agrostis* *Anthoxanthum*			
Stolons	R: *Cardaminopsis*	I: *Veronica ch.* *Veronica off.*		
Compact rhizomes			T: *Festuca* *Nardus* R: *Alchemilla*	T: *Carex* *Luzula* R: *Polygonum* *Ranunculus*

functionally distinct groups of species within the community. In seemingly homogeneous grasslands, this may be more difficult than in more open and/or structured communities. Species with high persistence and, as a rule, little long-distance spreading are typical matrix building species (mainly grasses and graminoids, but also dicotyledonous fortress species). However, not all grasses and graminoids behave as matrix-building species; the most notable exception is *Poa pratensis*; others are *Deschampsia*, *Anthoxanthum*, *Agrostis*. The matrix of these species is filled with moving components of the community, the guerrilla and annual species (Grubb 1986). Each of these coexisting groups has unique mobility properties. These properties can, under certain circumstances, act as the sole mechanism for species coexistence, as demonstrated by different types of spatial models (Bell 1984; Karlson & Jackson 1981) and may be particularly important in grassland communities, where resource-niche differentiation may be absent (Mahdi, Law & Willis 1989) and where regeneration after disturbance is rare (Grubb 1977).

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