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Fine-scale spatio-temporal patterns in a mountain grassland: do species replace each other in a regular fashion?

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Abstract. Long-term 'high spatial resolution' permanent plot data were used to determine whether fine-scale species replacements in space occur more often than expected on the basis of random processes, and to test whether these replacements are species-specific. Monte Carlo tests were used. There was no indication of significance in associated positive change (species A increased when B increased); the overall number of significant results was not higher than expected on a random basis. For associated negative change, or replacements (species A increased when B decreased) the overall number of significant results was significantly higher than expected. Significant reciprocal replacements between *Deschampsia flexuosa, Festuca rubra* and *Nardus stricta* were frequent; changes in *Anthoxanthum alpinum* and *Polygonum bistorta* were uncorrelated with changes of the former three. The first three species thus use the 'same' space. Both the latter species often reproduce by seeds and their turnover is much higher. The prevalence of negative correlations of changes (*i.e.* correlation of increase with decrease) supports the concept of an internal structuring within the grassland community.

Keywords: Functional differentiation; Monte Carlo test; Permanent plot; Spatial resolution.

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

Introduction

Recent studies of grasslands have shown a considerable degree of species dynamics at a scale of a few centimetres (Thórhalsdóttir 1990a; Herben et al. 1990; van der Maarel & Sykes 1993; Sykes et al. 1994; Silvertown et al. 1994). In the mountain grasslands of the Krkonoše Mts. temporal autocorrelation of even the slowest growing clonal species (such as *Nardus stricta*) approaches zero over 5 to 7 yr (Herben et al. 1995a). This means that over an interval of several years, the whole spatial structure of the grassland is entirely reshuffled. These dynamics are, to a large extent, due to the clonal growth of the component plants (Law et al. 1993; Herben et al. 1995a). The growth of these clonal plants is to some degree responsive to their environment (de Kroon et al. 1994). In a closed sward, however, the environmental heterogeneity has its own spatio-temporal patterns (Oborny 1994) since this heterogeneity is partly due to the growth of other plants, which are often clonal as well. Such dynamics potentially show a quite complex behaviour (Hogeweg 1988); though such behaviour was shown by modelling studies (Silvertown et al. 1992; van der Laan 1994), virtually no information on it is available from real communities.

Clearly, the high spatial dynamics of individual species should be associated with the spatial replacements of the mobile species. Are these replacements entirely random or is there any regularity in them?

A few experimental studies (Thórhalsdóttir 1990b; Silvertown et al. 1994) have shown that under conditions which standardize the number of interspecific contacts, individual pairs of species show different levels of intensity of pairwise horizontal overgrowing. This is similar to the processes known from marine sessile invertebrates (Paine 1984; Karlsson & Jackson 1981) and cryptogamic plants (Woolhouse et al. 1985). Given the high spatio-temporal patterns of the undisturbed grassland swards, it is very likely that this pairwise specificity should have some effects on the fine-scale replacements amongst the component species.

In this study, we attempt to discover any structure in such replacements using permanent plots in a mountain grassland. The fine-scale recording system in a long-term set of permanent plots (Herben et al. 1990, 1993, 1995a) enables us to observe pairwise species-replacements at the scale of 3.3 cm × 3.3 cm. This allows (1) identification of replacements which occur more often than expected and (2) testing whether these replacements are species-specific, i.e. whether, in closed vegetation, individual species pairs differ in the intensity of replacements. We used a Monte Carlo approach to account for the spatial dependence in the recording system. In this way we derived the expected distribution under the assumption of no correlation, and compared it with the observed values.

Methods

Study site

The study site is located in a mountain grassland in the Krkonoše Mts. in the northern part of the Czech Republic at the Severka settlement, ca. 3 km NW of Pec pod Sněžkou at 50° 41' 42" N, 15° 42' 25" E, at an altitude of ca. 1100 m. The area has a harsh climate; mean temperature in the warmest month (July) at the nearby climatic station of Pec pod Sněžkou, ca. 900 m a.s.l., was 13.7 °C (in 1989). The study site experiences a long winter with a thick snow cover, usually lasting from November until the end of April. The studied grasslands are not entirely natural; they are maintained by mowing. However, since their establishment about 300 yr ago they have developed a quite stable species composition, owing to stability in management (see also Herben et al. 1993). The traditional management of the meadows consisted of mowing once a year and manuring once in several years.

There are only five principal species in the plots: *Anthoxanthum alpinum*, *Deschampsia flexuosa*, *Festuca rubra*, *Nardus stricta* and *Polygonum bistorta* (henceforth referred to as *Anthoxanthum*, *Deschampsia*, *Festuca*, *Nardus* and *Polygonum*, respectively). Although the system is species-poor at a larger scale, relatively many species coexist at the fine scale, with a species density of 2 - 4 species/10 cm^2 and 6 - 10 species/2500 cm^2. According to the Braun-Blanquet classification of the Krkonoše grasslands (Krahulec 1990) the study grassland can be classified as the *Sileno-Nardetum pleurozietosum* (*Nardo-Agrostion*, *Nardetalia*).

Data collection

Four permanent plots of 50 cm × 50 cm were established in the site in 1984-1985. The plots were marked by plastic tubes driven 20 cm into the soil. A sampling frame with a grid of 15 × 15 cells of 3.3 cm × 3.3 cm was put in a fixed position through steel rods mounted to the frame which fitted into the plastic tubes. In this way the position of the frame deviated maximally 5 mm from year to year. In the cells of these plots the number of modules (shoots for grasses, leaves for *Polygonum bistorta*) of each species was counted every year in the middle of July until 1995. Small *Polygonum bistorta* seedlings with only juvenile leaves were omitted. Flowering shoots were counted separately.

Since the reported study was a part of a larger experimental study of grasslands, two plots (S1 and S3) were manured in autumn 1985 and in 1989 (cow manure following the traditional treatment performed at these plots). This amounted to adding the following amount of nutrients (g/m^2): Total N = 17, NO_3-N = 0.2, NH_4-N = 3.8, PO_4-P = 2.4, pH = 7.7. The overall dynamics of the plots is described in more detail in Hadincová et al. (subm.). Since the differences between the manured and non-manured plots are small, both at the large scale (Hadincová et al. subm.) and at the fine scale (this study), we are treating them as replicates here.

Data analysis

Successive recordings of the cells in exactly the same positions allowed us to search for correlated patterns within species pairs. Two types were searched: (1) difference in behaviour of a (target) species between cells differing in occupation by another (conditioning) species; (2) correlated changes of two species within cells.

Cells with the target species present were classified to form a two-way table by (a) the presence of the conditioning species at time 1, and (b) the behaviour of the target species from time 1 to time 2 (decrease vs. no decrease; see Fig. 1A). To account for the quantity of the conditioning species, the cell was treated as 'conditioning species present' only if the shoot number in that cell exceeded a specified limit. Two different limits were used for each species, which corresponded (after rounding off) to the 50 % (median) and 75 % quartile of the per cell shoot number distribution (with zero cells excluded). These values were for *Anthoxanthum* 3 and 5 shoots per 3.3 cm × 3.3 cm cell, for *Deschampsia* 8 and 12 shoots, *Festuca* 3 and 5 shoots, and *Nardus* 5 and 9 shoots.

In each of these cells, the behaviour of the target species – decrease vs. increase or no change from time 1 to time 2 – was determined, and the association of the target species behaviour and the presence of the conditioning species was assessed using the φ coefficient calculated as $\varphi = \sqrt{\chi^2/n}$ (Pielou 1977). In addition, the Pearson correlation between the quantity of the conditioning species and the change of the target species was calculated.

For testing correlated changes of two species only cells with both species present at time 1 were used in the analysis. In each of these cells, the behaviour of both species from time 1 to time 2 was assessed (increase, decrease, no change). This yields a 3 × 3 contingency table. Cells were then pooled as follows (see Fig. 1B) to create two 2 × 2 tables: increase of A/no increase of A vs. decrease of B/no decrease in B. The association within the two resulting 2 × 2 tables (the other with A and B swapped) was again measured by the φ coefficient. The Pearson correlation coefficient of the change of the species A and B was also calculated.

All pairwise combinations of the five important species – *Anthoxanthum*, *Deschampsia*, *Festuca*, *Nardus* and *Polygonum* – were tested. The comparison was

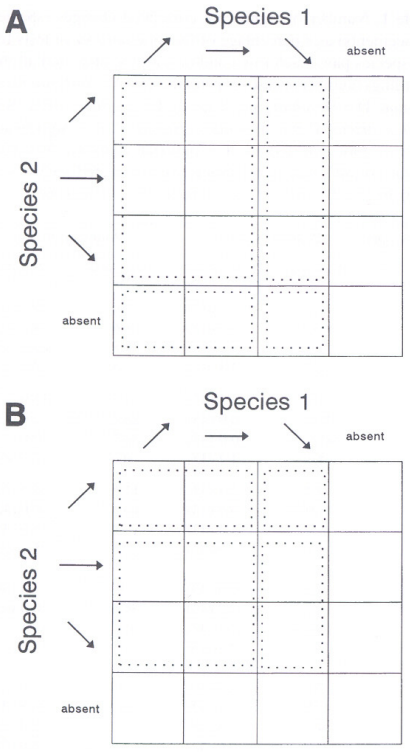

Fig. 1. Contingency tables used to study correlated species changes. The basic 4 × 4 grid covers all possible situations of the behaviour of two species when two recordings are compared (arrows indicate increase, no change, decrease; 'absent' means absent in both recordings). The way the 2 × 2 tables used for testing are formed is indicated by dotted boxes. Cells of the 4 × 4 grid not covered by the boxes were omitted from the particular type of analysis. (A). Effect of the presence of species 2 on changes in species 1; (B) correlation of the increase of species 2 with the decrease of species 1.

made over a 1-yr interval.

The grid data include many data points which are not statistically independent due to the autocorrelation structure within the grid; therefore the permutation procedure (Palmer & van der Maarel 1995) was used to estimate probabilities of the Type I error. This approach allows the examination of deviations from randomness in the species response for each plot and each time period separately. In each permutation, the grid of the conditioning species was shifted by a randomly chosen number of cells in X and Y directions, and the φ coefficient between the shifted grid of the conditioning species and the original grid of the target species was calculated. The shifted grid was 'wrapped around'. 1000 permutations were carried out, and the probability of the real data correlation coefficients in the distribution of values arising from permutations was determined. One-tail probabilities were used. The testing was carried out at the nominal $P = 0.05$ level. Essentially the same procedure was used to determine the probability of the Type I error for both point correlation and Pearson correlation coefficients: when correlated changes were tested, the shifted species was shifted identically at both times 1 and 2. This 'uncoupled' the behaviour of both species, but left the spatio-temporal structure of each species intact. In this procedure, the sample size is determined only after random shifting which may produce spurious significance if the correlation depends on the sample size. However, the variation of the sample size was small enough to make such an effect unlikely.

The procedure described above provides one test for each species pair in two successive recordings for one plot. Since further analysis would involve multiple significance testing, two procedures were adopted to correct for the random Type I errors resulting from the multiple tests. First, for each technique (Pearson correlation vs. point correlation, positive or negative associations), an assessment of the likelihood of the overall number of significant results was made using binomial distribution (event probability = 0.05; number of trials = number of all tests, i.e. number of species pairs × number of plots × number of recordings). This allowed the assessment of the total number of significant results expected under the hypothesis of no underlying effect, but did not identify any structure in the positive results. To determine this, similar tests were made for each species pair (across plots and recordings). Here the binomial distribution was used, with:

– event probability = 0.05;
– number of trials = number of plots × number of recordings;
– application of the Bonferroni correction instead of using usual significance levels, in order to correct for the number of tests performed in parallel, i.e. 20 being the number of species pairs.

The dependence of the number of significant responses on the year of recording and plots was tested using the log-linear model. A three way table was formed (response significant vs. year vs. plot fertilized or not). The effect of year was considered significant if the fit of the loglinear model with terms *response*, and *year* × *plot* was significantly improved by adding the interaction term *year* × *response*. The effect of plot was tested in the same way.

Results

Correlation between presence of one species and change of another species

We distinguish between positive and negative correlations – measured by the Pearson correlation coefficient. No positive correlations were found significant. The overall number of significant negative correlations was higher than expected on a random basis – a negative correlation means that a decrease in the target species was positively correlated with the number of shoots of the conditioning species. Similar effects were not detected by the φ coefficient with either limit of the conditioning species presence.

At the level of species pairs, very few pairs showed a significant correlation. *Deschampsia* significantly decreased in the presence of *Festuca* (as measured by the Pearson correlation coefficient); *Anthoxanthum* decreased in the presence of *Polygonum* (both with Pearson and the φ coefficient).

Correlated changes of species (species replacements)

For positive associations, i.e. species A increases when species B increases, the overall number of significant results was not higher than expected on a random basis. For negative associations – species A increases when species B decreases – the overall number of significant results was high and was very unlikely as the result of random processes only ($P < 0.0001$; binomial distribution). This overall result was obtained both with the Pearson correlation coefficient and the φ coefficient.

Table 1. Number of significant correlated changes (species replacements) as a percentage of the total number of tests for that species pair. Each row combines all the plots and all the recordings (number of cases in parentheses). A = *Anthoxanthum alpinum*; D = *Deschampsia flexuosa*; F = *Festuca rubra*; N = *Nardus stricta*; P = *Polygonum bistorta*. PLT = significant effect of plot detected by the loglinear analysis. Asterisks indicate significance at the Bonferroni-corrected levels: + = $P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Species pair	Pearson correlation		Point correlation	
	Negative	Positive	Negative	Positive
A-D	4.7	2.3 (43)	0.0	9.3 (43)
A-F	14.0 +	0.0 (43)	11.6	9.3 (43)
A-N	11.6	0.0 (43)	4.8	0.0 (42)
A-P	4.7	2.3 (43)	5	2.5 (40)
D-A	4.7	4.7 (43)	2.3	11.6 (43)
D-F	39.5 ***	0.0 (43)	26.2 *** PLT	2.4 (42)
D-N	41.9 ***	0.0 (43)	30.2 ***	0.0 (43)
D-P	4.7	4.7 (43)	0.0	2.3 (43)
F-A	9.3	2.3 (43)	11.6	2.3 (43)
F-D	41.9 ***	0.0 (43)	16.3 *	0.0 (43)
F-N	16.7 *	2.4 (43)	19.4 *	5.6 (36)
F-P	0.0	0.0 (43)	12.8	5.1 (39)
N-A	9.3	0.0 (43)	10	7.5 (40)
N-D	51.2 ***	0.0 (43)	36.6 ***	0.0 (41)
N-F	18.6 **	2.3 (43)	21.2*	6.1 (33)
N-P	2.3	2.3 (43)	10	0.0 (30)
P-A	7.0	4.7 (43)	7.0	0.0 (43)
P-D	4.7	0.0 (43)	0.0	4.8 (42)
P-F	4.7	2.3 (43)	7.1	2.4 (42)
P-N	2.3	0.0 (43)	8.3	5.6 (36)
Overall test	17.2 ***	1.5 (860)	12.6 ***	2.7 (851)

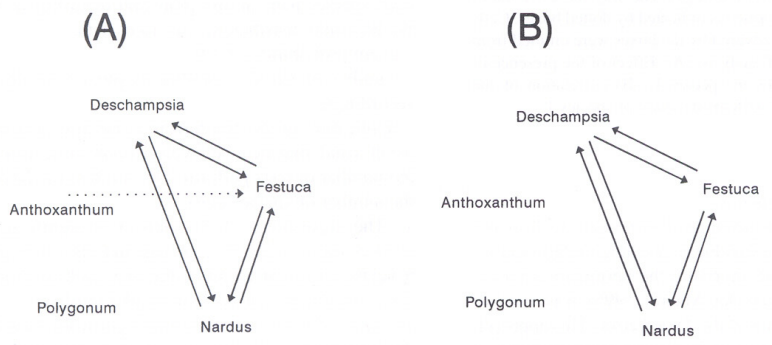

Fig. 2. Correlated changes of species. A species at which an arrow is pointing decreases while the species from which the arrow is pointing increases. Significance level $P < 0.05$ (*Anthoxanthum* - *Festuca* $P < 0.10$). A - association measured by the Pearson correlation coefficient, B - association measured by the φ coefficient.

Fig. 3. Idealized structure of the grassland stand.

A closer analysis of the number of significant results within species pairs revealed that some species pairs showed negatively-correlated behaviour much more often than expected on the random basis (Table 1), though no significant correlation was found in more than half of the possible cases (see Table 1). Many species showed the number of correlations significant at the Bonferroni corrected significance level $P = 0.05$. The log-linear analysis of the frequencies of significant responses within these pairs revealed only one significant relationship with plot: *Deschampsia-Festuca* (Table 1) and none with season. *Deschampsia, Festuca* and *Nardus* occurred in the negatively correlated pairs more often than *Anthoxanthum* or *Polygonum* (Fig. 3).

As expected from the overall test, pairs with consistently positively correlated behaviour were much more rare. Some pairs showed it more frequently than expected, but nowhere was the probability of the number of occurrences from the appropriate binomial distribution lower than the Bonferroni-corrected significance level $P = 0.05$.

Discussion

Limitations of the approach

Since the dataset is multidimensional (five species), but it is studied only by two-dimensional projections, confusion of the direct species-to-species interactions with compound effects involving more than two species may be possible (Wooton 1993). However, since the number of species is rather low (the median and mode of the species number per cell is 2; the average ranges around 2.5), the likelihood of the compound effects is low.

Another potentially serious limitation comes from different quantities of the four studied species and their different spatial patterns. Since the power of the tests to detect species replacements depends on the number of cells occupied, the power is different for each species pair in each plot. The tests performed at the same nominal probability of the Type I error, have different probabilities of the Type II error. This limitation is difficult to remedy; we believe that this is not a serious obstacle, since the frequencies of the component species, though different, are never extremely low, which would make the test very weak. Further, precise estimation of the power is generally unattainable (Toft & Shea 1983) and in this respect this study does not differ from other ecological studies.

Functional differentiation within the community

The structure of the replacement graphs shows at least two 'functional groups' of species within the community. The high frequency of significant reciprocal replacements between *Deschampsia, Festuca* and *Nardus* identifies these species as essentially using the 'same space' within the community. These species also show the slowest spatial dynamics (Herben et al. 1995a) and may be considered to form the 'matrix' of the community. Though using the space in the same way, their growth form is rather different (Fig. 3), ranging from the tussocky *Nardus* to rhizomatous tussocky *Deschampsia* and *Festuca*.

At the level of replacements, the other two species seem to behave independently of the former three. *Anthoxanthum* is a fast-growing species with high shoot turnover, high seedling recruitment and high spatial dynamics (Durasová unpubl. data; Herben et al. 1995a). In contrast to the three 'matrix' species this species penetrates through the matrix of them, both by seedlings and vegetative tiller growth, probably at a much faster rate than the other species (Fig. 3). *Polygonum*, a dicot species, has an entirely different morphology and hierarchy of response than the grasses. It shows a strong plastic response at the level of leaf size and shoot size, but a much weaker response at the level of leaf number. Its below-ground morphology seems to be almost independent of the presence of any grass species, but it seems to show a strong response to rhizome size (Pecháčková unpubl.), which cannot be detected directly by shoot counts only. This species also recruits new plants from seeds.

Anthoxanthum and *Polygonum* also show less detectable correlations with weather variables than the former three (see Herben et al. 1995b). They clearly belong to functional groups different from the group of *Deschampsia, Festuca* and *Nardus*. However, the fixed spatial resolution of 3.3 cm × 3.3 cm and the temporal resolution of one year limit the possibility to identify other processes operating at different scales. This concept of the functional differentiation within the community is fully scale-dependent.

The prevalence of negatively-correlated changes, i.e. one species replacing another, seems to support the idea of an internal structuring in the community (see Wilson & Roxburgh 1994; Wilson 1995). Several studies of the fine-scale pattern in grasslands have shown a limitation to the number of species at plot sizes around 1 cm^2 (Watkins & Wilson 1992). Though this limitation has been attributed to the limitation of the number of modules per plot of such a small size and thus may be only a statistical artifact (Watkins & Wilson 1992; Lepš 1995; van der Maarel et al. 1995), simulation studies show this need not always be the case (Klimeš 1995). At any rate, if there is a limitation of the species number per small plot, the fine-scale spatio-temporal patterns should take the form of correlated increases vs. decreases in any stationary system.

However, observation of the process without support of manipulative experiments can hardly provide evidence for the underlying mechanism and distinguish between the mechanistic effect of competition and the statistical effect of the module number limitation (Hastings 1977; Goldberg 1990; Lepš 1990). In the studied grasslands, a removal experiment in the same grasslands revealed changes in species density and spatial behaviour (Herben et al. subm.) when one species of the system was removed. This demonstrates that the species in the system do compete. Still, such an experiment can hardly demonstrate the actual role of competition in shaping the community. Law et al. (1993) argued persuasively that competition, though experimentally demonstrable, need not necessarily play an important role in chalk grasslands. Their contention is that in the natural range of densities, the species' response curve to density is too flat to cause any response to changes in density. If this is also true for the grassland under study, the replacements may result from processes other than competition, even if the species are involved which compete with each other.

However, the negative correlation of change does not concern *Polygonum* and *Anthoxanthum*. Hence only the three former species – *Deschampsia, Festuca* and *Nardus* – are subject to some structuring process; it does not matter whether this process takes the form of a limited number of modules per area or has a functional basis such as competition.

The studied grassland system is remarkably stable in spite of the pronounced fine-scale spatio-temporal change (Herben et al. 1993). The stability of the system depends, among other things, on the regularity of the species-species replacements. The information on their regulation is very limited and variation in the environment (e.g. weather variation) can play an important role here (Fowler 1990; Hara 1993, 1994). Interestingly, some correlations between species performance and weather variables are opposite for *Deschampsia* vs. *Festuca*, for example new shoot formation and June temperature, see Herben et al. (1995b).

In contrast to correlated changes (replacements), there is almost no structure in the correlation of change vs. presence of the conditioning species. The quantity of any species *per se* is probably not a good predictor of its future behaviour, and thus also of the correlation with the change of another species.

Can interactions in the system be species-specific?

The replacements detected by the current study could result from several mechanisms (competition, growth form of component species, intrinsically limited module life span, etc.). However, if interspecific competition is one of the factors determining their frequency, the partial species-specificity of these replacements may seem to be at odds with the concept of diffuse competition between plants (see Goldberg & Werner 1983; Keddy 1990). Is there any reason to believe that the competitive interactions in this system have an additional species-pair specific component?

Whereas most of the data on vertical competition (overtopping) show it is primarily influenced by plant

size (Keddy 1990; Gaudet & Keddy 1995), this is not necessarily true for spatial spreading (horizontal competition). There is some evidence that grasses may indeed show some species-pair specificity in spatial spreading. Both Thórhalsdóttir (1990b) and Silvertown et al. (1994) showed that the ability of a grass to invade its neighbour's space and the resistance to invasion were uncorrelated; if the competition were species-pair unspecific, these quantities should be perfectly negatively correlated. An independent study performed in the studied grassland (Herben et al. subm.) also reports a certain species-specific type of response to neighbour removals in some grasses.

Therefore the species-specificity of interactions cannot be excluded. Though the overall role of competition in producing the replacements is unclear, the species specificity in competition may perhaps be sufficient to account for the structured replacements observed in this study. In reality, however, the fine scale of the species spatial pattern in grasslands could make the species-specific competition appear diffuse at the larger scale, since in a large sample, any species has all other species as its neighbours (Mahdi & Law 1987). The species specific effects could only be revealed by an analysis performed at a very fine spatial scale.

The existence of species specific interactions may have profound effects on community dynamics (Silvertown & Dale 1991). Notably, the spatially constrained competitive interactions will make the result of competitive processes dependent on species spatial pattern (Silvertown et al. 1992). Given that the interactions between species are intransitive, it may also be a powerful mechanism for species coexistence (Karlsson & Jackson 1981).

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