



Assembly rules during old-field succession in two contrasting environments

E. Ruprecht^{1,*}, S. Bartha², Z. Botta-Dukát² and A. Szabó¹

¹ Department of Taxonomy and Ecology, Babeş-Bolyai University, Republicii street 42, R-400015 Cluj Napoca, Romania. Fax: + 40264431858

² Institute of Ecology and Botany of the Hungarian Academy of Sciences, Alkotmány út 2-4, H-2163 Vácrátót, Hungary

* Corresponding author. E-mail: ruprecht@grbot.ubbcluj.ro

Keywords: Plant interactions, Soil, Spatial organization, Spatial scale, Species association, Structure.

Abstract: Studies addressing the question of how communities develop reported contrasting temporal patterns of species associations during succession. Several hypotheses were formulated about succession, but a general explanation of community assembly is missing. We analysed trends of species associations during old-field succession in two contrasting habitats: the first with chernozemic brown forest soil and temperate climate, and the second with sand soil and dryer climate. Significant pair-wise associations were calculated across a range of spatial scales. Comparing the two succession seres, one under harsh and the other under favourable environment, we attempted to make generalisations about species relation patterns. We found no trend but fluctuation in the level of community organization during succession. None of the existing succession models explained our results about changes in spatial structure of grassland communities during succession. Fluctuation in the number of significant associations was more intense and took longer under less favourable environmental conditions. Our results suggest that the stressed habitat type posed stronger constraints on species coexistence during succession than the favourable habitat did, but validating this hypothesis needs further investigations.

Nomenclature: Flora Europaea

Introduction

The question of how species infiltrate into a community, and the general principles of their co-occurrence are popular topics in community ecology attracting the interest of many plant and animal ecologists. These rules, known as 'assembly rules' since Diamond (1975), define how populations combine to form a community.

Most studies address the question of how species live together by explaining observed diversity patterns in different kinds of natural communities (e.g., Zobel 1992, Wilson et al. 1995, Weiher et al. 1998, Watkins and Wilson 2003). Fewer case studies deal with assembly rules during community formation and, interestingly, these investigations have led to different results (e.g., Hogeweg et al. 1985, O'Connor and Aarssen 1987, Lepš and Buriánek 1990, Myster and Pickett 1992, Gitay and Wilson 1995). From divergent concepts regarding changes in community structure during the process of community

formation Gitay and Wilson (1995) formulated testable hypotheses:

a) The 'gradient-in-time' hypothesis (Peet 1992) supposes that species are arranged along a temporal gradient based on their biological characteristics. In this way, the strength of spatial associations between species should not change with time, since species composition is controlled to an equal extent by environmental variation (Gitay and Wilson 1995);

b) According to the 'competitive-sorting model' (Peet 1992), the initial composition of a community after disturbance is a matter of chance, but as succession develops the community composition becomes more predictable. In this way, the number and strength of species associations will increase during succession (Gitay and Wilson 1995);

c.) The ‘three-phase’ model, formulated first by Greig-Smith (1952), delimits three phases at the level of community organisation during succession. In the first phase of succession the number of species associations is low because of random colonisation events. In the middle phase there is a well-marked non-randomness, a high number of associations appear that can be attributed to the environmental heterogeneity and interdependence between species. In the last phase of succession, there is very little interdependence of species again (Greig-Smith 1952).

These suggestions were based mainly on theoretical deductions supported by few case studies which applied various and often non-comparable methods, with different temporal and spatial scales. Although this topic has a long history of scientific research, our knowledge about changes in the spatial structure of plant communities in the course of succession is not yet crystallised in a generally operational theory. Finding a common concept would not have only theoretical significance, but it is becoming more and more indispensable for practice, especially in restoration ecology (Booth and Swanton 2002, Temperton et al. 2004). Since many attempts to create plant communities have failed, many ecologists plan to consider assembly rules in their restoration efforts in order to make the results more appropriate to their goals (Lockwood 1997).

Comparative studies, using the same sampling protocol and methodology, are needed in order to elucidate contradictory perceptions about the changes in fine-scale vegetation structure during community formation and to explore general trends. Here we make an attempt at finding common trends in species associations during old-field succession by comparing two seres from contrasting (a favourable and a harsh) environments.

Plot size influences the probability of finding a given species combination (Podani et al. 1993), because spatial patterns and underlying mechanisms are scale dependent (Wiens 1989), as well as the scale at which the association between two species can be revealed is influenced by the frequency of the species. Studies restricted to a single (often the finest) scale, or to a few arbitrarily chosen scales only, will not succeed in exploring all the possible associations between species, thus considerable information about community structure may remain hidden (Bartha and Kertész 1998).

In this study, we compare trends in plant-plant associations during grassland formation in two sites with contrasting environmental characteristics: on sand soil and semiarid, warm temperate climate (Fülöpháza, Hungary)

and on chernozemic brown forest soil with clayish substrate under the temperate continental climate (Suatu, Romania). Non-randomness in pair-wise plant associations based on presence/absence data was revealed and the proportion of significant associations was calculated in a series of gradually increasing scales in different stages of succession. The objective of this study is to answer the following question: Which of the existing models of succession is effective in explaining patterns during grassland formation?

Materials and methods

Study sites

Suatu (46°46'N, 23°58'E, 328-485 m a.s.l.) is in the central part of the Transylvanian Lowland (Câmpia Transilvaniei), Romania. The natural vegetation is forest-steppe/forest with a mixture of oak and oak-hornbeam woodlands, semi-dry grasslands and dry steppes. Soils are chernozemic brown forest soils mostly on clayish substrate, rich in nutrients and good water holding capacity (Jakab 1972). The climate is temperate continental; mean annual precipitation is 615 mm, maximum precipitation occurring in June, July, and August; mean annual temperature is 8.5 °C (Kun et al. 2004).

Secondary succession on abandoned agricultural fields was followed by investigating fields abandoned 1, 4, 6, and 14 years ago. The date when the fields were abandoned (2003, 2000, 1998 and 1990, respectively) was obtained by asking landowners. For the purpose of having a reference for the possible endpoint of succession, a semi-natural grassland was also investigated. The reference grassland studied was closed, dominated by *Festuca rupicola*, and it was used as a pasture for cattle. All the fields and the reference grassland were situated within a 2.5 km × 2.5 km area. General succession characteristics based on data about vegetation closure (total cover and total frequency of species), species number and the length of the period annuals dominate in the studied time interval are given in Table 1.

Fülöpháza (46°52'N, 19°24'E) is in the Kiskunság National Park, on the Danube-Tisza Interfluve, central part of Hungary. The natural vegetation is forest-steppe with a mixture of sand steppes, oak woodlands, open sand grasslands, and meadows in the depressions. Soil is blown sand and humous sandy soil of alkaline reaction, high carbonate content (CaCO₃, MgCO₃) (Várallyay 1993) and low humus content (0.66% in the 0-10 cm of soil) (Kovács-Láng et al. 2000). The climate is warm temperate, with sub-Mediterranean influence; mean annual precipitation is 517 mm, maximum precipitation occurring in

Table 1. Some important vegetation characteristics during succession in the sites studied. Total frequency is the summed frequency value of each species from a transect. Vegetation cover is the sum of cover values for all species present.

Environment	Time interval (years)	Vegetation cover*	Total frequency of species / transect	Dominance of annuals*	Total species number / transect	Speed of succession*
Favourable	1-14	85-130%	103-403	1 year	35-65	Fast
Stressed	2-36	50- 70%	82-178	5 years	17-27	Slower

*Data obtained from Ruprecht (2005) for the favourable environment (Suatu) and Csecserits and Rédei (2001) for the stressed environment (Fülöpháza).

May and November, mean annual temperature is 10.3 °C. The duration of the semiarid period is four month, thus the climate is strongly semiarid (Borhidi 1993). There are strong seasonal and daily fluctuations in temperature and air humidity and uneven temporal distribution in precipitation (Várallyay 1993).

Secondary succession on abandoned agricultural fields was followed by investigating fields abandoned 2, 7, 28, and 36 years ago. The date when the fields were abandoned (2000, 1995, 1974 and 1966, respectively) was obtained by analysing aerial photographs originating from different years. The reference grassland studied was an open sand grassland dominated by *Festuca vaginata*, typical for the Danube-Tisza Interfluve. All the fields and the reference grassland were situated within a 1.5 km × 0.5 km area.

Vegetation sampling

At both sites, old-fields of different ages were sampled including a reference grassland that represents the possible end-point of the studied succession seres. The smallest scale was chosen so as to correspond to the average size of plant individuals or ramets. In order to have multiple replicates, 1040 microquadrats of 0.05 m × 0.05 m size were sampled contiguously along a 52 m long circular belt transect, one transect in each old-field and grassland. Sampling was made in May 2004 at Suatu, and May 2002 and 1997, respectively, in the case of the old-fields and the grassland at Fülöpháza. Presence of species was recorded in each microquadrat. We took the samples from homogeneous vegetation patches in order to exclude large-scale heterogeneity, thus we considered our samples stationary. Old-fields and reference grasslands from a site were chosen in a way to have the same habitat conditions: slope angle, exposure, soil type, moisture conditions. Chronosequences were compiled in each case and vegetation characteristics were followed through time.

Data analysis

Spatial associations were computed between two species (*A* and *B*) by the maximum likelihood Chi-square statistic (the mutual information between the species) calculated from 2 × 2 contingency tables (Kullback 1959, Legendre and Legendre 1998):

$$I(A,B) = 2*[m \ln m + a \ln a + b \ln b + c \ln c + d \ln d - (a+c)\ln(a+c) - (b+d)\ln(b+d) - (a+b)\ln(a+b) - (c+d)\ln(c+d)]$$

where *a*, *b*, *c* and *d* correspond to the notations of the 2 × 2 contingency table, and *m* is the sample size. Note that $0 \leq I(A,B) \leq 2m \ln m$.

In order to evaluate species coexistence or avoidance, we applied a null model showing the expectation in a random situation, and tested the statistical significance of departure from this expectation. All possible associations under the null model were generated by systematic, step-by-step shifting. In case of each species pair, the spatial position of one of the species was shifted step-by-step in relation to the other species along the circular transect. Shifting maintained the spatial pattern of each species, but changed the relative (interspecific) positions of the species (Fig. 1, Palmer and van der Maarel 1995, Bartha and Kertész 1998). The relatively small number of different relative positions (1040) of two species made the use of systematic shifting possible. It is better than random shifting because it generates all possible cases under the null hypothesis.

Probability of Type I error was expressed as the relative frequency of associations in the null model which were equal to or higher than the observed one (Legendre and Legendre 1998). Critical value for significance was 0.05. We made multiple comparison thus the experiment-wise error rate (Rice 1989) and false discovery rate (Verhoeven et al. 2005) were higher than 5%. The pair-wise associations are not independent from each other, thus the usual corrections cannot be applied. Therefore, the 10

Table 2. The 10 most abundant species included in the analysis of the Suatu transects. After species names in the Cat. column a combined category is indicating the life form (first letter) and forb (F) or graminoid (G) status (second letter) of the species. Life form categories are: a (annual), b (biennial) and p (perennial). Species relative frequencies are given in case of each transect. G: reference grassland.

Species	Cat.	Years since abandonment				
		1	4	6	14	G
<i>Papaver rhoeas</i>	aF	15.58				
<i>Elymus repens</i>	pG	13.46	76.25	15.77		
<i>Setaria pumila</i>	aG	12.02				
<i>Stachys annua</i>	aF	9.90				
<i>Convolvulus arvensis</i>	pF	9.33	24.04			17.60
<i>Crepis foetida</i> ssp. <i>rhoeadifolia</i>	aF	8.94				
<i>Matricaria perforata</i>	aF	8.08				
<i>Consolida regalis</i>	aF	3.27				
<i>Conyza canadensis</i>	aF	2.40	35.00			
<i>Bifora radians</i>	aF	2.12				
<i>Hieracium praealtum</i> ssp. <i>bauhinii</i>	pF		28.27	13.37		
<i>Anthemis arvensis</i>	aF		9.71			
<i>Oxalis stricta</i>	aF		8.17			
<i>Cichorium intybus</i>	bF		8.17			
<i>Symphytum officinale</i>	pF		5.96			
<i>Arenaria serpyllifolia</i>	aF		5.67			
<i>Lactuca serriola</i>	aF		4.90			
<i>Koeleria macrantha</i>	pG			41.83	34.90	23.37
<i>Leontodon hispidus</i>	pF			20.29	33.17	
<i>Medicago lupulina</i>	aF			14.52		
<i>Festuca pratensis</i>	pG			13.65	34.62	24.71
<i>Daucus carota</i>	bF			13.65		
<i>Plantago lanceolata</i>	pF			12.98	20.77	
<i>Trifolium repens</i>	pF			12.60	22.69	
<i>Trifolium arvense</i>	aF			11.25		
<i>Achillea collina</i>	pF				58.17	36.35
<i>Festuca rupicola</i>	pG				29.14	80.87
<i>Thymus pannonicus</i>	pF				20.67	37.02
<i>Plantago media</i>	pF				15.77	
<i>Dorycnium pentaphyllum</i> ssp. <i>herbaceum</i>	pF				13.08	
<i>Medicago sativa</i> ssp. <i>falcata</i>	pF					24.33
<i>Elymus hispidus</i>	pG					15.87
<i>Thesium linophyllum</i>	pF					15.39
<i>Filipendula vulgaris</i>	pF					14.04

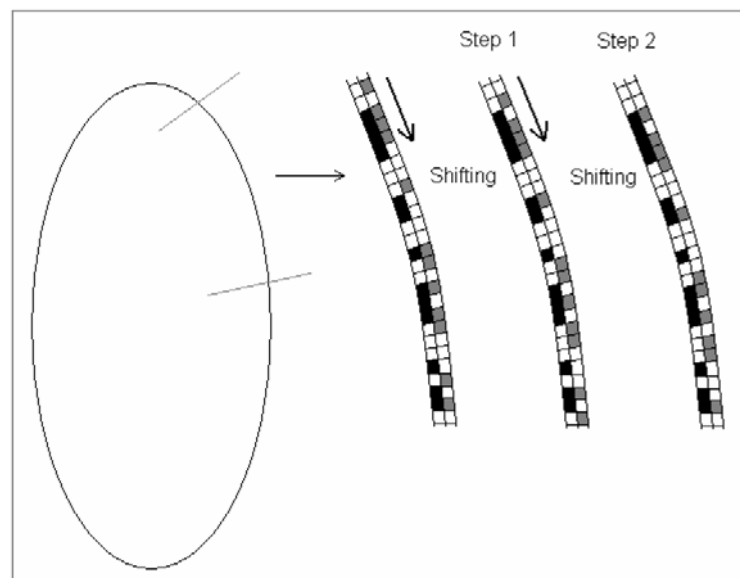


Figure 1. Systematic step-by-step shifting the spatial position of one species from a pair (species 1: grey) in relation to the other species (species 2: black) along the circular transect. The first two steps of the shifting procedure are presented on the figure.

Table 3. The 10 most abundant species included in the analysis of the Fülöpháza transects. After species names in the Cat. column a combined category is indicating the life form (first letter) and forb (F) or graminoid (G) status (second letter) of the species. Life form categories are: a (annual) and p (perennial). Species relative frequencies are given in case of each transect. G: reference grassland.

Species	Cat.	Years since abandonment				
		2	7	28	36	G
<i>Bromus tectorum</i>	aG	96.64	5.10			
<i>Cerastium semidecandrum</i>	aF	34.90				2.50
<i>Arenaria serpyllifolia</i>	aF	15.48		3.27	7.12	18.75
<i>Silene conica</i>	aF	11.54	1.83			
<i>Crepis foetida</i> ssp. <i>rhoeadifolia</i>	aF	3.94	3.65			
<i>Ambrosia artemisiifolia</i>	aF	3.27				
<i>Secale sylvestre</i>	aG	2.02				
<i>Cynodon dactylon</i>	pG	2.02	2.69			
<i>Medicago minima</i>	aF	1.83	8.75			
<i>Bassia laniflora</i>	aF	1.64	41.25	6.25	4.33	14.62
<i>Poa angustifolia</i>	pG		84.71			
<i>Elymus repens</i>	pG		13.37			
<i>Festuca pseudovina</i>	pG		3.94			
<i>Bromus hordeaceus</i> ssp. <i>hordeaceus</i>	aG		2.21			
<i>Festuca vaginata</i>	pG			44.52	64.42	48.08
<i>Stipa borysthenica</i>	pG			6.44		15.19
<i>Polygonum arenarium</i>	aF			6.15	5.39	
<i>Dianthus serotinus</i>	pF			4.90		
<i>Fumana procumbens</i>	pF			3.08		12.31
<i>Artemisia campestris</i>	pF			2.31		
<i>Salsola kali</i> ssp. <i>ruthenica</i>	aF			1.35		1.64
<i>Minuartia glomerata</i>	aF			1.25	3.85	
<i>Equisetum ramosissimum</i>	pF				7.69	
<i>Dichanthium ischaemum</i>	pG				5.10	8.37
<i>Eryngium campestre</i>	pF				2.89	
<i>Teucrium chamaedrys</i>	pF				2.79	
<i>Syrenia cana</i>	pF				2.69	
<i>Poa bulbosa</i>	aG					34.23
<i>Conyza canadensis</i>	aF					2.12

most abundant species were included in the analyses in case of each transect (Tables 2 and 3) in order to equalize the number of tests performed. Thus experiment-wise error rate and false discovery rate were set to be the same in each analysis. None of the species included in the analyses had a frequency less than 1%.

All statistics were calculated across a range of scales from 0.05 m × 0.05 m to 0.05 m × 2 m by merging two, then three, then four, ..., and finally 40 consecutive plots by subsequent computerised sampling in 14 spatial steps. This was an automated procedure for taking simulated units from an appropriate sampling universe (Podani 1987). In this way, we calculated species associations in a series of gradually increasing plot sizes. Using a series of spatial scales but remaining within a smaller scale interval we hope to approach the total number of possible species associations without crossing the border between two hierarchy levels or a boundary of large-scale spatial heterogeneity.

The number and the proportion of significant associations (proportion = % of the total possible paired associations) appearing in any of the scales was calculated for each old-field and grassland, and a temporal sequence was compiled.

Results

In case of both succession seres studied, in the beginning of the process there were mostly short-lived species present, while in the middle and later stages it was characteristic that perennial grasses became dominant together with a high frequency of some subordinate forbs (Tables 2 and 3). Under harsh environmental conditions at Fülöpháza, vegetation was open, with a low total frequency of species even in the middle and later stages of succession, while in case of Suatu (more favorable environment) the species frequencies were low only in the first year, and vegetation became more closed during the process (Tables 1, 2 and 3).

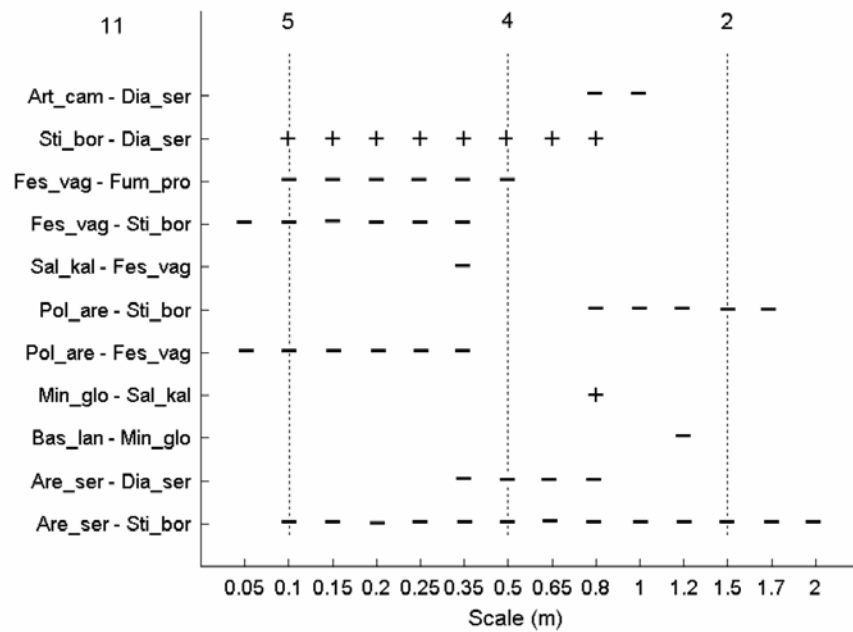


Figure 2. The total number of significant ($p < 0.05$) paired associations between 10 species is 11 in the case of the 28 year old field at Fülöpháza, when calculated at multiple spatial scales. Scale is given in the figure as the length (m) of the sampling unit, width is constantly 0.05 m. On the y axis the significant associations between species pairs are given. Species are: *Arenaria serpyllifolia* (Are_ser), *Stipa borysthena* (Sti_bor), *Dianthus serotinus* (Dia_ser), *Bassia laniflora* (Bas_lan), *Minuartia glomerata* (Min_glo), *Salsola kali* ssp. *ruthenica* (Sal_kal), *Polygonum arenarium* (Pol_are), *Festuca vaginata* (Fes_vag), *Fumana procumbens* (Fum_pro), *Artemisia campestris* (Art_cam). Significant positive (+) and negative (-) associations are marked on the figure. If we use one arbitrarily chosen scale (dotted vertical lines), we will find, for example, 5 ($0.05 \times 0.1 \text{ m}^2$), 4 ($0.05 \times 0.5 \text{ m}^2$), or 2 ($0.05 \times 1.5 \text{ m}^2$) associations only.

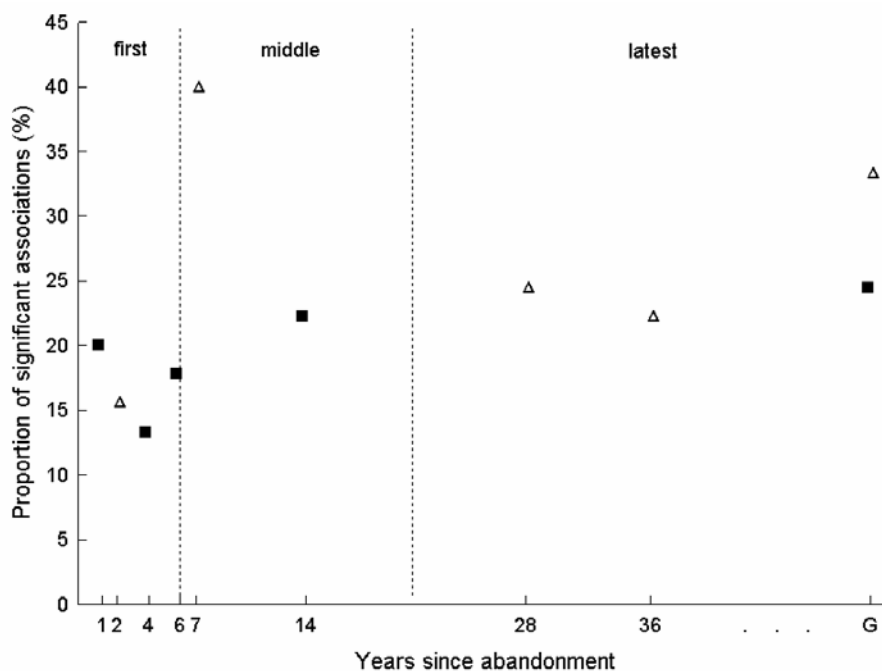


Figure 3. Proportion of significant ($p < 0.05$) plant-plant associations (% of all possible paired associations) during grassland succession in the studied sites. Full squares = favourable habitat, chernozemic soil (Suatu); open triangles = stressed habitat, sand soil (Fülöpháza); G = the grassland used as reference. Different aged old-fields and reference grasslands are arranged in three main time intervals (delimited by dotted lines) corresponding to the main stages of succession: first, middle and latest.

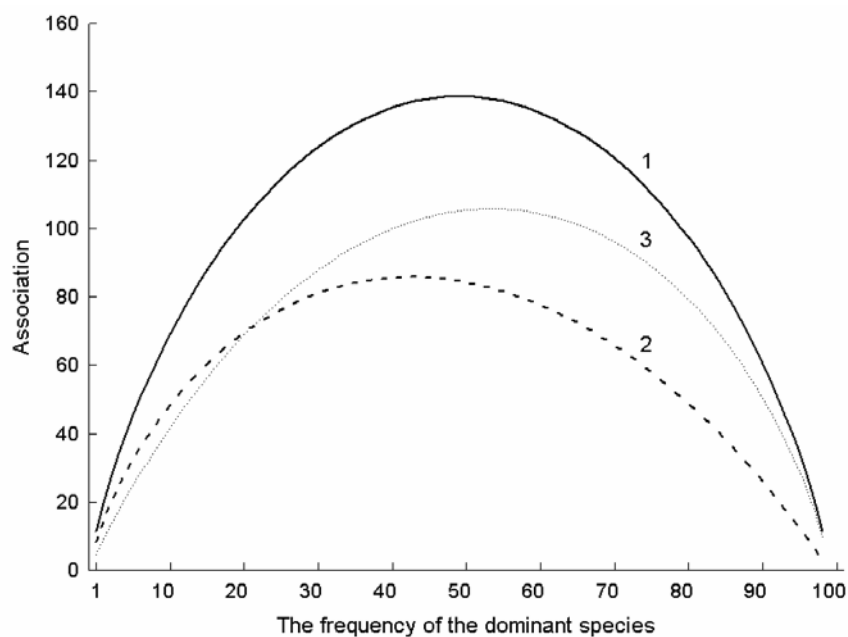


Figure 4. Association between two species, a dominant (high frequency) and a subordinate (low frequency), depends on the strength of the effect the dominant has on the subordinate species and also on the probability of occurrence of the dominant. Three cases are presented on simple, non-spatial artificial data: (1) the subordinate cannot establish in the presence of the dominant, but given its high dispersal ability, it occurs in every locality where the dominant is missing; (2) the dominant is strongly inhibiting the occurrence of the subordinate (the probability of establishment is 20%), meanwhile the subordinate can occur in every locality, where the dominant is missing; (3) the subordinate cannot establish in the presence of the dominant, but when the dominant is missing, the establishment probability of the subordinate is only 90%. The subordinate cannot affect the occurrence of the dominant, thus the strength of the interaction between the two species depends on the degree the presence of the dominant is inhibiting the probability of occurrence of the subordinate. The dominant is conceived as biotic environment of the subordinate, thus the degree of environmental heterogeneity depends on the frequency of the dominant. The strength of the association between the two species (the degree of vegetation heterogeneity) reaches its maximum, when the frequency of the dominant is approximately 50%. If the dominant has very low or very high frequency, the heterogeneity is low (Botta-Dukát and Bartha, in preparation).

On average, 18.3% (Suatu) and 25.5% (Fülöpháza) of the possible species combinations were significant in the studied succession seres. Applying multiple spatial scales was more advantageous for approaching the total number of paired associations than using only one, arbitrarily chosen scale, which we demonstrate here on one data set (Fig. 2).

We found no monotonic trend in the proportion of species associations during succession ('gradient-in-time' hypothesis, 'competitive-sorting model'), and if the studied stages were arranged in three main time intervals (first, middle, latest) in order to test the 'three-phase model' also, no unimodal relationship could be observed. In both sites, the proportion of significant associations fluctuated in time (Fig. 3). The fluctuation was moderate at Suatu and intense at Fülöpháza, and the proportion of significant associations in the succession sere on sand (Fülöpháza) in the 7th, 28th year and in the case of the reference grassland was higher than in any stage of the succession sere on chernozemic soil from Suatu (Fig. 3).

Discussion

Associations between plant species originate not only from direct species interactions; in fact, they express the spatial heterogeneity of vegetation. Thus, a great deal of spatial constraints do not result from plant-plant interactions but from spatial segregation due to dispersal limitation or environmental heterogeneity (Greig-Smith 1983, Dale et al. 1991). Using a shifting null-model we could filter out spatial relations originating from the aggregated distribution of plant species. Some studies use spatially restricted models (e.g., patch-based null model) to filter out environmental effects (patchiness) from the resulting patterns (Watkins and Wilson 1992, Wilson and Gitay 1995) in the hope of obtaining only the real or direct interactions (e.g., competition, facilitation) between species.

Environmental heterogeneity can be caused by abiotic and biotic factors. Accompanying species are also part of the environment if they affect the spatial distribution of

the studied species. Thus, the frequency of species forming the biotic environment will also influence the number of significant associations of the studied species (Fig. 4). The abiotic environment changes during succession (e.g., Vitousek and Walker 1987, Osbornová et al. 1990), but abiotic changes are generally caused by the species present (e.g., nitrogen-level of the soil depleted by a species, or light interception affected by shading). Thus, the temporal and spatial heterogeneity of the abiotic environment is closely connected with the heterogeneity of the biotic environment. Separating these two components of the environment is arbitrary and often impossible. Therefore, we consider that assembly rules originate not only from direct plant-plant interactions but more generally from environmental constraints.

Common trends in community organization during old-field succession

We found no monotonic or regular trend in species coexistence during succession. The only pattern common to both seres is that there is a fluctuation in the proportion of significant associations. None of the succession models presented in the introduction explains our results on trends of pattern development. In the following, we recall three theories and analyse why our results are different from the expectations.

According to the ‘gradient in time’ hypotheses summarized by Peet (1992), “because species differ from each other, the success of species will change continuously along an environmental gradient”. This concept supposes, that “the successional sequence should be orderly in the sense that there are sets of allowable species for any point along the sequence” (Lawton 1987, Tilman 1988). Changing environmental conditions (e.g., nutrient depletion) will govern succession, and the strength of spatial associations between species will not change during this process (Gitay and Wilson 1995). This hypothesis presumes that environmental factors are changing with the same rate in the whole area, but in reality, changes in the environmental conditions take place heterogeneously in space and time (e.g., Pickett et al. 2001).

The ‘competitive sorting model’ states, that “the initial composition of a community is unpredictable..., few individuals are present and competition is low. However, as population sizes increase during succession, competition intensifies” (Peet 1992). This hypothesis was initially developed from the observation made by Margalef (1963, 1968) on marine phytoplankton. This model presumes that the environmental heterogeneity is constant during succession. In the first phase of succession plant species can hardly render environmental heterogeneity because

dispersal limitation, thus the initial composition is a matter of chance. Later, the community structure becomes more and more predictable, since species are arranged based on their adaptations to particular site conditions. Contrary to the presumption of this model, environmental heterogeneity is changing through succession (Armesto et al. 1991) mainly because aggregated pattern of dominant species makes heterogeneity in the environment of subordinates.

In the ‘three-phase model’, the initial species composition is said to be unpredictable because random colonisation of species. In the second phase there is a larger-scale heterogeneity when species are arranged in discrete patches of the environment based on their requirements (sharing with each other a patch or avoiding each other by occupying different patches). In the final phase, heterogeneity is small or very small-scaled (Greig-Smith 1952). That is why the degree of community organization follows a unimodal curve during secondary succession. This relationship is explained as being governed by changes in the scale of environmental heterogeneity during succession, as well as by the strength of direct effects of species to each other (Greig-Smith 1952). This hypothesis, approaching a more elaborated concept about succession, is still oversimplified, because it distinguishes only three phases during this process. We consider that there are several phases during succession (‘multiple phase model’ cf. Bartha et al. 2000), and the environmental heterogeneity is continuously changing in space and time with successive phases of increasing and decreasing heterogeneity, giving rise to a fluctuating pattern at the level of community organization.

Results of earlier case studies are diverse, supporting some of the theoretical models. Hogeweg et al. (1985) found increasing trend in the number of species associations during succession (supporting the ‘competitive sorting model’). Others delimit characteristic phases during this process (Greig-Smith 1952, Gitay and Wilson 1995; supporting the ‘three-phase model’). There are studies reporting monotonously decreasing trends in the number and strength of species association (Aarssen and Turkington 1985, O’Connor and Aarssen 1987, Myster and Pickett 1992). We found no trend but fluctuation in the proportion of species associations during secondary succession. Our results are in line with the findings of Lepš and Buriánek (1990) and Bartha et al. (2000).

How can results be so different? One of the explanations can be the various spatial scales at which these studies were carried out. As we demonstrated, spatial scale influences the number of detected species associations (Fig. 2). Another explanation is that most of the studies men-

tioned above (including ours) characterise succession based on a few stages, and if the fluctuation in the level of spatial structure is the emerging characteristic of vegetation succession, choosing a few random points from a temporal sequence we can get potentially all kinds of temporal trends.

In our study, we found that ‘assembly’ and ‘disassembly’ phases are alternating (Belyea and Lancaster 1999) during secondary succession. This fluctuation in the level of community organization can be due to the temporal and spatial changes in environmental heterogeneity (e.g., changes in dominant species can have a strong influence on the structural characteristics of the vegetation, see Fig. 4).

Environmental differences

Fluctuation in the level of community assembly was more intense in the site with sand soil and dryer climate (harsh environment). One possible explanation is that in the semiarid environment, aboveground plant cover is discontinuous because the strong limitation of soil water, thus resource islands are formed beneath individual plants (Burke et al. 1998). Over time, colonization of new individuals (developing resource islands) and death of others (reduction in resources) can cause intense structural transformations by modifying spatial heterogeneity.

Based on our findings that the proportion of significant associations between species was higher in some stages of the succession under less favourable environment than during any stage of the succession under more favourable environmental conditions, we hypothesise that under harsh environmental conditions stronger assembly rules operate in the course of grassland formation (Wilson et al. 1995, Wilson and Whittaker 1995). However, demonstrating the general validity of our findings related to differences in community assembly between harsh and favourable environments, and revealing the causes of such differences needs further investigations.

Conclusions

In our study we analysed trends in species associations during old-field succession in two contrasting environments. The general view appearing in both seres analysed is that community structural characteristics are fluctuating during succession, and fluctuation rather than any regular trend in plant-plant associations is the characteristic feature of the succession process. We set up a hypothesis that under harsh environmental conditions assembly rules operating in the course of community

formation are stronger than under more favourable habitat conditions.

Acknowledgments. We thank N. Bauer, M. Deák, M. Enyedi, A. Fenesi, T. István, A. Kun, B. Lhotsky, B. Papp and T. Rédei for assistance during the field work, M. Kertész for his useful comments on an earlier draft and Kyle Kenyon for improving the English. E.R.’s work was supported by the Arany János and Domus Hungarica Foundation, and the Institute of Ecology and Botany of the Hungarian Academy of Sciences helped a lot by making her work possible there. We acknowledge the support of the National Development Program (NKFP 3B/0008/2002) and the Hungarian National Science Foundation (OTKA T 032630 and K 62338).

References

- Aarssen, L. W. and R. Turkington. 1985. Vegetation dynamics and neighbour associations in pasture-community evolution. *J. Ecol.* 73:585-603.
- Armesto, J. J., S. T. A. Pickett and M. J. McDonnell. 1991. Spatial heterogeneity during succession: a cyclic model of invasion and exclusion. In: J. Kolasa and S. T. A. Pickett (eds.), *Ecological Heterogeneity*. Springer-Verlag, New York, Inc. pp. 256-269.
- Bartha, S. and M. Kertész. 1998. The importance of neutral-models in detecting interspecific spatial associations from ‘trainsect’ data. *Tiscia* 31:85-98.
- Bartha, S., S. T. A. Pickett and M. L. Cadenasso. 2000. Limitations to species coexistence in secondary succession. In: *Proceedings IAVS Symposium*. Opulus Press, IAVS, Uppsala. pp. 55-58.
- Belyea, L. R. and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402-416.
- Booth, B. D. and C. J. Swanton. 2002. Assembly theory applied to weed communities. *Weed Science* 50:2-13.
- Borhidi, A. 1993. Characteristics of the climate of the Danube-Tisza Mid-Region. In: J. Szujkó-Lacza and D. Kováts (eds.), *The Flora of the Kiskunság National Park*. Hungarian Natural History Museum. pp. 9-20.
- Burke, I. C., W. K. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R. Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy and R. A. Gill. 1998. Plant-soil interactions in temperate grasslands. *Biogeochemistry* 42:121-143.
- Csecserits, A. and T. Rédei. 2001. Secondary succession on sandy old-fields in Hungary. *Appl. Veg. Sci.* 4:63-74.
- Dale, M. R. T., D. J. Blundon, D. A. MacIsaac and A. G. Thomas. 1991. Multiple species effects and spatial autocorrelation in detecting species associations. *J. Veg. Sci.* 2:635-642.
- Diamond, J. M. 1975. Assembly of species communities. In: M. L. Cody and J. M. Diamond (eds.), *Ecology and evolution of communities*. Harvard University Press, Cambridge. pp. 342-444.
- Gitay, H. and J. B. Wilson. 1995. Post-fire changes in community structure of tall tussock grasslands: a test of alternative models of succession. *J. Ecol.* 83:775-782.
- Greig-Smith, P. 1952. Ecological observations on degraded and secondary forest in Trinidad, British West Indies. II. Structure of the communities. *J. Ecol.* 40:316-330.
- Greig-Smith, P. 1983. *Quantitative Plant Ecology*, 3rd edition. Blackwell Scientific Publications, Oxford.
- Hogeweg, P., B. Hesper, C. P. van Schaik and W. G. Beefink. 1985. Patterns in vegetation succession, an ecomorphological study.

- In: J. White (ed.), *The Population Structure of Vegetation*. Dr W. Junk Publishers, Dordrecht. pp. 637-666.
- Jakab, S. 1972. Observații pedogeografice și pedomorfologice în Cîmpia Transilvaniei (Pedogeographic and pedomorphogenetic observations in the Transylvanian Plain). *Știința Solului* 10:55-69.
- Kovács-Láng, E., Gy. Kröel-Dulay, M. Kertész, G. Fekete, S. Bartha, J. Mika, I. Dobi-Wantuch, T. Rédei, K. Rajkai and I. Hahn. 2000. Changes in the composition of sand grasslands along a climatic gradient in Hungary and implications for climate change. *Phytocoenologia* 30:385-407.
- Kullback, S. 1959. *Information Theory and Statistics*. John Wiley and Sons, New York.
- Kun, A., E. Ruprecht and A. Szabó. 2004. Az Erdélyi-medence bioklimatológiai jellemzése (The bioclimatological characteristics of the Transylvanian Basin (Romania)). *Múzeumi Füzetek* 13:63-81.
- Lawton, J. H. 1987. Are there assembly rules for successional communities? In: A. J. Gray, M. J. Crawley and P. J. Edwards (eds.), *Colonization, Succession and Stability*. Blackwell Scientific Publications, Oxford. pp. 225-244.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*, 2nd English edition. Elsevier, Amsterdam, The Netherlands.
- Lepš, J. and V. Buriánek. 1990. Interspecific associations in old-field succession. In: F. Krahulec, A. D. Q. Agnew, S. Agnew and J. H. Willems (eds.), *Spatial Processes in Plant Communities*. SPB Academic Publisher, The Hague. pp. 31-47.
- Lockwood, J. L. 1997. An alternative to succession: Assembly rules offer guide to restoration efforts. *Restoration & Management Notes* 15:45-50.
- Margalef, R. 1963. On certain unifying principles in ecology. *Am. Nat.* 97:357-374.
- Margalef, R. 1968. *Perspectives in Ecological Theory*. University of Chicago Press, Chicago, Illinois.
- Myster, R. W. and S. T. A. Pickett. 1992. Dynamics of associations between plants in ten old fields during 31 years of succession. *J. Ecol.* 80:291-302.
- O'Connor, I. and L. W. Aarssen. 1987. Species association patterns in abandoned sand quarries. *Vegetatio* 73:101-109.
- Osbornová, J., M. Kováčová, J. Lepš and K. Prach (eds.). 1990. *Succession in Abandoned Fields. Studies in Central Bohemia, Czechoslovakia*. Kluwer Academic Publishers, Dordrecht.
- Palmer, M. W. and E. van der Maarel. 1995. Variance in species richness, species association, and niche limitation. *Oikos* 73:203-213.
- Peet, R. K. 1992. Community structure and ecosystem function. In: D. C. Glenn-Levin, R. K. Peet and T. T. Veblen (eds.), *Plant succession: Theory and Prediction*. Chapman & Hall, London. pp. 103-151.
- Pickett, S. T. A., M. L. Cadenasso and S. Bartha. 2001. Implications from the Buell-Small Succession Study for vegetation restoration. *Appl. Veg. Sci.* 4:41-52.
- Podani, J. 1987. Computerized sampling in vegetation studies. *Coenoses* 2:9-18.
- Podani, J., T. Czárán and S. Bartha. 1993. Pattern, area and diversity: the importance of spatial scale in species assemblages. *Abstracta Botanica* 17:37-51.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.
- Ruprecht, E. 2005. Secondary succession on old-fields in the Transylvanian Lowland (Romania). *Preslia* 77:145-157.
- Temperton, V. M., R. J. Hobbs, T. Nuttle and S. Halle. 2004. *Assembly Rules and Restoration Ecology. Bridging the Gap between Theory and Practice*. Island Press, Washington.
- Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, USA, New Jersey.
- Várallyay, Gy. 1993. Soils in the region between the rivers Danube and Tisza (Hungary). In: J. Szujkó-Lacza and D. Kovács (eds.), *The Flora of the Kiskunság National Park*. Hungarian Natural History Museum. pp. 21-42.
- Verhoeven, K. J. F., K. L. Simonsen and L. M. McIntyre. 2005. Implementing false discovery rate control: increasing your power. *Oikos* 108:643-647.
- Vitousek, P. M. and L. R. Walker. 1987. Colonization, succession and resource availability: ecosystem-level interactions. In: A. J. Gray, M. J. Crawley and P. J. Edwards (eds.), *Colonization, Succession and Stability*. Blackwell, Oxford. pp. 315-339.
- Watkins, A. J. and J. B. Wilson. 1992. Fine-scale community structure of lawns. *J. Ecol.* 80:15-24.
- Watkins, A. J. and J. B. Wilson. 2003. Local texture convergence: a new approach to seeking assembly rules. *Oikos* 102:525-532.
- Weihner, E., G. D. P. Clarke and P. A. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81:309-322.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3:385-397.
- Wilson, J. B. and H. Gitay. 1995. Limitations to species coexistence: evidence for competition from field observations, using a patch model. *J. Veg. Sci.* 6:369-376.
- Wilson, J. B. and R. J. Whittaker. 1995. Assembly rules demonstrated in a saltmarsh community. *J. Ecol.* 83:801-807.
- Wilson, J. B., M. T. Sykes and R. K. Peet. 1995. Time and space in the community structure of a species-rich limestone grassland. *J. Veg. Sci.* 6:729-740.
- Zobel, M. 1992. Plant species coexistence – the role of historical, evolutionary and ecological factors. *Oikos* 65:314-320.

Web site

Flora Europaea – <http://rbg-web2.rbge.org.uk/FE/fe.html> (accessed on 15 November 2006).

Received November 6, 2006
 Revised January 11, 2007
 Accepted February 16, 2007