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LANDSCAPE AND COENOLOGICAL DIFFERENTIATION OF *BRACHYPODIUM PINNATUM* GRASSLANDS IN HUNGARY

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Taxonomic nomenclature: Soó (1980)

Abstract. Secondary *Brachypodium pinnatum* grasslands are typical in low precipitation areas of Hungary after clearing of the oak forest. These grasslands contain steppe species and shade tolerant forest species in varying proportions. Quantitative results from the Institute of Ecology and Botany research site in the Gödöllő Hills support the proposition of an intense differentiation. For one thing, a spatial-floristic gradient is revealed. Along this, the representation of the forest species and that of the steppe species show opposite trends. A sharp hierarchical group structure is also revealed. This is characterised by the separation of the types dominated by forest species from other types dominated by the steppe species. While the two species groups tend to mutual exclusion under strong coenological and environmental selective pressures, interestingly, no evidence suggests that the species of the *Brachypodium pinnatum* grassland have an aggressive trait sufficient to endanger biodiversity. The paper presents the detailed results and also the description of analytical techniques.

Introduction

Arid and semiarid grasslands, characterised by *Festuca rupicola,* have wide distribution in the Carpathian Basin. Developmentally these grasslands represent mostly the final stage of secondary succession. The intermediate stage, with dominant *Brachypodium pinnatum,* is less common. Interestingly, the *Brachypodium pinnatum* grassland exists in the form of a stable, primary community as well, but only on dry, poor quality soils in oak openings, which Schmotzer & Vojtkó (1996) discovered.

Past *Brachypodium pinnatum* grassland research included sites abroad (Bobbink & Willems 1987, 1991, 1992, Bobbink *et al.* 1989, Willems 1990, Willems & Bobbink 1990 among others), and also in Hungary (Schmotzer & Vojtkó 1996, Varga-Sipos & Varga 1996). We draw attention to a strikingly "loose" syntaxonomic nomenclature:

Polygalo majori-Brachypodietum pinnati
Lino tenuifolio-Brachypodietum pinnati
Hypochoerio-Brachypodietum pinnati

(c.f. Dostal 1933, Klika & Hadac 1944, Wagner 1941, Soó 1964, 1968, Borhidi 1996). The confusion in this should not be surprising when we consider the usual local nature of the grassland studies.

The views regarding the ecological role of *Brachypodium pinnatum* grassland are conflicting. This is not surprising either, considering the broad differences in initial conditions in the sites, such as in the oak forest clearings (Soó 1959, 1964) at one extreme and abandoned vineyards (Baráth 1963) at the other extreme, possibly in different vegetation zones. The coenological tables in the mentioned works show varying levels of diversity and also extensive floristic differences among regions and sites. Questions thus are raised that, to be answered, require appropriate field surveys and data analysis, with focus upon community and patch level spatial pattern. Motivation for new research came also from recent suggestions regarding the substantial influence of the impact of the broader surroundings on local processes. We point in this regard to ornithological and botanical studies (Freemark & Merriam 1986, Raivio & Haila 1990, Pearson 1993, Rescia *et al.* 1997).

The objective of the present paper is to clarify the role of the coenological factors and landscape in population and community level selection within a study site. The data set is thus in part floristic and in part environmental. Different study scenarios could be conceived under the circumstances. We opted for stratification of the environment (landscape compartments), species populations (forest and steppe groups) and communities (vegetation types) as the first step, followed by data collection (in quadrats) and statistical analysis by appropriate methods. This scenario hands us a set of results that we can interpret and from which we are able to draw general principles about the *Brachypodium pinnatum* grassland.

Study site

We surveyed a roughly 0.3 km by 2 km stretch of land situated 25 km east of Budapest in the Gödöllő Hills (Fekete et al. 1996). The land surface in the area is 200-230 m above sea level. The site encloses one side of a valley with steep slopes and numerous side ravines. The climate is transitional between the continental climate of the Great Plain and the sub-continental climates of the mountains. The mean annual temperature at the site is 9°C and the mean annual precipitation is about 600 mm. Brown forest soils (chernozemic type) are typical on the loess substrate.

The oak *(Quercus pubescens)* forest of the site was cleared in the early 1900s (Military survey II. 1883, III. 1943). The forest fragments remaining in the site occur in the company of much scrub vegetation (mainly *Crataegus)* and grassland communities (mainly *Brachypodium pinnatum*). The vegetation is now categorised as a part of the Forest-Steppe Zone.

Data and methods

We completed field survey in 1992-1993 in the course of which we have taken phytosociological relevés of fifty-two 4m x 4m quadrats in *Brachypodium* grassland. In total we have 156 species. We give the presence-absence scores in Table 1 and a vegetation map with quadrat locations in Fig. 1. Other maps presented show variation of species richness (Fig. 2) and the number of forest and steppe species (Fig. 3a,b). The maps cover the NE facing side of the valley, drawn from aerial photographs (1:2000 scale) and quadrat data. We note that the cut-off patch size in the maps is 5 m across. Land surface characteristics such as steep slope segments and sharp ridges between the lateral ravines were the main criteria to guide the subdivision of the area into 10 landscape compartment units (Fig. 2). The southwest facing side of the ravines is extremely dry. Interesting to observe in the site also how effective is the influence of the lateral ridges in constraining the anthropogenic activities.

Data evaluations used cluster analysis, ordination techniques, and other statistical methods. Specifically, we present results from divisive association analysis (Podani 1979), seriation analysis (Podani 1993, 1994), canonical contingency table analysis (Orlóci 1991a), information analysis (Orlóci 1991b), and a new method of topological similarity/dissimilarity analysis (Appendix). In statistical inference we rely on randomisation testing (see the Appendix).

The coenological pattern in detail

It is seen from Fig. 1 that oak specimens occur sporadically as individual trees and also in groups on the site. *Brachypodium pinnatum* and *Bromus erectus* grassland types dominate in some parts of the site and *Crataegus monogyna* in other parts. We know that *Bromus erectus* spread quickly in the company of xerophilous steppe species after clear cutting. This grassland type does not represent a stable steppe vegetation and are gradually converted by natural processes into a *Festuca rupicola* grassland type which is the stable formation. Small patches of the latter also occur in the study site. In addition to the above-mentioned vegetation types, the steep south-facing slopes hold extensive stands of *Chrysopogon gryllus* and *Carex humilis*. These are typical in oak openings and represent a reservoir for steppe plants.

In the forest remnants, *Brachypodium pinnatum* forms the sparse undergrowth layer, closely resembling in physiognomy the xerothermic oak forests of the Pannonian region. Since *Brachypodium pinnatum* occurs in almost all of the forest remnants, we have no doubt that its presence in the open habitats can be explained by invasion from the forest. Characteristically, the *Brachypodium pinnatum* cover is complete in the non-forest sites.

The main compositional variants of the *Brachypodium pinnatum* grassland carry either the characteristic species of the dry Oak forest *(Quercetea pubescentis-petraeae)* or the xerophilous steppe. We found 23 species in the dry oak forest to which we will refer as "forest species". The most frequent of these include in order of decreasing frequency: *Betonica officinalis, Viola hirta, Campanula persicifolia, Carex michelii, Veronica chamaedrys, Campanula bononiensis, Trifolium alpestre, Chrysanthemum corymbosum, Dictamnus albus.* Only some of the *Brachypodium pinnatum* stands are able to preserve shade-tolerant forest species. Others become inundated by the invading xerothermic steppe species. The steppe variant includes 58 species from the *Festucetalia valesiacae Festuco - Brometea* of which the most common ones are: *Festuca rupicola, Medicago falcata, Veronica austriaca, Thalictrum minus, Adonis vernalis, Phleum phleoides, Astragalus onobrychis, Chamaecytisus austriacus, Euphorbia pannonica, Helianthemum nummularium ssp. obscurum.* We refer to this group as the "steppe species". Where *Crataegus monogyna* does not form a dense layer, it occurs in mixed types with *Brachypodium pinnatum* or *Bromus erectus* (Fig. 1).

Floristic gradient and coenological group structure in *Brachypodium* grassland

The general pattern of entries in Table 1 reveals a dominant one-dimensional floristic gradient. This gradient is marked by the shifting presence scores of the forest species and steppe species.

Presence-absence based clustering by divisive information analysis produced the dendrogram in Fig. 4. Two well-defined groups of quadrats are revealed: 30 without *Bromus erectus* (a shade intolerant species), but with forest species present, and 22 with *Bromus erectus* present. In the 30-quadrat group *Centaurea sadlerana* is responsible for the next

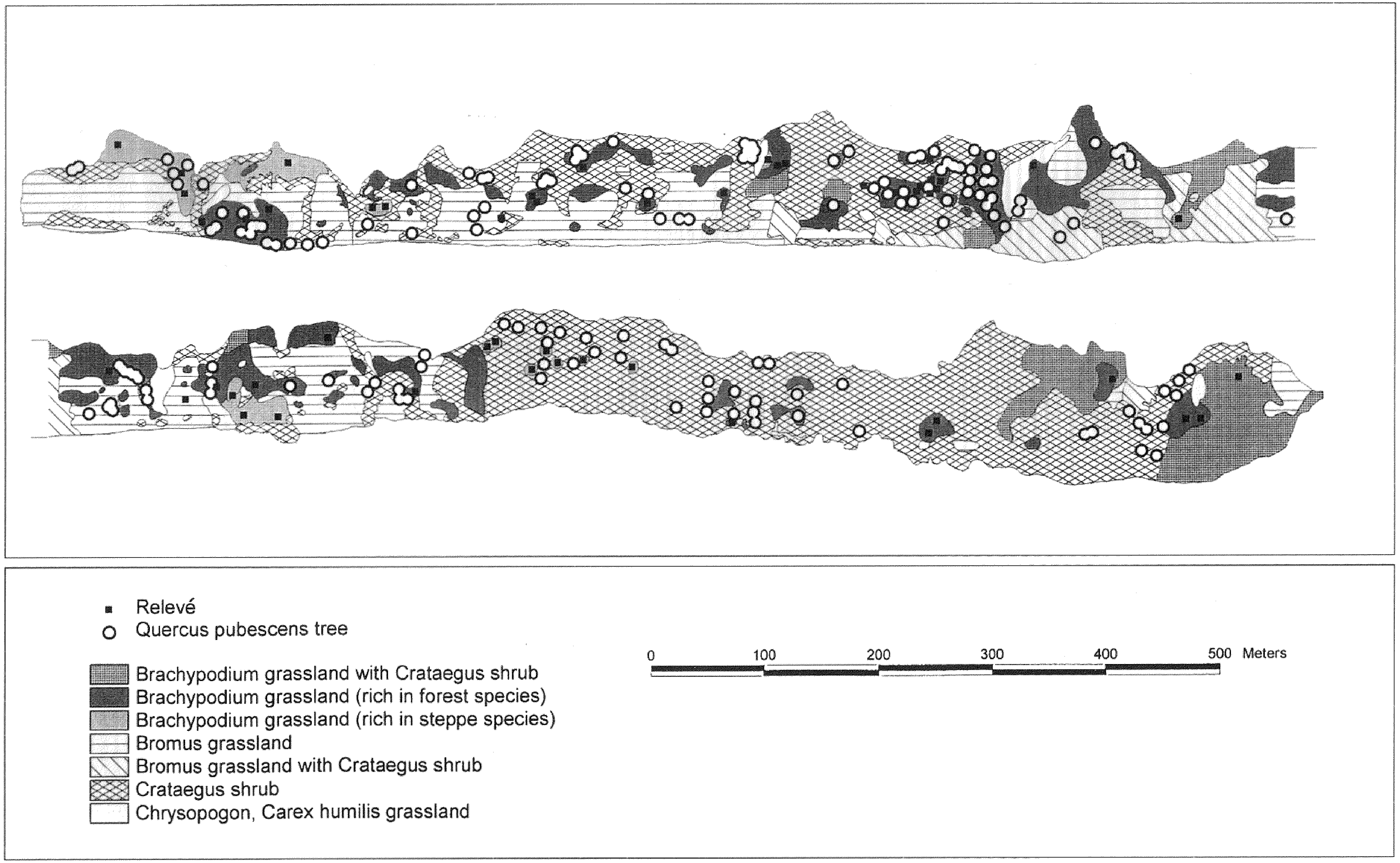

Figure 1. Vegetation map of the NE facing side of study area. Types are recognised by dominance.

Table 1. Phytosociological data matrix of 52 relevés arranged in order obtained by seriation analysis. Forest species: bold type. Steppe species: italics.

	23	4	1	20	2	27	22	51	33	35	15	44	21	5	43	36	45	6	31	26	32	29	28	7	12	30	10	52	49	8	18	47	3	46	37	24	14	13	41	39	11	16	48	38	9	40	17	34	50	19	42	25
Chrysopogon gryllus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stellaria graminea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linum catharticum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Medicago lupulina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thesium arvense	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scabiosa ochroleuca	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhinanthus minor	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bothriochloa ischaemum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Falcaria vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Briza media	0	1	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carlina vulgaris	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salvia pratensis	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrostis stolonifera	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Koeleria cristata agg.	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Luzula campestris	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leontodon hispidus	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthericum ramosum	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asparagus officinalis	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Vincetoxicum hirundinaria	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex caryophyllea	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex humilis	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium glaucum	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia pannonica	1	0	1	0	0	0	0	1	1	1	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bromus erectus agg.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asperula cynanchica	0	1	0	0	0	0	0	1	0	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola rupestris	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Helianthemum ovatum	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum serotinum	1	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chamaecytisus austriacus	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thlaspi jankae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veronica austriaca	0	0	0	0	0	1	1	0	1	0	0	1	1	1	1	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astragalus onobrychis	0	1	1	1	0	1	0	1	1	0	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium montanum	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dianthus pontederae	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscari comosum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Lotus corniculatus	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eryngium campestre	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Medicago falcata	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	1	0	1	0	0	0
Phleum phleoides	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	1	0	1	1	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Potentilla heptaphylla	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calamagrostis epigeios	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Achillea pannonica	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Thalictrum minus	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0
Hieracium bauhinii agg.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centaurea sadlerana	1	0	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Knautia arvensis	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Adonis vernalis	1	0	0	0	1	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0
Teuchrium chamaedrys	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	0	0	0	0
Seseli annuum	0	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0
Carex michelii	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Festuca rupicola	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	0
Filipendula vulgaris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0
Galium verum	0	1	0	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0	1	0
Campanula rotundifolia agg.	0	1	0	1	0	0	1	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0
Plantago media	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0

Verbascum speciosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thymus pannonicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachypodium pinnatum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Coronilla varia	1	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0
Fragaria viridis	1	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	0	0	1	1	0	0	1	0	1	1	0	0	1	0	1	1	0	0
Pimpinella saxifraga	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	0	1	0	0	0	0
Stachys recta	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Rumex acetosa	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	1
Ranunculus polyanthemos	0	0	0	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	0	0	1	1	0	0	1	1	1	1	1	1	0	1	1	0	0	1	1	0	0	0	1	1	1	0	0	1	1	0	1	1	0	0
Agropyron repens	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0
Campanula glomerata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0
Allium sphaerocephalum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrimonia eupatoria	1	0	1	0	0	0	1	0	1	1	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	0
Betonica officinalis	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	0	0	0	1	0
Arrhenatherum elatius	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	1	1	0	0	1	0	1	0
Salvia nemorosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dictamnus albus	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0
Viola hirta	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	1	0	1	1	1	0	0	1	0	0	1
Dactylis glomerata	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1	0	0	0	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	0	1	1	1	1	0	1	1	0	0
Veronica chamaedrys	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0
Crataegus monogyna	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	0
Sedum maximum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Hypericum perforatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dianthus collinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysanthemum corymbosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	0	1	1	0	0	1	0
Silene vulgaris	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	1	0	1	1	1	0	1	0	1	0	0	1	0	1	0	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
Euphorbia cyparissias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	1	0	1
Astragalus glycyphyllos	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Campanula persicifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	0	1
Viscaria vulgaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium alpestre	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0	0	1	1	1	0	1	0	0	0
Poa pratensis agg.	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	0	1	0	1	0	0	0	1	0	0
Quercus pubescens	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	1	1
Rubus fruticosus agg.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0
Allium paniculatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Rosa canina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Centaurea pannonica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Campanula bononiensis	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	1
Galium mollugo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Ajuga genevensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Clinopodium vulgare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	1	0	0	0	1	0	1
Rhamnus catharticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
Vicia tetrasperma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Prunus spinosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	1
Pulmonaria mollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1
Ulmus minor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0
Acer campestre	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Festuca heterophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0
Peucedanum cervaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolum pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Ranunculus illyricus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Moehringia trinervia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Primula veris	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	1	1	1
Vicia tenuifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Euonymus europaea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0
Polygonatum latifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Poa compressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Carex pairae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Galium aparine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Fallopia dumetorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Hersperis tristis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

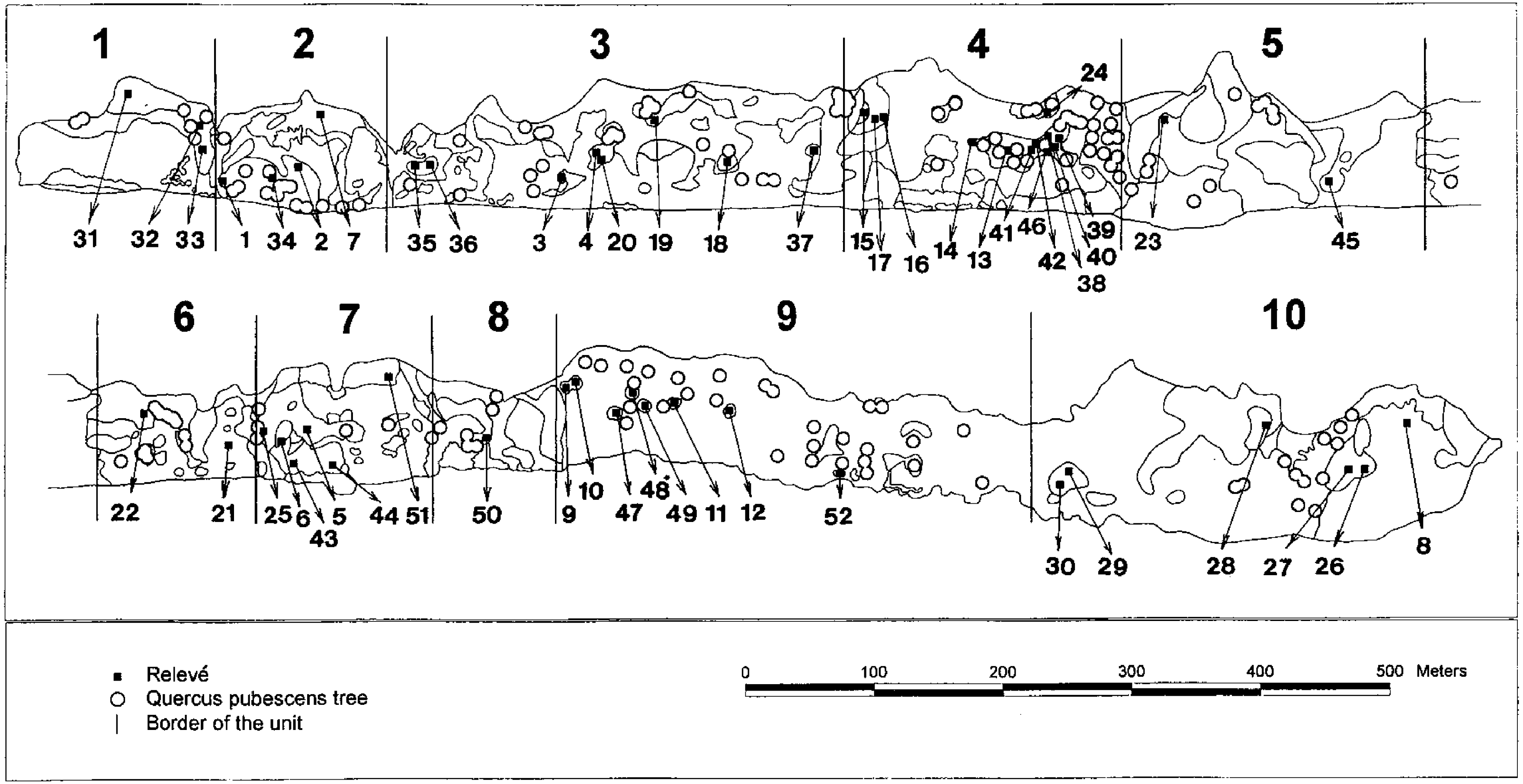

Figure 2. Map showing the distribution of species richness on the study site. Ten landscape compartments are identified. Numbers of species are shown at quadrat locations. Legend: full square quadrats, circle individual Quercus tree.

division. This division separates forest quadrats which contain steppe species from those in which the steppe species are absent. The steppe species dominate the 22-quadrat group. One of the subgroups in this group lacks forest species. Thus by divisive clustering two large groups of quadrats and four smaller groups were isolated, each interpretable in terms of the two contrasting species groups, forest and steppe.

Species richness and landscape compartments in quadrats

It is clear from Fig. 3a,b that forest and steppe species occur in different numbers in the quadrats. It is also clear that there is much variation in richness within the compartments. To quantify these, we performed on the data in Fig. 3a,b tests with null states defined as equidistributions (Orlóci 1991b and references therein). The method is an analysis of I-divergence information (Orlóci and Orlóci 1995). For the two species groups we give richness data by landform compartment (1 to 10) and corresponding statistics in the following:

(a) forest species

1: 4,6,6
2: 3,2,4,2
3: 2,4,1,4,3,2,2,4
4: 3,4,7,4,7,8,9,6,4,6,7,10
5: (empty compartment)
6: 5,3
7: 5,5,6,4,5,3
8: (one observation)
9: 5,11,5,9,7,7,8,7
10: 6,6,6,6,2,8
$2I_{total} = 50.02$, $P=0.451$
$2I_{between\ compartments} = 26.760$, $P=0.001$
$2I_{within\ compartments} = 23.265$, $P=0.989$

(b) steppe species

1: 20,16,14
2: 19,11,4,8
3: 17,17,8,1,2,10,10,4
4: 21,4,3,3,1,1,4,5,7,7,2,2
5: 7,12
6: 9,12
7: 2,12,12,21,16,14
8: (one observation)
9: 11,7,3,12,16,6,15,12
10: 15,9,8,13,13,15
$2I_{total} = 190.396$, $P=0.001$
$2I_{between\ compartments} = 56.217$, $P=0.001$
$2I_{within\ compartments} = 134.179$, $P=0.001$

Note: empty compartments or compartments with a single value cannot be used in the analysis.

The associated probabilities in the above and in all of the following cases were determined via randomisation experiments. The reasoning for and methods of randomisation are discussed in the Appendix. The key quantity to consider is $2I_{within\ compartments}$. This is so because when $2I_{within\ compartments}$ is large, having a small probability of occurring by chance under the null state, variation of species richness within the compartments is significant and the $2I_{between\ compartments}$ quantity is ambiguous for interpretation. In 2I terms the landscape units do appear to be selective in serving as refugia for forest species, but do not appear to sort the steppe species in any non-random manner.

Joint distribution of forest and steppe species

We performed a Chi-squared test on the data in Table 2. The test shows significant ($\chi^2=12.63$, $p=0.0035$), but a numerically weak tendency of exclusion ($r_{rows,columns}=-0.27$, $p=0.0159$).

Thoughts on neighbourhood effects

Closer inspection of the patches pattern (Fig. 1) on the ground reveals that the extent of transformation of the Brachypodium pinnatum grassland to steppe grasslands can be different even within a single stand. In landscape compartment 2, for example, the main portion of the *Brachypodium pinnatum* stand is a forest-type, but at the edges, adjacent to a large *Bromus erectus* stand, two of the quadrats (1,2) show invasion of steppe species. Such diminishing resistance against invading xerophilous species is evident also within the small *Brachypodium pinnatum* patches surrounded by the *Bromus erectus* stand, such as in quadrats 4, 20, and 21, as well as in the neighbourhood of the *Chrysopogon gryllus* community such as in quadrat 15. By inference, we see reason to suggest that floristic differentiation in the study site is in large part a function of the vegetation patch's response to their immediate coenological environment.

Linkage of landscape compartments and vegetation types

The relevant contingency data and the deviations from random expectation are given in Table 3. The deviations from random expectation are potted by table columns in Fig. 5. We present a canonical ordination of the column and row vectors of the same table in Fig. 6 (see method in Orlóci 1991a). Examined on this basis, the linkage of vegetation types and landscape compartments is strong. In Chi-squared terms, the relationship is highly significant ($\chi^2=1079$, $P=0.00001$), albeit somewhat muddled by much random variation (mean square contingency coefficient 0.181). We see the nature of the linkage by inspecting the magnitude and sense of the deviations from the null state (horizontal line) in Fig. 5. Under the null sate the linkage would be ruled completely by chance. Whether positive or negative, deviation values reveal tendencies in landscape compartment preferences and exclusions. Among the cases most striking is Type 6. This type has strong linkage to landscape compartment 9,

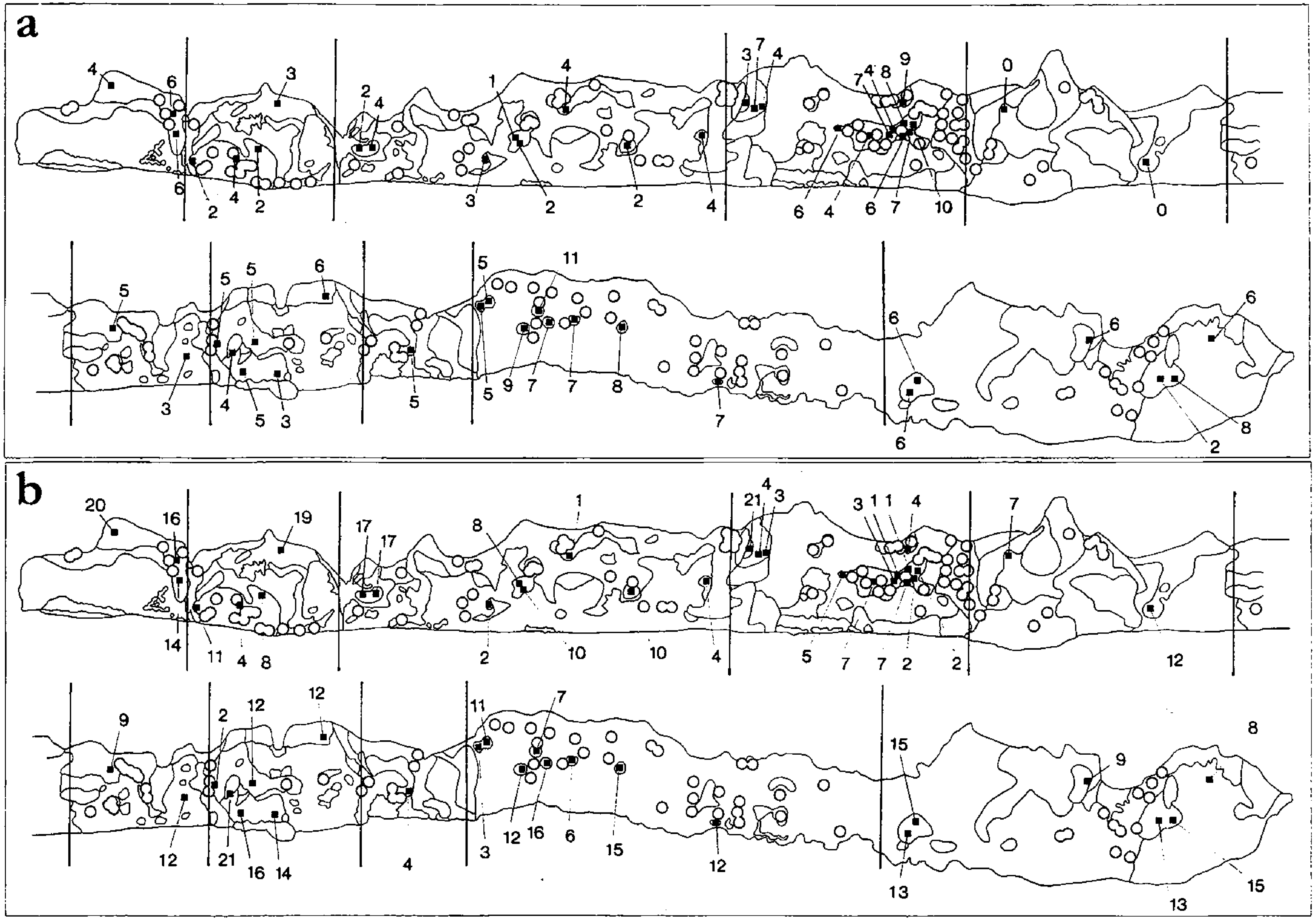
a
4 6 3 2 4 1 4 3 7 4 7 4 8 9 0
6 2 4 2 3 2 2 4 6 4 6 7 10 0
5 5 5 6 5 11 6 6
3 4 5 3 5 5 9 7 7 8 7 6 2 8
b
20 16 19 17 17 8 1 21 4 3 3 1 1 4 7
14 11 4 8 2 10 10 4 5 7 7 2 2 12
9 2 12 12 11 7 15 9 8
12 21 16 14 4 3 12 16 6 15 12 13 13 15

Figure 3 (opposite page). Map showing the distribution of forest (a) and steppe species (b) richness. Numerical labels refer to species numbers at quadrat locations.

weaker linkage to compartment 5, and a tendency to exclusion in the other compartments. The pairing of types by the similarity of their deviation graphs in Fig. 5 is mimicked by the pairing of points in Fig. 6 (top stereogram). The comparison of the upper and lower stereograms (Fig. 6) allows us to find correspondence between the vegetation types and landscape compartments. While the pairing of vegetation type 1 to landscape type 10, 5 to 5 and 6 to 9 is unambiguous, pairing of the others is not as clear.

Distribution of steppe type and forest type quadrats among landscape compartments

We can see in Table 4 that six of the ten landscape compartments include both types of quadrats, steppe and forest, but not in equal numbers. To test the idea of differential preferences further, we examine the joint distribution of forest and steppe quadrat types with landscape compartment being the pairing criterion. We use for this a topological index (see description in the Appendix). The corrected index value turns out to be 47.8%. Being less than 50%, the observed value indicates discordance. But in this case the value of the index is very close to the theoretical expectation, 50%. In fact the left tail probability 0.393 induce us to conclude that statistically the two quadrat types, forest and steppe, are sorted independently among the landscape compartments. This finding is consistent with what we have already shown for Fig 3a,b: while forest species richness is distributed selectively over the landscape compartments, the steppe species do not appear to be distributed that way.

General discussion

The results presented in the paper suggest characteristics that we believe can be expected as a rule in secondary *Brachypodium pinnatum* grasslands. For one thing, we can expect well-struck floristic gradient and group structure. We can also expect a major discontinuity separating the early successional stage with a rich complement of forest species from the later successional stage with many steppe species. The linkage of this shift to landscape types is clear in the case of forest species, but not so clear in the case of the steppe species.

Our results bring into focus the selection and differentiation problem on the forest to steppe vegetation gradient. The dynamics on this gradient involve penetration and gradual saturation of the grassland by xerophilous steppe species. In the early successional stage on our site the cover value of *Brachypodiumpinnatum* is 60 to 70%, the stand is closed and dense, and the height of the grass layer is about 50 cm. The

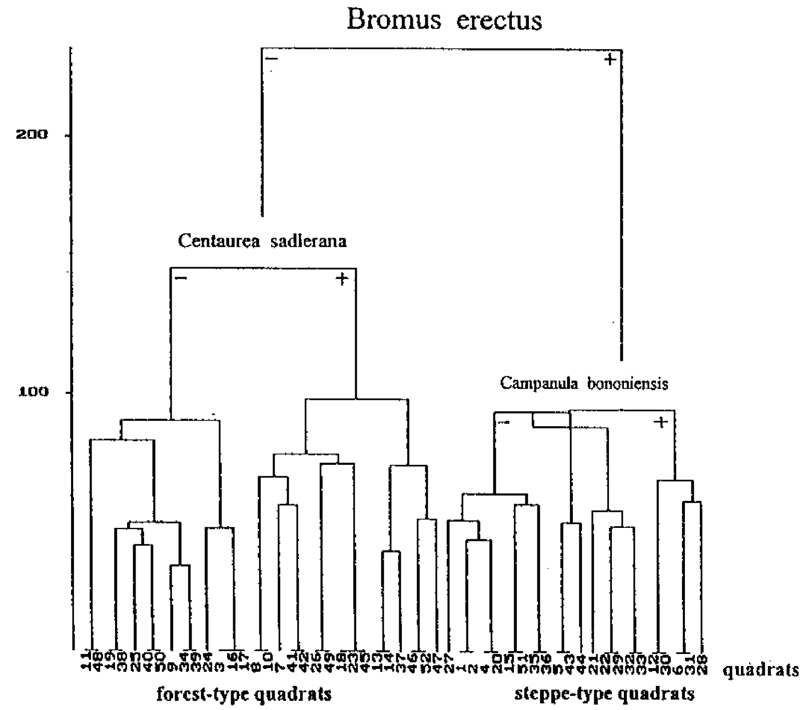

Figure 4. Cluster analysis of the 52 quadrat sample by association analysis. See the description of details in the main text and the method in Podani (1979). Four groups of quadrats: 11 to 17 - many forest species; 8 to 47 - many forest species and some steppe species; 27 to 44 - many steppe species and some forest species; 21 to 28 - steppe species and no forest species.

average number of forest species is about 8. Some locally rare forest plants such as *Bromus ramosus ssp. benekeni, Festuca heterophylla, Moehringia trinervia, Polygonatum odoratum, Vicia dumetorum* occur exclusively in the early stage. *Festuca rupicola*, the dominant species of steppe grasslands, is present in almost every site but usually with only a meagre 1 or 2 percentage cover. Other steppe species are rare, usually less than 4 in number. The late successional stage is extreme. Total vegetative cover is 45 to 50%, and plant height is much stunted. Forest species are either absent or their numbers are significantly reduced. An increasing number of steppe species appear, reaching 15 to 20 in total. Their cover may be as high as 30 to 40%. The percentage cover of *Festuca rupicola* is 5 to 25%, but it can reach 50%.

Table 2. Joint distribution of forest and steppe species among 52 quadrats. Entries represent quadrat numbers.

Number of forest species	Number of steppe species			Total
	1-6	7-12	13-	
1-3	1	11	6	18
4-6	7	6	5	18
7-	9	2	5	16
Total	17	19	16	52

Table 3. Distribution of vegetation types among landscape compartments. Entries in the body of the table represent percentages on a m^2 basis. Part A: raw data. Part B: deviations from random expectation.

PART A

Landscape compartments	Vegetation types						
	1	2	3	4	5	6	7
1	0	0	20.5	58.7	0	20.8	0
2	0	26.7	15.9	34.9	0	20.1	2.4
3	1.8	13.3	0.7	44.6	0	38.7	0.9
4	4.5	30.8	0.8	3.5	9.7	50.7	0
5	11.6	1.9	0	18.6	42.9	18.5	6.5
6	0	23.2	0	65.9	0.7	5.3	4.9
7	2.3	33.1	11.9	43.8	0	8.9	0
8	0	30.8	0	29.4	0	38.7	1.1
9	0	2.9	1.9	.3	0	94.9	0
10	36.8	6.6	0	5.1	1.7	48.9	0.9

PART B

	1	2	3	4	5	6	7
1	-5.7	-16.93	15.33	28.22	-5.5	-13.75	-1.67
2	-5.7	9.77	10.73	4.42	-5.5	-14.45	.73
3	-3.9	-3.63	-4.47	14.12	-5.5	4.15	-.77
4	-1.2	13.87	-4.37	-26.98	4.2	16.15	-1.67
5	5.9	-15.03	-5.17	-11.88	37.4	-16.05	4.83
6	-5.7	6.27	-5.17	35.42	-4.8	-29.25	3.23
7	-3.4	16.17	6.73	13.32	-5.5	-25.65	-1.67
8	-5.7	13.87	-5.17	-1.08	-5.5	4.15	-.57
9	-5.7	-14.03	-3.27	-30.18	-5.5	60.35	-1.67
10	31.1	-10.33	-5.17	-25.38	-3.8	14.35	-.77

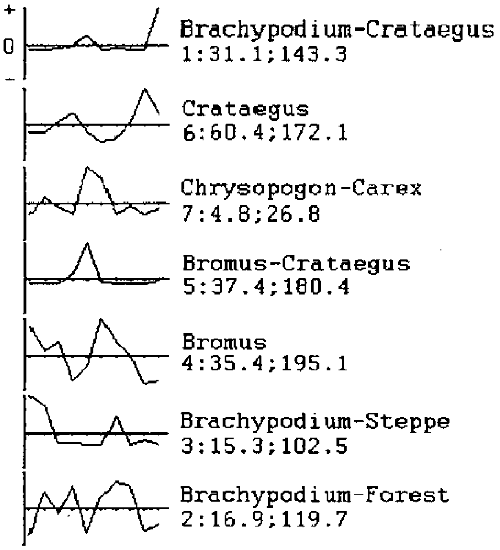

Figure 5. Deviation profiles of vegetation types as identified. Deviations (+,-) are plotted on vertical axis relative to random expectation (zero line). Tick marks on horizontal axis correspond to landscape compartments in the order of the rows of Table 3. Graphs are equal size, but the scales are different (see Table 3b). By the graph's shape, types {1,6}, {7,5}, and {4,3} are natural pairs with similar preferences for landscape compartment. Type 2 is an outlier. Legend to number strings {a: b; c} -- a column number in Table 3, b highest peak in deviation units, c size of I-divergence information for the profile.

Table 4. Distribution of forest and steppe quadrats among landscape compartments. Part A contains the classification of quadrats in accordance with Figs. 4. Part B contains the frequencies. Entries in column b are adjusted to correct for differential sampling intensity in the two groups.

Part A. Sampling unit inventory

Landscape compartment	Forest type quadrats	Steppe type quadrats
1		31 32 33
2	7 34	1 2
3	3 18 19 37	4 20 35 36
4	13 14 16 17 24 38 39 40 41	15 42 46
5	23 45	
6		21 22
7	25	5 6 43 44 51
8	9 50	
9	10 11 47 48 49 52	12
10	8 26	27 28 29 30

Part B. Contingency table

Landscape compartments	Forest type quadrats		Steppe type quadrats
	a	b	c
1	0	0	3
2	2	1.7	2
3	4	3.5	4
4	9	7.7	3
5	2	1.7	0
6	0	0	2
7	1	0.9	5
8	2	1.7	0
9	6	5.1	1
10	2	1.7	4
	28	24	24

As for *Brachypodium pinnatum*, its vitality is low, its growth is stunted, and has yellow leaves.

One may wonder if there is in fact order in the appearance of the steppe species. In forest stands, steppe species invasion is very much restricted. Indeed, we rated 39 of the 58 steppe species to be unsuited to invade the forest. There are no early successional steppe species. *Asperula cynanchica, Astragalus onobrychis, Carex humilis, Euphorbia pannonica, Taraxacum serotinum,* and *Thalictrum minus* enter in the late succession phase. Other late successional steppe species include *Campanula sibirica, Helictotrichon pratense, Hippocrepis comosa, Hypochoeris maculata, Lavathera thuringiaca, Medicago lupulina, Ranunculus illyricus, Trinia glauca, Viola ambigua* and *Orchis ustulata*, but we found these in only one or two sites. Finally, the *Brachypodium pinnatum* type and the xerophilous grasslands can have practically identical composition, except for the presence of *Brachypodium pinnatum*. Complete replacement of this by *Festuca rupicola* or by other steppe grasses could take a long period of time.

An answer to the question whether landscape compartments affect the spatial distribution and differentiation of the *Brachypodium pinnatum* grassland is a complicated matter, to say the least. It is our opinion that compositional differentiation is primarily coenological, a consequence of local dynamics within and among patches in their immediate neighbourhood. This opinion is also supported by Pearson (1993) and Rescia et al. (1977).

When we compare our results to others we are convinced that the behaviour of the principal species of the *Brachypodium pinnatum* grassland shows much plasticity over the different climatic regions. In the area of calcareous grasslands of humid regions the increasing dominance of *Brachypodium pinnatum* poses a real treat to biodiversity (Bobbink & Willems 1987, 1992, Schlaepfer 1997) and the

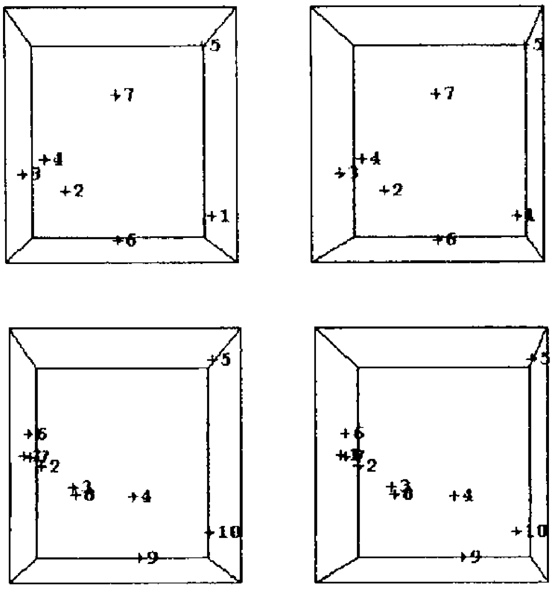

Figure 6. Stereo mapping of vegetation types (upper pair) and landscape compartments (lower pair) based on scores from canonical contingency table analysis of the data in Table 3. Note the pairing of vegetation types as points in a manner consistent with the similarities of graphs in Fig 5. Also note the comparability among the stereo pairs. For example, points 1 and 10, 6 and 9, 5 and 5, etc. The stereo mappings reinforce an impression of linkage between landscape pattern and vegetation pattern.

control of this species is understandably an imperative of grassland management. We see no invasive behaviour of that type in the *Brachypodium pinnatum* grassland species in our region. By reasoning on the basis of Hungary's vegetation map, we feel justified to expect replacement of the *Brachypodium pinnatum* grasslands in the course of secondary succession by the xerophilous grassland types dominated by other *Poaceae* species. We believe that the replacement will come by *Festuca rupicola* mainly as the result of coenological selection.

Schmotzer and Vojtkó (1997) investigated the variability of *Brachypodium* grasslands in the Bükk Mountain of Hungary. They found that these grasslands are mainly secondary in forest habitats in each of four altitude zones. These authors show close correspondence between the floristic composition of the *Brachypodium pinnatum* grasslands and the herb layer of forests in the forest-steppe zone. For climatic and edaphic reasons, natural gaps are formed in the forest where numerous steppe species occur. This being the case, a good part of the *Brachypodium pinnatum* grassland flora is in fact present in the sites *ab ovo*. For edaphic reasons, a forest of similar physiognomy develops in the Hornbeam-Oak zone where the floristic similarity of grassland and forest is highest. In the zone of the closed forests (Turkey Oak and Beech), the grassland flora is supported by migration, mainly from the outside and under the influence of anthropogenic and other perturbation. Based on consideration of these, Schmotzer and Vojtkó (1997) concluded that the floristic differences among *Brachypodium pinnatum* grasslands are accounted for by differences in the forests communities from which they derived. Their conclusion, and also that presented by Lausi and Nimis (1985), suggest the existence of an underlying natural law of universal validity, regarding the linkage of the floristic composition of secondary vegetation and the primary vegetation in an area.

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Appendix

Randomisation in the statistical tests

Statistical calculations hand us estimates of population values, but the absolute size of an estimate may not be a sufficient basis of interpretations. Take for example a sample Chi-squared value, such as $\chi^2=12.63$ (Table 2). This is a completely ambiguous quantity for interpretation when taken by itself. If the value of the associated mean square contingency coefficient is also given, here 0.121, one can have a better but not yet a complete notion about the relative strength of association. This is considering the fact that the closer the value of the mean square contingency coefficient approaches unity the sharper the detected relationship. But we would not pay much attention to the Chi-squared value or the mean square contingency coefficient if we could not show that the observed value is an uncommon value, meriting the statistical verdict of "significance". The technical problem in making a decision on "commonness" is one in determining the probability of a statistic having value at least as extreme as the observed when chance rules the relationship. We need the probability distribution of the statistic. If the probability associated with the observed value is high we declare commonness.

In the specific case of Table 2, we have two ways to go about to find a probability. We may invoke some very basic statistical axioms, assume that these are valid under the circumstances, and then fall back on solving the Chi-squared probability integral. This avenue of approach gives us the probability 0.0132. All this is mathematically elegant and simple, but unfortunately it could be utterly unreliable. There are two main conceptual concerns in this: (i) The circumstances we have assumed may not exist. (ii) A theoretical distribution function may not be available for the specific type of statistic that we elected to use. The solution lies in randomisation testing. In this, the probability is empirically derived based on information in the sample data. The *modus operandi* of this depends on the definition of the "null state". In the example of Table 2, it appears reasonable to stipulate the null state as the unhindered chance mingling of forest and steppe species in the sampling site with totals retained by the species entities. This is in fact the condition that has analogue in the method that A. Fisher used when he calculated exact probabilities for 2 x 2 tables. To understand where in the manipulations with Table 2 randomisation occurs, we go to the basic observational vector that happens to be 52-valued in the case of each species. The second element in Table 2 implies that in 11 of the 52 cells the number of forest species was 1, 2 or 3 when the number of steppe species was 7, 8, 9, 10, 11 or 12. Actually, the counting is within quadrats. Randomisation is the chance permuting the elements within a 52-valued vector according to random numbers. Permutations could be applied to both species types, but it is sufficient to permute only one.

Considering Table 2, the empirical Chi-squared probability distribution is generated by recursive application of two computational steps: (i) construction of a 3 x 3 table based on the 52-valued vectors after each serge of random permutations; (ii) computation of a new value for Chi-squared for each new table. When we perform these steps a very large number of times, we find that the proportion of all the tables with Chi-squared vale equal to or greater than 12.63 is about 0.01251. The fact that this value is close to the theoretical value is not a guarantee that it will be close in all other cases. Clearly, in the light of the small probability we have to regard the relationship in the observed table an uncommon one that could not easily arise unless the spatial distribution of the forest and steppe species over the quadrats did have some strong landscape and/or coenological constraint. The computations are automatically performed in Valerio De Patta Pillar's application program MULTIV (vpillar@ecologia.ufrgs.br). We note the low values of both the mean square contingency coefficient and r for Table 2 associated with very low probabilities. These tell us that the linkages are significant, albeit numerically weak and negative. These are conditions symptomatic of processes that are synchronous, but muddled by much random variation. Translated into other terms, we may say that the disappearance of forest species and the establishment of steppe species are fuzzy processes. We know for sure that the invasion of steppe species is likely to precede by a long shot the disappearance of the forest species.

Regarding Table 3, randomisation involves the assumption that the vegetation stand's coenological type bears no predictive value for its landscape type affiliation. In other words, the null state is a condition that involves a chance arrangement of coenological types among the landscape compartments. The randomisation algorithm is now different from what we use in the test of Table 2. The reasons for this are two folds. First, simple permutation of numbers in the table's rows would be forced, considering that the things we are dealing with have real size in area units. Second, the linkage or association of area units of the types and landscape compartments is in question. From these flows the null state of no association defined in terms of the unrestricted random assortment of the vegetation type units among the landscape compartments. The same mode of randomisation is used, but for a different reason, in the I-divergence analysis that we presented in connection with Fig. 4a,b.

For relevant materials on the basics and applications of randomisation testing, the theory and applications, readers are referred to Edgington (1995), Manly (1997), Pillar and Orlóci (1996), Legendre and Anderson (1998), and the references therein.

Manipulations of the Chi-squared quantity

While we formulate the null state as a state of "no association", actually the property we are testing in Table 3 is the random manner of peaking of values in the table cells, or equivalently the strength of specificity of the peaks to landscape compartments. Chi-squared gave an overall test for this. We can of course be very specific, and also more revealing, if we consider the partitions of the total Chi-squared. We can obtain partitions by different methods, such as singular value decomposition in canonical contingency table analysis (see Orlóci 1991a and references therein) or by the simple I-divergence method (see Orlóci 1991b). The former provides for parsimonious summarisation (see Figs. 5,6), while the latter supplies the results that we present as the last number in each number string in Fig 6 and in the section on the analysis of Figs. 4a,b.

The topological index

We may consider the entries in Part B in Table 4 as coordinates of a complex surface on which each cell of the table is represented by a point. There are two sets of points, one set for forest-type quadrats and another set for steppe-type quadrats. The two sets are identically ordered by the landscape classification and for that reason points from the two sets are uniquely paired.

Here in this analysis we are interested to see how co-ordinated is the spatial relationship of the two sets of points. To quantify this, we compare every point pair to every other pair in the sample. This gives us 45 distinct comparisons in the example. In the course of comparisons we assign a score (+, 0, or -) to each point according to the following set of simple rules: "+" assigned if point *P* of the chosen pair is down-slope in relation to the same type of point *U* in the compared pair, "0" if *P* and *U* are at same elevation, "-" if *P* is up-slope. Now if we complete the scoring for the two types of points over all paired comparisons, the topological index for the two types, forest and steppe, is given by

$C_{forest,steppe} = M/(s(s-1)/2)$

In this, M is the number of matching scores and s the number of point pairs. To illustrate the calculations by example, we consider a trivial data set:

#	Forest	Steppe
1	3	5
2	1	1
3	8	4
4	1	6

The assignment of signs is

```
Forest - + - + 0 -
Steppe - - + + + +
```

Corresponding to these is

$C_{forest,steppe} = 2/6 = 0.333$ or 33%

We can perform on the index a randomisation experiment to find its empirical probability distribution under the null state of sero relationship, but in this case randomisation is by permuting the elements in one column of the data set.

A further thought regards the 0 elevation differences of *P* and *U*, i.e., a perfectly flat region of the geometric model. Dealing with real numbers, 0 difference would be very unnatural to obtain, considering that it would require two co-ordinates to be identical. This ambiguity has a solution through replacement of zeros by " +" or "-" scores selected by an even chance or some other way. If we followed this, which we did not in the example, we would have:

```
F - + - + + -
S - - + + + +
```

The topological index would be 3/6.

It is important to realise that the topological index has a range from 0 to 1, or from 0 to 100%). Within this range concordance is measured in the upper portion and discordance in the lower portion. The expectation under the null state is 0.5 or 50%. For Table 4 we have 9 {+,+} matches, 7 {-,-} matches, and 1 {0.0) matches, a total of 17 matched scores. The index value is 17/45=0.378 or 37.8%.

Further pointers are in order regarding expectations and a bias correction. The experimental expectation for the topological index in Table 4b, under the assumption of independence, is 39.9%. The bias is 10.1% and the adjusted index value is 47.8%. The associated left tail probability is 0.393.

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