Testing community assembly predictions for nominal and continuous plant traits in species-rich grasslands

Testování predikcí utváření druhově bohatých lučních společenstev na základě kontinuálních a kategoriálních vlastností rostlin

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Schamp B., Hettenbergerová E. & Hájek M. (2011): Testing community assembly predictions for nominal and continuous plant traits in species-rich grasslands. – Preslia 83: 329–346.

We investigated patterns of trait-based community assembly in grasslands sampled along a moisture gradient (216 species) using three continuous species-level traits (maximum species height, minimum species height, seed mass), as well as seven nominal traits (flowering phenology, fruit type, pollen vector, clonal growth organs – CGOs, branching type, leaf distribution, lateral spread), some of which are unusual in that a species may possess more than one state per trait simultaneously (e.g. CGO). Additionally, this study tests whether patterns of assembly vary with plot biomass and moisture using both presence-absence and abundance-weighted analyses (two plot sizes: 25×25 cm, 75×75 cm). Plant species in these grasslands were randomly organized with respect to both maximum and minimum species height; however, coexisting plant species had a significantly smaller mean seed mass than expected by chance, and were significantly convergent in seed mass, consistent with observations from one previous study, and with theory related to environmental or competitive filtering. These patterns were consistent across plot sizes, and were similar whether analyses were abundance-weighted or not, although partitioned analyses show that these patterns are most pronounced in wet grasslands. Grasslands were non-randomly assembled with respect to five of our ten traits including seed mass, fruit type, CGO, branching type and leaf distribution. Among these, only patterns of branching type clearly conformed to the predictions from Limiting Similarity Theory, suggesting that variation in this trait may contribute to species coexistence in these grasslands. In two cases (fruit type, branching type), results differed in significance depending on whether analysis used presence-absence or abundance data; incorporating abundance may be more relevant, however, cover-based abundance measures in small plots can bias trait representation in favour of size over ramet number. In general, patterns were consistent across the two plot sizes. For four traits (seed mass, flowering phenology, leaf distribution and lateral spread) plot-level effect sizes of our tests varied significantly with plot-level biomass production; the slope of these relationships was positive for seed mass, but negative for flowering phenology, leaf distribution and lateral spread. For seven of ten traits, plot-level effect sizes varied significantly with plot-level soil moisture, with positive regression slopes for some traits (flowering phenology, leaf distribution), and negative slopes for others (minimum height, seed mass, fruit type, pollen vector, CGO). These results indicate that community assembly rules related to different functional traits can be responsive to variation in either biomass or soil moisture, or both.

K e y w o r d s: coexistence, diversity, environmental filtering, functional diversity, limiting similarity, plant functional traits, trait convergence, trait dispersion, trait divergence

Introduction

An increased interest in functional diversity, perhaps a more ecologically meaningful sub-set of taxonomic diversity (McGill et al. 2006, Messier et al. 2010, Webb et al. 2010), has emerged within the field of ecology, placing a greater emphasis on studies exploring the importance of variation in species-level traits in driving deterministic patterns of commu-nity assembly (e.g. Weiher et al. 1998, Weiher & Keddy 1999, Franzén 2004, Stubbs & Wilson 2004, Mouillot et al. 2005b, Grime 2006, Schamp et al. 2008, 2010, Schamp & Aarssen 2009). Coincident with this focus on functional variation has been the develop-ment and refinement of theories related to trait-based community assembly (e.g. Weiher & Keddy 1995, Weiher et al. 1999, Grime 2006, Wilson 2007), as well as a renewed interest in testing predictions that coexisting species should differ with respect to traits related to resource requirement (i.e. Limiting Similarity Theory; MacArthur & Levins 1967).

While progress has been made, advancement has been limited by available trait data, and perhaps by the limited availability of programs/algorithms for the appropriate null models that have emerged as standard for testing predictions related to trait over- and underdispersion (trait convergence/divergence, trait spread or clustering) (Weiher et al. 1998, Stubbs & Wilson 2004, Mouillot et al. 2005a, Schamp et al. 2008, 2010, de Bello et al. 2009, Schamp & Aarssen 2009). Consequently, a great deal more work is required to explore the consistent contribution of functional traits to community assembly; four chal-lenges exist within the framework of this field. First, evidence thus far, although limited, suggests that patterns of trait-based assembly are scale-dependent (Stubbs & Wilson 2004, Schamp et al. 2008, Messier et al. 2010); most studies thus far have focused on a single scale of analysis (e.g. Weiher et al. 1998, Franzén 2004, Schamp & Aarssen 2009). Further studies are needed that assess the influence of particular traits across scales both within and among communities. Second, a limited number of traits have been considered, most of which have been chosen largely for convenience, rather for their potential importance in community assembly (but see Stubbs & Wilson 2004). However, selecting recognized functional traits is perhaps only one available solution to this problem. The current approach, which has focused on species-level traits that are readily available either in the literature, or in databases, is beneficial because it allows researchers to explore the poten-tial influence of species-level traits that have been hitherto unexplored in the area of com-munity ecology. This approach should be extended, albeit with care to avoid problems with multiple tests, to also explore possible correlations between traits being examined, as a way of more clearly assessing which traits are driving patterns. One approach would be to collapse many continuous traits into a few ordination axes. Third, few studies have explored these patterns using nominal traits (but see Stubbs & Wilson 2004, Schamp et al. 2010). Such studies should be expanded, to enable researchers to both (i) address current theoretical predictions regarding trait dispersion, and (ii) use existing null model tests to objectively determine which traits can accurately be described as "functional traits". Fourth, several studies have found contrasting results related to the dispersion of plant spe-cies traits. For example, Franzén (2004) observed that seed mass was significantly underdispersed within a grassland community. This contrasts with a study by Schamp et al. (2008) in which species in an old-field plant community were neither significantly over- or underdispersed with respect to this trait. Similarly, Weiher et al. (1998) found evi-dence that maximum species height was overdispersed among wetland plots, while

Schamp et al. (2008) and Schamp & Aarssen (2009) found no significant pattern for this trait in an old-field community, and among forest communities, respectively. These limited results suggest that patterns may be both scale- and community/habitat specific, with differences in findings possibly linked to a number of factors. Several approaches may be used to address these challenges. Large-scale studies examining many different functional traits will come with time, and will play an important role. In the meantime, immediate progress can be made through multiple studies targeting different communities, and a variety of functional trait data. While this is a problem, it is also clear that the approach taken has yielded interesting results, and has accomplished a great deal in the development of statistical techniques for assessing deterministic trait-based community assembly (e.g. Weiher et al. 1998, Franzén 2004, Stubbs & Wilson 2004, Schamp et al. 2010).

Furthermore, what may appear to be confusingly diverse patterns among the small number of studies that have been done, may yet reveal consistency when additional consideration is given to such issues as scale of analysis (also plot size), the relative contribution of non-native species to communities, and successional stage. This work will be aided by the growing number of trait databases becoming available, e.g. LEDA Traitbase (Kleyer et al. 2008) or CLO-PLA database (Klimešová & Klimeš 2006, 2008, Klimešová & de Bello 2009), as well as the proliferation of public databases connecting researchers with community data that may be combined for more comprehensive analyses (e.g. connection with large vegetation-plot databases; Schaminée et al. 2009). A larger number of studies exploring these patterns are required to test predictions related to the general influence of particular traits on plant community assembly.

This study sets out to address several of the issues surrounding research exploring the influence of important species-level traits on community dynamics. We use a large data set consisting of paired plots (two plot sizes) sampled along the existing moisture gradient in species-rich grasslands and a collection of 10 species-level traits, to test the following questions: (i) Are the chosen species-level traits, several of which have been highlighted as playing important roles in vegetation processes (e.g. plant height in competition and invasion: Gaudet & Keddy 1988 and Schamp & Aarssen 2010, respectively; CGOs in local dispersal: Klimeš 2008, Klimešová & Klimeš 2008), significant drivers of non-random species organization in a species-rich grassland? (ii) Are predictions related to Limiting Similarity Theory more generally supported in a species-rich grassland community, where potential for overlap in resource requirements among species may be expected to increase the instances of interspecific competition? (iii) Do observed patterns differ for different plot sizes and when presence-absence vs abundance data is used? (iv) Do assembly patterns vary across gradients of plot-level biomass production and soil moisture, as expected if these gradients are related to environmental stress (Weiher & Keddy 1995), and consistent with patterns observed for some species-level traits in other studies (Schamp et al. 2008, 2010)?

Materials and methods

Study sites

All study localities are situated in Central Europe in Western Carpathian Mountains on the southern part of the border between Czech and Slovak Republic, with most localities in the Bílé Karpaty Mountains. This area is formed by flysh – the bedrock is composed of

alternating claystones and sandstones. The annual mean precipitation is approximately 700 mm and the annual mean temperature is about 8 °C (Miklós 2002, Tolasz 2007). The altitude of localities varies between 270 and 550 m a.s.l. (average 442 m). The grasslands in the study area are floristically unique (Hájková et al. 2011).

The study system is a mosaic of small (several square metres) spring calcareous fen sedge-moss wet grasslands scattered within herb-rich semi-dry grasslands. The soil moisture varied from 98% in wet plots to 19% in plots located in neighbouring semi-dry grasslands. Fen vegetation consists mostly of small sedges and non-sphagnaceous mosses, as well as a variety of grasses and herbs (the *Caricion davallianae* alliance, cf. Hájek et al. 2006), while semi-dry grassland vegetation is characterized primarily by grasses, herbs and sedges and is classified within *Festuco-Brometea* class (alliance *Cirsio-Brachypodion pinnati* and *Bromion erecti*). Fen-grassland transitions are sometimes formed by vegetation dominated by herbs, grasses, taller sedges and rushes, classified within *Calthion* alliance.

Field sampling

All field data were collected between June and July during the years 2005–2008. Data collection always consisted of establishing one linear transect (8–30 m) extending from the wettest part of spring fen grassland to dry grassland on 15 localities. The number of plots recorded per fen (5 to 16 plots) depended on size of the spring fen grassland; data from 126 plots (of the size 75 × 75 cm) were recorded. The exact distance between the centres of neighbouring plots was 2 metres. Within each larger plot (75 × 75 cm), a smaller, nested sample (25 × 25 cm) was recorded and standing plant biomass was collected. In each plot, species cover was estimated using a nine-grade scale (van der Maarel 1979). Biomass was subsequently dried at 60 °C for several days and weighted. Soil moisture in the upper most soil horizon was measured for each 25 × 25 cm plot during the driest period of the year (July to September; ThetaProbe, soil moisture sensor ML2x).

The nomenclature of plant species follows Kubát et al. (2002), syntaxonomical nomenclature is according to Chytrý (2007).

Species-level plant traits

Species-level plant traits (Electronic Appendix 1) were obtained from multiple sources: (i) Czech flora (Kubát et al. 2002): maximum and minimum species height; (ii) BiolFlor database: flowering phenology, fruit type, pollen vector (Klotz et al. 2002); (iii) CLO-PLA database: clonal growth organs (CGOs), branching type, leaf distribution, lateral spread (Klimešová & Klimeš 2006, 2008, Klimešová & de Bello 2009). Seed mass data were taken from the Ecological Flora of the British Isles online database (Fitter & Peat 1994), from the Seed Information Database (Royal Botanic Gardens Kew 2008) and from Moles et al. (2005). Additional seed mass data were obtained for nine additional species by weighing between 30–100 seeds per species (depending on availability) from samples in the Seed and Fruit Collection of the Institute of Botany of the ASCR (http://www.ibot.cas.cz).

Some trait data were not available for some species. Missing trait data were dealt with in two ways: (i) by calculating the average proportion of species in plots that were missing data for each trait; (ii) the use of sensitivity tests to test whether the results of our tests differed when a subset of plots consisting of less missing trait data were analyzed (see below). For presence-absence data, the proportion of missing trait data was measured as the number of

species per plot with missing trait data divided by the total number of species in that plot. For abundance analyses, the proportion of missing trait data was calculated as the abundance of species in a plot with missing trait data divided by the total abundance of plants in that plot. In general, missing data made up only a small proportion of the species in plots (Electronic Appendix 2); flowering phenology contained the highest proportion of missing data, and consequently was used in the aforementioned sensitivity analysis.

Analysis: continuous and nominal plant traits

We used an established null model to test for deterministic (i.e. non-random) organization of plant species according to three continuous plant traits: maximum height, minimum height (presumably observed at reproductive maturity) and seed mass. We tested for trait-advantages using a test statistic developed by Schamp & Aarssen (2009; mean trait value) and tested for evidence of either over- or underdispersion (also divergence vs convergence; trait spread vs clumping) using previously developed test statistics (Stubbs & Wilson 2004, Schamp et al. 2008, Schamp & Aarssen 2009). Patterns related to trait overdispersion/divergence/spread support theoretical predictions under Limiting Similarity Theory (MacArthur & Levins 1967), and patterns of underdispersion support theoretical predictions of trait convergence due to competitive filtering (Grime 2006), or environmental filtering (Weiher & Keddy 1995). This analysis compares different measures of trait distributions to a distribution of the same measures generated by randomly assigning traits among all species in the community (i.e. null distribution; Schamp et al. 2008, 2010, Schamp & Aarssen 2009). Distributions of each community-level test statistic were generated from 5000 randomizations of the trait matrix. All null model tests are two-tailed tests, with P-values calculated as:

$$P = MIN\ [2S/(3001), 2L/(3001)]$$

with S and L equal to the number of randomized test statistics greater than or equal to, or less than or equal to the measured test statistic respectively (cf. Bersier & Sugihara 1997, see also Schamp et al. 2008, Schamp & Aarssen 2009). All analyses were carried out in Matlab® using code developed by Schamp. Separate analyses were conducted using presence-absence data as well as abundance data; these two approaches can produce different results (e.g. Schamp et al. 2008).

We used several test statistics (trait distribution measures), all of which have previously been used in similar analyses (e.g. Stubbs & Wilson 2004, Schamp et al. 2008). In each case, the statistic is calculated for each plot and trait, and the mean of all plot-level values (i.e. community mean) is used as the test statistic. These include: (i) Mean – This measure was used to assess whether one end of a given trait distribution is favoured or not (Schamp & Aarssen 2009). If coexisting plants have a greater maximum height than expected, for example, this may be interpreted as evidence that tall plants are favoured. (ii) Range – This measure is the maximum trait value minus the minimum trait value for a particular plot. When this test statistic is larger than expected by chance, this can be taken as evidence for Limiting Similarity Theory, and if it is smaller than expected, it is accepted as evidence of significant trait convergence. (iii) Mean Nearest Trait Distance (meanNTD) – This was calculated for each plot by ordering species from smallest to largest for each trait, and

determining the mean difference in trait value (Euclidean) between each species and its closest neighbour. The mean of plot-level meanNTD among all plots was used as the measure of how spaced species are with respect to traits, within plots. Higher meanNTD values than expected support Limiting Similarity Theory (Weiher & Keddy 1995), and smaller meanNTD values suggest trait convergence (Grime 2006). (iv) Variance in Nearest Trait Distance (varNTD) – This is the variance in those distances among coexisting species described for meanNDT; this is a measure of how regularly spaced coexisting species are with respect to each trait. Values of varNTD that are lower than expected have been cited as support for Limiting Similarity Theory (Stubbs & Wilson 2004). (v) Richness – This test statistic was used for nominal/categorical traits and is a measure of the number of categories represented within a sample. If richness is higher than expected by chance, this would suggest evidence of limiting similarity, and a lower than expected value of richness would indicate that some trait categories are favoured over others. This measure is less useful for traits with few categories, as possible variation in richness among plots tends to be low, or in some cases non-existent. (vi) Evenness – This statistic was also used with categorical data and is a measure of how evenly represented different categories were within samples. This measure addresses concerns that functional diversity should be measured both in terms of richness and evenness (Mason et al. 2005, Mouillot et al. 2005a). High evenness is taken here as evidence in support of Limiting Similarity Theory, while lower evenness than expected would indicate some categories are more favoured. For traits with few categories, high evenness may also result if species richness is lower than expected; this is because a plot represented by a single category for a trait would be measured as maximally even. We discuss these issues in the results as they arise.

Analysis: nominal traits for which a species may possess multiple states

Some potentially informative categorical traits pose problems for analysis because categories for that trait may not be mutually exclusive, meaning that some species may have multiple trait-states for a given categorical trait. A given species, for example, may possess several different CGOs at the same time, so for this particular trait, that species has multiple values. To handle this, the same model was employed as described above; however, distributions of traits for plots were composed of all trait-states represented, so for presence-absence data, the number of trait-states for a given plot was equal to the number of trait values exhibited by the species in that plot. In general, the trait distribution contained more values than there were species in that plot. If a given species possessed three different CGOs, this was represented in plots by all three trait-states, contributing the same level of trait variation as would three different species with one CGO each. Similarly, for abundance analyses with such traits, the number of trait-states in a given plot was generally higher than the total plant abundance for that plot. In the current analysis, it is therefore assumed that each species displays all possible states for such traits, in each plot. This may be unreasonable, and we recommend that future studies actually measure what states are displayed for each of these traits in each plot. As with other nominal traits, the same two test statistics were calculated (richness, evenness).

Sensitivity analysis

To test whether missing trait data may have impacted our results, we re-ran our tests for flowering phenology, the trait with the highest proportion of missing data (4.6% missing per plot for presence-absence data; 5.5% missing per plot for abundance data; Electronic Appendix 2). These tests included only plots for which all species-level flowering phenology data were available (n = 68 plots for 25 × 25 cm plots; 38 plots for 75 × 75 cm plots).

Community assembly along gradients

For one plot size (25 × 25 cm plots) we tested whether the plot-level effect sizes of our tests were responsive to plot-level variation in productivity and soil moisture by using regressions to test for directional changes in effect sizes (z-scores) of our tests among 25 × 25 cm plots (biomass was not collected for 75 × 75 cm plots). Z-scores for each plot and each test statistic were calculated as (O–M)/S, where O is the observed value for each test statistic and plot, and M and S are the mean and standard deviation respectively for each test statistic across 5000 randomizations of the trait distribution for the study plots (Schamp & Aarssen 2009, Schamp et al. 2010).

Analysis of wet and dry grasslands separately

Because it is possible that investigations of limiting similarity across gradients may bias results against supporting limiting similarity, which may likely be most strongly expressed in more homogeneous conditions, we also analyzed wet and dry grassland plots separately (wet grasslands: 52 plots; dry grasslands: 51 plots), excluding plots that were of intermediate moisture.

Results

Continuous plant traits

Species coexisting in our study plots were randomly organized with respect to maximum and minimum species height (Table 1). Additionally, our results indicate that coexisting species have significantly smaller seed masses than expected by chance (25 × 25 cm: P = 0.0092; 75 × 75 cm: P = 0.00016), and that seed size is significantly convergent in 25 × 25 cm plots (range: P = 0.0084; meanNDT: P = 0.0056; varNDT: P = 0.0016) and in 75 × 75 cm plots (range: P = 0.00012; meanNDT: P = 0.0012; varNDT: P = 0.0148). These patterns are reported for presence-absence analyses; however, in general, abundance-based analyses produced similar results, excepting results for meanNDT and varNDT, which generally do not produce significant results for abundance data because of the heavy weight placed upon these values by abundant species, the nearest neighbour of which will always be conspecifics with the same trait value.

Nominal plant traits

Because seven traits were examined at two scales and using two test statistics as well as both presence-absence and abundance data, we confine our written report to significant results, and refer readers to Table 2, which summarizes the results from all analyses.

Table 1. – Results from trait dispersion analysis on three continuous species-level traits: maximum height, minimum height (minimum size at reproduction), and seed mass. Analyses used presence-absence and abundance data from 126 plots for each of two plot sizes (25 × 25 cm, 75 × 75 cm). P-values indicate whether plots are overdispersed (Obs > Exp), or underdispersed (Obs < Exp) for the trait of interest. Bold values signify type-I error rates at α < 0.05 (i.e. P-values).

		Presence-absence				Abundance			
	Test statistic	Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp	
	Plot size (cm)	25 × 25	75 × 75	25 × 25	75 × 75	25 × 25	75 × 75	25 × 25	75 × 75
Maximum height	Mean			0.376	0.522			0.428	0.652
	Range			0.421	0.438			0.416	0.441
	Mean NTD			0.813	0.741			0.506	0.673
	Var NTD			0.438	0.092			0.291	0.273
Minimum height	Mean			0.266	0.251	0.603	0.527		
	Range			0.704	0.523			0.968	0.791
	Mean NTD			0.908	0.639			0.855	0.148
	Var NTD			0.436	0.056			0.537	0.062
Seed mass	Mean			**0.009**	**< 0.001**			**0.011**	**0.004**
	Range			**0.008**	**< 0.001**			**0.004**	**0.003**
	Mean NTD			**0.006**	**0.001**		0.958	0.661	
	Var NTD			**0.002**	**0.015**			0.414	0.918

Table 2. – Results from trait dispersion analysis on seven nominal traits. P-values indicate whether plots are richer (Richness: Obs > Exp), or poorer (Richness: Obs < Exp) in terms of variation in these traits, and whether these traits are more evenly (Evenness: Obs > Exp), or less evenly (Evenness: Obs < Exp) distributed within plots. Studied traits include flowering phenology (month of flowering), fruit type, lateral spread, pollen vector, leaf distribution, clonal growth organ and branching type. The last four of these traits are unique in that a single species can have multiple values; for example, a species may be both insect and wind pollinated. This was incorporated into the analysis. Bold values signify type-I error rates at α < 0.05 (i.e. P-values).

		Presence-absence				Abundance			
	Test statistic	Obs > Exp		Obs < Exp		Obs > Exp		Obs < Exp	
	Plot size (cm)	25 × 25	75 × 75	25 × 25	75 × 75	25 × 25	75 × 75	25 × 25	75 × 75
Flowering phenology	Richness		0.730	0.994		0.993	0.722		
	Evenness	0.125	0.870			0.087	0.852		
Fruit type	Richness			0.301	0.508			0.296	0.455
	Evenness			**0.009**	0.090			**0.001**	**0.021**
Pollen vectors	Richness		0.244	0.777		0.699	0.7028		
	Evenness	0.713			0.663			0.555	0.124
Clonal growth organ	Richness			0.416	0.838		0.678	0.879	
	Evenness			**0.003**	**0.010**			**0.001**	**0.002**
Branching type	Richness	0.058	**0.042**			0.774	0.647		
	Evenness			0.034	**0.047**			0.511	0.178
Leaf distribution	Richness			0.020	**0.002**			0.082	**0.006**
	Evenness	**0.001**	**0.006**			**0.001**	**0.001**		
Lateral spread	Richness			0.689	0.689			0.694	0.689
	Evenness			0.710	0.710			0.709	0.573

In 25 × 25 cm plots, coexisting species were also non-randomly organized with respect to several nominal plant traits. In these small study plots, several traits were significantly less evenly distributed among coexisting species, indicating that some trait-states are favoured in plots (fruit type: P = 0.0088; CGOs: P = 0.0028; branching type: P = 0.0336). Each of these patterns was accentuated when analyses were weighted by abundance.

Also in 25 × 25 cm plots, coexisting species were observed to be more even than expected by chance with respect to leaf distribution (P = 0.0012); however, plots were also significantly less rich with respect to this trait (P = 0.02), indicating that low richness in this trait may have resulted in higher evenness (Table 2).

In 75 × 75 cm plots, similar patterns were observed, with coexisting species being less even than expected by chance with respect to two categorical traits (CGOs: P = 0.0104; branching type: P = 0.0468); significance of these results were higher when weighted by abundance (Table 2). Coexisting species in these plots were also less even than expected in regard to fruit type; however, this result was only significant for the abundance-weighted analysis (P = 0.0212). At this plot size, coexisting species were also possessed of a significantly richer number of branching types than expected by chance, a result expected under Limiting Similarity Theory (P = 0.0416).

Sensitivity test results

When flowering phenology analyses were run only using plot data for which all trait data were known (0% missing trait data/plot), coexisting species were randomly organized with respect to flowering time (Electronic Appendix 3). This finding is no different from that observed when the entire data set was analyzed; no further interpretation of these results was pursued.

Community assembly along gradients

For 25 × 25 cm plots, patterns of organization in relation to traits were generally poorly responsive to plot level biomass (Tables 3–4). However, the tendency for coexisting plant species to be of smaller mean seed mass in plots was significantly higher in plots with high biomass (P = 0.048; Table 3), the opposite of the pattern expected if assembly rules for this trait are driven by environmental stresses (Weiher & Keddy 1995, Weiher et al. 1998). Among nominal traits, coexisting species tended to be less rich in flowering phenologies in plots with high biomass. This pattern was also observed for leaf distribution, and for lateral spread (Table 4). Coincident with the tendency for coexisting species to be less rich in leaf distribution in plots with high biomass, species were also less even in the distribution of different lateral spread strategies (P = 0.002).

Patterns varied significantly along the moisture gradient in this study for seven of ten traits (minimum height, seed mass, flowering phenology, fruit type, pollen vector, CGO and leaf distribution; Table 4). Plot-level effect sizes increased significantly with plot-level soil moisture for flowering phenology and leaf distribution, and decreased significantly for minimum height, seed mass, fruit type, pollen vector, CGOs. Importantly, slopes of these relationships were extremely close to zero and for most traits (but see flowering phenology) explained only a very small portion of the variance in observed effect sizes.

Table 3. – Results from regression analyses testing whether plot-level effect sizes of our tests for each continuous trait and each test statistic change predictably with above-ground dry biomass production, and moisture of plots (25 × 25 cm plots). All regressions have a sample size of 126 plots; bold values signify type-I error rates at α < 0.05 (i.e. P-values).

Plot characteristic	Trait	Test statistic	Slope	R2	P-value
Plot biomass	Maximum height	Mean	0.011	0.020	0.114
		Range	0.005	0.005	0.435
		Mean NTD	0.006	0.008	0.327
		Var NTD	0.005	0.012	0.230
	Minimum height	Mean	0.006	0.006	0.378
		Range	0.004	0.004	0.460
		Mean NTD	0.005	0.008	0.332
		Var NTD	0.005	0.013	0.202
	Seed mass	Mean	0.012	0.031	**0.048**
		Range	0.004	0.007	0.348
		Mean NTD	0.003	0.004	0.480
		Var NTD	0.019	0.004	0.127
Plot moisture	Maximum height	Mean	–0.003	0.021	0.108
		Range	0.001	0.002	0.611
		Mean NTD	0.002	0.006	0.409
		Var NTD	0.002	0.025	0.080
	Minimum height	Mean	–0.005	0.050	**0.012**
		Range	–0.001	0.001	0.762
		Mean NTD	–0.0004	0.001	0.811
		Var NTD	0.001	0.010	0.266
	Seed mass	Mean	–0.010	0.211	**< 0.001**
		Range	–0.005	0.093	**< 0.001**
		Mean NTD	–0.004	0.075	**0.002**
		Var NTD	0.0002	0.001	0.767

Analysis of wet and dry grasslands separately

When wet and dry grasslands were considered separately, which was done to ensure that patterns reflecting limiting similarity were not obscured by the inclusion of plots along the moisture gradient, no new evidence of overdispersion for our traits was uncovered either in wet (Electronic Appendix 4, 6), or dry (Electronic Appendix 5, 7) grasslands. However, in dry grasslands, significant underdispersion observed for seed mass in the larger analysis was no longer apparent (Electronic Appendix 4), although it remained for wet grasslands (Electronic Appendix 5). Significant underdispersion observed in the larger analysis was also removed in dry grasslands for fruit type, CGO and branching type (Electronic Appendix 6), although this change varied depending on plot size and the use of abundance-weighting in analyses. In dry grasslands, branching types were significantly more evenly represented in 25 × 25 cm plots than expected by chance; however, significance was marginal and would be erased by any effort to protect for multiple tests (P = 0.046; Electronic Appendix 6).

Discussion

Deterministic assembly of grassland communities

Our results indicate that plant species within this grassland mosaic are organized deterministically into plots of two different sizes, with respect to several plant traits. Significant patterns of either under- or overdispersion, or favoured trait-states were observed for five of the ten traits examined (Table 1). This finding supports the logic of a swelling interest in the impact of functional trait variation on patterns of plant community assembly (e.g. Weiher & Keddy 1995, Grime 2006, McGill et al. 2006, Wilson 2007). Additionally, our findings support the assertion (Schamp et al. 2010) that hitherto unrecognized functional plant traits can be discovered through the use of these models (e.g. fruit type, CGOs, branching types, lateral spread; Table 2).

Observed patterns reflected predictions from Limiting Similarity Theory for branching type in our larger plot size, with coexisting species being significantly richer in classes of this trait than expected by chance (Table 2). Additionally, branching types were less evenly distributed among coexisting species in these plots than expected by chance, such that richness was higher, but evenness was lower. Thus, in terms of richness, predictions from Limiting Similarity Theory are supported, but in terms of evenness, they are not. Regardless, this can be viewed as supporting evidence that different branching types may contribute to coexistence via limiting similarity in these grasslands. Contrastingly, leaf distribution classes were significantly more evenly represented among coexisting species for both plot sizes; however, in both cases, coexisting species were significantly less rich in leaf distribution class than expected. In these cases, many plots were represented by only a single leaf distribution class, and therefore are significantly more even than expected by virtue of low richness. These findings illustrate the complexities of recognizing evidence of limiting similarity for nominal plant traits. The latter problem is less likely for nominal traits for which there are many different states (e.g. leaf distribution: 3 states vs CGO: 17 states). Care should be taken in interpreting this type of result as conclusive evidence supporting Limiting Similarity Theory.

Our results provide evidence of significant underdispersion (i.e. convergence) of several traits, in support of predictions by Grime (2006) that traits related to competition will be convergent as dominant trait states outcompete less competitive states. Additionally, these results are consistent with predictions from Weiher & Keddy (1995) that traits related to environmental tolerance will be convergent. Coexisting species possessed a smaller mean seed mass than expected by chance, and were significantly underdispersed for this trait at both plot sizes; these patterns were generally supported independent of whether presence-absence or abundance data were used (Table 1). This result is consistent with patterns observed by Franzén (2004) in a grassland community, but contrasts with patterns observed by Schamp et al. (2008) in an old-field community. Further testing should be conducted to determine whether dispersion patterns related to seed mass vary across a successional gradient. These patterns held in wet grasslands when these were considered separately (Electronic Appendix 5), but were not as prominent in dry grasslands (Electronic Appendix 4). This is further evidence that trait-based filtering of species will be accentuated in some environmental conditions (Weiher & Keddy 1995). Additionally, a number of nominal traits were less evenly distributed among coexisting species than expected by chance, which suggests that some nominal traits are favoured over others.

Fruit type, CGOs and branching type were traits following this pattern (Table 2). These patterns were consistently observed for both plot sizes, with the exception that fruit type underdispersion was only significant at $\alpha = 0.05$ when analyses were weighted by abundance. These findings indicate that these traits are important for community assembly, and that particular trait states are favoured within communities.

Presence-absence vs abundance analyses

In a previous study, Schamp et al. (2008) observed that although significance of patterns did not differ between analyses using abundance vs presence-absence data, in some cases patterns that tended towards overdispersion for one type of analysis tended towards underdispersion when the other type of analysis was employed, suggesting that the choice of which analysis type to use may be important. Our results take this suggestion further by demonstrating that the use of these different analyses can lead to differences in the significance of observed results. For example, coexisting species for both plot sizes were significantly convergent in seed mass for all four test statistics employed when presence-absence data were used in analyses; however, when abundance data were examined, the spacing among individuals in seed mass was not significantly lower than expected (meanNDT; Table 1), nor less variable than expected (varNDT; Table 1). Part of this difference comes from the fact that in abundance analyses, individual plants count as individuals but still contribute species-level traits such that variation in both meanNDT and varNDT are driven primarily by the randomization procedure which randomizes traits across all species, but conserves abundance patterns. The conservative nature of our randomization procedure, which keeps abundance patterns in the community static, may contribute to this observed result, and will necessarily be more true for certain test statistics, as illustrated in our seed mass results (Table 1). This will not be the case for similar observations for test statistics used to examine nominal traits. So the observations that results change in P-value across the α threshold for branching type at both plot sizes, and for fruit type at the 75×75 cm plot size, yields stronger support for the assertion that the use of abundance data in analysis can play an important role in testing these patterns.

Interpretations of patterns

While we observed several patterns of deterministic community assembly for the traits examined, a great deal of trait-variation explored did not contribute to significant patterns of over- or underdispersion. Random assembly with respect to these traits may indicate that variation in these traits is unimportant in driving the organization of species within these grassland communities. In particular, it suggests that variation in these traits do not likely contribute to the filtering of species along biomass or moisture gradients in grasslands, or differential resource use in these communities. It is possible that these patterns will differ in other communities, or at different plot sizes than those considered here.

The observed pattern of random species organization with respect to maximum species height (Table 1) is consistent with findings by Schamp et al. (2008) in an old field community, and those of Stubbs & Wilson (2004) for three plot sizes in sand dune communities. However, these results differ from findings by Schamp & Aarssen (2009) for forest communities where tall plant species were overrepresented relative to what was expected by chance, and from findings that coexisting species in wetlands are overdispersed with respect to

maximum height (Weiher et al. 1998), and those of Stubbs & Wilson (2004) who observed significant underdispersion with respect to plant height at one plot size. These findings also do not support the theoretical prediction of overdispersion for this trait by Weiher & Keddy (1995). Lastly, effect sizes of our tests for this trait did not vary predictably with plot biomass, while Schamp & Aarssen (2009) observed that taller plant species were overrepresented to a greater degree in more productive forest plots. A multi-community study will be required to determine whether inconsistency in community assembly rules related this trait results from variation along successional gradients, different scales of analysis, or the varied context with which this trait may contribute both to niche differentiation (i.e. overdisperion), or asymmetrical competition, which would lead to underdispersion (Grime 2006, Scheffer & van Nes 2006, Schamp et al. 2008). Coexisting species were also randomly assembled with respect to minimum species height. This trait was examined as a result of its potential advantage in low resource habitats where survival might be improved when resource requirements, which will be size related, are small. It is possible that this trait will be more important in more nutrient limited communities than those studied here.

Coexisting species were also significantly underdispersed at both plot sizes with respect to seed mass; with small species also being significantly overrepresented in our vegetation plots (Table 1); this effect was also prominent within wet grasslands when these were considered separately (Electronic Appendix 5), but not in dry grasslands (Electronic Appendix 4). Evidence suggests that large seeds have a higher probability of successful recruitment than small seeds (Turnbull et al. 1999). Multiple studies, for example, have demonstrated that large seeds have a survival advantage that is more pronounced in shaded habitats (Moles & Westoby 2004, Bruun & ten Brink 2008). Donath & Eckstein (2010), by analogy, found that large-seeded species had a fitness advantage only when seeds were shed beneath a ground cover. Drought is another factor that may be advantageous for large-seeded species (Bruun & ten Brink 2008). As our study system is composed of wet to semi-dry, open mown grasslands, these potential advantages of large seeds may have disappeared, leaving small-seeded species with an advantage. This pattern could result from smaller-seeded species having better dispersal ability within grasslands; such an advantage could also be mediated by seed quantity, given that seed mass is generally negatively correlated with seed production (Paul-Victor & Turnbull 2009). A larger number of seeds could result in a larger number of seedlings, which may be advantageous in mown grasslands where seedling mortality may be high after mowing. Such different responses of functional traits to different vegetation management regimes have been repeatedly demonstrated (e.g. Kahmen & Poschlod 2008, Klimešová et al. 2008); however, management effects are difficult to generalize as some traits may respond non-linearly to different management intensities (Saatkamp et al. 2010). When wet and semi-dry grasslands were considered separately, small seed size appeared to be clearly advantageous within wet grasslands (Electronic Appendix 5). This may illustrate the important contribution of dispersal ability in seed mass convergence, as small wet patches are in fact isolated habitat islands in the matrix of semi-dry grasslands. The important role of dispersal limitation of wetland vascular plants in the discrete spring fen habitat in the study area has been clearly demonstrated in a previous study (Hájek et al. 2011). Nevertheless, small seeds are somehow favoured in semi-dry grasslands as well (Table 3). We also analyzed a larger data set sampled in a single large semi-dry grassland (the Čertoryje Nature Reserve) and found a similar pattern of underdisperion with respect to seed-mass (B. Schamp, E. Hettenbergerová & M. Hájek, unpublished data).

We also observed non-random patterns of dispersion for CGOs; evenness of CGO representation among coexisting species was significantly lower than expected by chance, indicating that some CGO categories were favoured/overrepresented within plots. This finding supports the importance of CGOs as a functional trait that contributes to patterns of community assembly with particular clonal growth organs possibly contributing to a competitive advantage under different abiotic conditions (Wildová et al. 2007, Klimeš 2008, Klimešová & Klimeš 2008). For example, CGO evenness decreased with increasing moisture, indicating that the observed over-representation of some CGOs was accentuated in wet grasslands. While the slope of this relationship is extremely small, this is possibly due to the fact that some CGOs are overrepresented in general, affording limited opportunity for this to be accentuated at one end of a moisture gradient. However, this under-dispersion is also observed for CGOs for wet grassland plots, suggesting that even for portions of this gradient, some CGOs are favoured (Electronic Appendix 7). Sosnová et al. (2010) have observed the prevalence of rhizomatous plants in fens and bogs, while other clonal organs are only marginally represented, an observation that may explain these results. Species were randomly organized in plots with respect to lateral spread, another important clonal trait; however, coexisting species were richer in categories for this trait in low-biomass plots (i.e. higher richness; Table 4). This result may suggest a competitive advantage for fast spreading clonal plants in more nutrient-rich habitats (van Groenendael et al. 1996, Sosnová et al. 2010). The plot-level richness of leaf distribution in CGO (rosette, semi-rosette, no rosette) decreased with increasing plot biomass and decreasing soil moisture, which may coincide with the light regime experienced by these plants. Rosette plants are supported in low-productive vegetation with good light penetration through canopy of taller plants and may better survive mowing (Klimeš & Klimešová 2001). Tall grasses such as *Molinia arundinacea* were common dominants in our grasslands, restricting superior rosette plants if their above-ground biomass is high (Lepš 1999, Hájková et al. 2009).

We further demonstrated non-random dispersion of non-clonal nominal traits. Coexisting species had fewer representative pollen vectors and fruit types in fen grasslands (Table 4), characterized by wetter conditions and lower productivity. These conditions coincide with the prevalence of members of the *Cyperaceae*, which are mostly anemogamous plants producing achenes. On the other hand, coexisting species in wet grasslands were slightly richer in flowering phenology; although this pattern was not significant (Table 2), the effect size of this test increased significantly with plot moisture (Table 3). Additionally, flowering phenology was nearly significantly overdispersed when analyses examined only wet grassland plots (Electronic Appendix 7). Obviously, many phenological aspects alternate in small spring fen grasslands in the study area, starting with *Tussilago farfara* in early spring followed by *Eriophorum angustifolium* and *Dactylorhiza majalis* in spring, *Eriophorum latifolium* and *Epipactis palustris* in summer and *Parnassia palustris* and *Gentianopsis ciliata* in autumn. Evolution of different flowering phenologies may be driven by interactions with pollinators (e.g. Pleasants 1980, Devaux & Lande 2010), but in our case many examined plants are anemogamous and, the effects were lower for neighbouring drier plots. Coexisting plant species may also differ in phenology because flowering generally coincides with peak resource needs, such that species differing in flowering time may also avoid competition, as expected under Limiting Similarity Theory. Our results suggest that this pattern is confined to high moisture, low biomass parts of these grasslands, suggesting that tem-

Table 4. – Results from regression analyses testing whether plot-level effect sizes of our tests for each nominal trait and each test statistic change predictably with above-ground dry biomass production of plots (25 × 25 cm plots). All regressions have a sample size of 126 plots; bold values signify type-1 error rates at α < 0.05 (i.e. P-values).

Plot characteristic	Trait	Test statistic	Slope	R2	P-value
Plot biomass	Flowering phenology	Richness	–0.024	0.047	**0.015**
		Evenness	–0.004	0.001	0.722
	Fruit type	Richness	0.017	0.029	0.058
		Evenness	0.016	0.018	0.133
	Pollen vectors	Richness	0.020	0.024	0.082
		Evenness	–0.012	0.015	0.177
	Clonal growth organs	Richness	0.010	0.013	0.199
		Evenness	0.017	0.017	0.152
	Branching type	Richness	0.006	0.002	0.672
		Evenness	–0.011	0.014	0.181
	Leaf distribution	Richness	–0.027	0.095	**< 0.001**
		Evenness	–0.021	0.072	**0.002**
	Lateral spread	Richness	–0.025	0.035	**0.035**
		Evenness	–0.013	0.014	0.182
Plot moisture	Flowering phenology	Richness	0.019	0.285	**< 0.001**
		Evenness	0.003	0.006	0.394
	Fruit type	Richness	–0.007	0.043	**0.019**
		Evenness	–0.009	0.058	**0.007**
	Pollen vectors	Richness	–0.009	0.045	**0.017**
		Evenness	–0.002	0.006	0.408
	Clonal growth organs	Richness	–0.001	< 0.001	0.817
		Evenness	–0.020	0.202	**< 0.001**
	Branching type	Richness	0.008	0.023	0.090
		Evenness	–0.001	0.002	0.655
	Leaf distribution	Richness	0.007	0.068	**0.003**
		Evenness	0.004	0.021	0.103
	Lateral spread	Richness	0.003	0.006	0.377
		Evenness	0.005	0.019	0.123

poral niche partitioning may be more likely under particular environmental conditions. These wet fen grasslands are extremely phosphorus-limited (Rozbrojová & Hájek 2008) and species growing early in spring may gain the advantage in phosphorus uptake, thus the observed pattern for flowering phenology may be driven by a more general growth phenology pattern. Importantly, coexisting plant species were no more or less rich with respect to flowering phenology than would be expected by chance. It is possible that a different observation would be observed for plots at the more extreme end of a low biomass and high moisture gradient. Further studies focused more tightly on particular grassland types are therefore needed.

Additionally, coexisting species possessed a greater variety of fruit types than expected by chance. Fruit type is often strongly phylogenetically conserved and may here be an

indicator of phylogenetic overdispersion within plots (e.g. Tofts & Silvertown 2000, Prinzing et al. 2008). On the other hand, this pattern may be related to variable seed dispersal or anti-granivory strategies. While the intent of this study was to examine a large number of traits that may have yet unexplored consequences on community dynamics, where patterns have been observed, further analysis will be necessary to clarify underlying mechanisms for our observed patterns.

See http://www.preslia.cz for Electronic Appendix 1–7

Acknowledgements

Souhrn

Studovali jsme uspořádání společenstev ve vztahu k funkčním vlastnostem 216 druhů rostlin. Různě druhově bohatá travinobylinná společenstva jsme snímkovali podél vlhkostního gradientu od subxerotermních luk po vápnitá prameništní slatiniště. Použili jsme tři kontinuální vlastnosti druhů (maximální a minimální výška rostliny, hmotnost semen) a sedm kategoriálních vlastností (květní fenologie, typ plodu, přenos pylu, typ klonálních růstových orgánů, typ větvení, rozložení listů a boční šíření). Některé druhy byly přiřazeny k více než jedné kategorii v dané vlastnosti (např. typ klonálních růstových orgánů). Na dvou různých velikostech ploch (25 × 25 cm a 75 × 75 cm) jsme pomocí nulového modelu testovali, zda je uspořádání společenstev náhodné vzhledem ke studovaným vlastnostem rostlin, a to zvlášť pro prezenčně-absenční a zvlášť pro kvantitativní data. Na ploše 25 × 25 cm jsme testovali i vliv hmotnosti nadzemní biomasy a vlhkosti půdy na toto uspořádání. Zjistili jsme, že druhy byly ve zkoumaných společenstvech výškově náhodně rozmístěny a převažovaly druhy s lehčími semeny. Tento výsledek platil pro obě velikosti ploch, při použití jak prezenčně-absenčních, tak i kvantitativních dat. Studovaná společenstva byla nenáhodně uspořádána vzhledem k pěti studovaným vlastnostem (hmotnost semen, typ plodu, typ klonálních růstových orgánů, typ větvení a rozložení listů), avšak pouze výsledek pro typ větvení je v souladu s predikcemi Teorie limitující podobnosti (tj. rozdílnost vlastností v lokálním společenstvu). U typu plodu a typu větvení se výsledky výrazně lišily v závislosti na tom, zda byla použita prezenčně-absenční nebo kvantitativní data. Obecně ale platí, že výsledky byly stejné pro obě velikosti plochy, což naznačuje, že malá změna ve velikosti plochy nemá na výsledky analýz vliv. Pro některé testované vlastnosti jsme potvrdili významný vztah mezi rozložením vlastností rostlin ve společenstvu a produkcí biomasy nebo vlhkostí půdy, což naznačuje, že zákonitosti uspořádání společenstva vzhledem k různým funkčním vlastnostem rostlin mohou být závislé na množství produkované biomasy a na vlhkosti půdy. Když jsme datový soubor rozdělili podle vlhkosti, popisované nenáhodné rozmístění vlastností rostlin se mnohem více projevilo ve společenstvech slatinišť než subxerotermních luk, a to nejvíce v případě velikosti semen.

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