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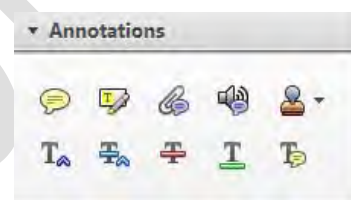
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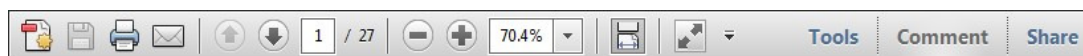
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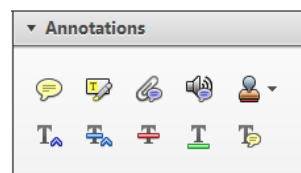**IMPORTANT:** <u>Do not click the "Complete Proof Review" button without replying to all author queries found on the last page of your proof</u>. Incomplete proof reviews will cause a delay in publication.

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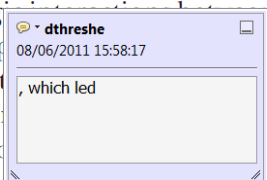### 1. Replace (Ins) Tool – for replacing text.

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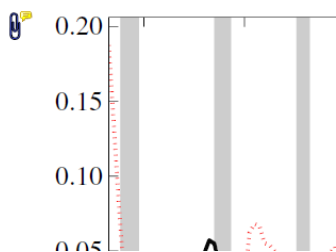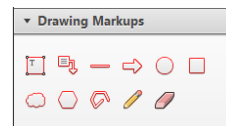
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Changes in assembly rules along a stress gradient from open dry grasslands to wetlands

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Summary

1. A central issue of community ecology is finding rules that explain the composition and abundance of coexisting species. Nowadays two main processes, environmental filtering and limiting similarity, are thought to play the main roles in structuring communities. Their relative importance under different environmental conditions, however, is still not properly clarified.

2. We studied the strength and the effect of environmental filtering (causing convergence) and limiting similarity (causing divergence) in 137 sample plots along an extremely long environmental gradient ranging from open sand grasslands to highly productive marshes, using a trait-based approach. The main environmental gradient (i.e. productivity) was characterized by the Normalized Difference Vegetation Index, an indicator of above-ground live biomass. Cover of the plant species was estimated visually. Values of 11 plant traits were collected from field measurements and data-bases. Mean and dispersion of the trait values of the plots were quantified by community-weighted means and Rao's quadratic entropy. Trait convergence and divergence were tested by randomization tests, followed by the study of changes in effect size along the productivity gradient by fitting generalized additive mixed models (GAMM).

3. For vegetative traits we found mainly convergence, indicating the filtering effect of environmental constraints, while traits related to regeneration showed divergence.

4. The strength of convergence in vegetative traits generally decreased as productivity grew, indicating that while under harsh conditions environmental constraints strongly limit the possible trait values, under more benign conditions various water and nutrient use strategies are adaptable. At high productivity, the strength of divergence in regenerative traits decreased. Since the larger diversity of vegetative traits found here reduces competition, the importance of diverse reproductive strategy is probably lower.

5. *Synthesis:* Our results partly support the stress-dominance hypothesis, but reveal that assembly rules are more complex. The relative importance of environmental filtering and limiting similarity depends on the trait and on the environmental conditions of the habitat. Traits related to resource use are generally limited by environmental filtering, and this restriction is weakening as conditions become more favourable, while traits related to regeneration are constrained by limiting similarity and are more diverse under harsh conditions.

Key-words: community assembly, determinants of plant community diversity and structure, effect size, environmental filtering, environmental gradient, habitat filtering, plant functional trait, productivity gradient

Introduction

Searching for assembly rules that explain or predict the species composition and abundance of a local community is a long-held issue of ecologists (Keddy 1992). Classical studies tried to find general rules in community assembly using species identities. Since identifying the species occurring in a community cannot give insight into the mechanisms underlying community assembly and provides little information about the function of the species, nowadays, the trait-based approach is the most widely used tool in exploring community assembly rules (McGill *et al.* 2006; Götzenberger *et al.* 2012). Focusing on traits instead of species identities may help us find general principles that are valid for communities

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building from different species pools (Fortunel *et al.* 2014). Also, using this approach allows quantitative comparisons to be made between communities that have hardly any or no species in common (Webb *et al.* 2010).

Several theories have been developed on the mechanisms that drive the dynamics of populations and thus determine species composition in a community. The possible processes can be organized into a series of filters selecting the species from the global species pool (Keddy 1992; HilleRisLambers *et al.* 2012). The list of possible processes includes dispersal limitation, environmental suitability, and interactions between co-occurring species. In a relatively small area, where dispersal limitation does not constrain the occurrence of species, the abiotic conditions strongly determine which species of the regional species pool can establish, survive and reproduce themselves. Only species with functional trait values adaptive in the given habitat can persist; thus, abiotic conditions limit the range of the possible trait values of the co-occurring plants. This process is called environmental filtering and it causes trait convergence (Keddy 1992). Species with overlapping functional trait ranges, however, use resources in a similar manner, and thus, the interspecific competition between them for resources presumably hinders co-occurring species with highly similar trait values. This limiting similarity of co-occurring species causes trait divergence in a given community (MacArthur & Levins 1967; Stubbs & Wilson 2004). If there is within-plot environmental heterogeneity, it may lead to within-plot spatial niche segregation that also can be interpreted as limiting similarity (Szilágyi & Meszéna 2009).

The two contrasting assembly processes, environmental filtering and limiting similarity, may occur for different niche axes (Weiher, Clarke & Keddy 1998; Cavender-Bares *et al.* 2004), and thus, the various functional traits may respond differently to the two filtering processes. Previous case studies (e.g. Swenson & Enquist 2009; Carboni *et al.* 2014; Wellstein *et al.* 2014) analysing traits separately found both trait convergence and trait divergence confirming this hypothesis. The traits that play an important role in the adaptation of the species to the given environmental conditions (Begon, Harper & Towsend 1996) or to the given level of non-regulating environmental variables (Krebs 2001) react intensely to environmental filtering, while traits related to resource acquisition are subject to limiting similarity (Weiher & Keddy 1995). Traits linked to competitive ability in asymmetric competition (e.g. height in competition for light) are often regarded as exceptions to this rule: in the case of these traits, convergence is expected (Grime 2006; Mayfield & Levine 2010). We do not share this view. Becoming more similar to the stronger competitor is an equalizing mechanism, while it is only stabilizing mechanisms that lead to stable coexistence (Chesson 2000) and these mechanisms are based on differences among species. For example Kohyama & Takada (2009) have shown that species asymmetrically competing for light can coexist if they differ both in height at maturity and fecundity.

The strength and the relative importance of environmental filtering and limiting similarity may change along productivity or stress gradients. While this hypothesis is widely accepted and proved by several case studies in various ecosystems (e.g. Mason *et al.* 2011, 2012; Pakeman 2011), there is still controversy over the direction and causes of the changes (Carboni *et al.* 2014). The stress-dominance hypothesis predicts that it is environmental filtering and the resulting trait convergence that plays the major role in harsher environments, while limiting similarity and the resulting trait divergence will be more important in more favourable habitats (Weiher & Keddy 1995; Swenson & Enquist 2007; Coyle *et al.* 2014). In line with the stress-dominance hypothesis, Mason *et al.* (2011) found that niche overlap decreased with increasing productivity, indicating that limiting similarity has a stronger effect in more productive habitats. On the other hand, the opposite trend, transition from trait divergence to trait convergence with increasing productivity was found in other studies (Pakeman 2011; e.g. Mason *et al.* 2012; Carboni *et al.* 2014). This is in agreement with Grime's prediction (2006, see also Mayfield & Levine 2010) that higher productivity should lead to trait convergence since increasing competition excludes species with traits associated with poorer competitive ability. Navas & Violle (2009) argued that trait convergence is expected at both ends of the productivity gradient, and trait divergence at medium productivity. Overall, there is still ongoing controversy on how the strength of trait divergence and convergence varies along productivity gradients.

Trends may depend on which traits are involved in the study (Bernard-Verdier *et al.* 2012; Spasojevic & Suding 2012) and which part of the stress gradient is sampled (Bernard-Verdier *et al.* 2012). Therefore, trait convergence/divergence patterns should be analysed along as long gradients as possible to test the predictions of the two competing theories, environmental filtering and limiting similarity. At the same time, the effects of other confounding factors, especially dispersal limitation should be reduced as much as possible. Sampling plots therefore have to be situated within a relatively small area, which limits the length of productivity gradients. As a consequence, previous studies were often conducted within a single habitat type [e.g. in dolomite (Bernard-Verdier *et al.* 2012), or wet grasslands (Carboni *et al.* 2014)]. The Kiskunság in Central Hungary is an ideal setting to overcome these limitations: due to its climate, diverse geomorphology and special soil characteristics, soil moisture availability is strikingly diverse, allowing us to study an extremely long productivity gradient within a relatively small area (Kovács-Láng *et al.* 2008). This gradient ranges from semi-desert like open sand grasslands through closed dry, mesic and wet grasslands to wetlands and reed beds.

The aim of this study was to answer the following questions:

1. Is there convergence, and for which traits?
2. Is there divergence, and for which traits?
3. Does their strength change with increasing productivity?
4. How do the optimal (mean) trait values and the values filtered out by environmental filtering vary along a productivity (stress) gradient?

We hypothesized that species composition is formed by both environmental filtering and limiting similarity and thus trait convergence and trait divergence could occur alongside each other. We expected convergent pattern for traits related to vegetative growth and divergence for traits related to regeneration. We expected that stress-dominance hypothesis would be proven, that is in the less productive part of the gradient environmental filtering, at the more productive part limiting similarity will play the major role in structuring communities.

Materials and methods

STUDY AREA

The Orgovány grassland site is located in the middle of Hungary in the Danube–Tisza Interfluve. It is part of the Sand Ridge Region in the Kiskunság National Park (see Fig. S1, Supporting Information). The climate is temperate with continental and Mediterranean features. The mean annual temperature is 10.5 °C, ranging from −1 °C in January to 22 °C in July. The mean annual precipitation is 550 mm, distributed unevenly; long and severe droughts in the summer are frequent (Borhidi 1993). The effect of drought is enhanced by the poor water retention capacity of the nutrient poor, coarse, calcareous, sandy soil; therefore, soil moisture content is the main limiting resource for vegetation. Due to the transitional climate and diverse geomorphology, habitat diversity is strikingly high. The area is in a transitional zone between forest and steppe vegetation zones, where the climate is incapable of supporting continuous closed forest vegetation. Therefore, prior to human impact the area was covered by forest patches dominated by pedunculate oak (*Quercus robur*), grasslands, and in the depressions, wetlands (Fekete, Somodi & Molnár 2010). The undulating surface of the region and the low water holding capacity of the sandy soil lead to fine-scale changes in vegetation: the top of the dunes feature semi-desert-like open sand grasslands, while in the depressions, where the roots of the plants can reach the water-table, meadows and marshes are abundant. The area was under strong human impact in recent centuries. Although there still exist large remnants of the semi-natural vegetation, most of the more productive grasslands were ploughed and used as arable fields, while the more elevated areas were often used as grazing field – typically for sheep. In the 1980s, numerous arable fields were abandoned and were either planted with alien tree species, mainly black locust (*Robinia pseudo-acacia*) and black pine (*Pinus nigra*) or left aside for spontaneous succession.

Our research was carried out in a 5 km × 13 km area (centred on 46°51′N, 19°27′E, 105–130 m a.s.l.) covered mostly by semi-natural vegetation, where productivity is primarily determined by the availability of soil moisture. The plant communities present in the area ranged from semi-desert-like open grasslands to marshes and reed beds, thus forming an extremely long productivity gradient. The area is protected; thus, in the dry habitats there is no human disturbance and the wet meadows are under conservation management – that is, they are mechanically mowed once a year.

VEGETATION SAMPLING AND ENVIRONMENTAL CHARACTERIZATION

Vegetation was sampled by 137 plots in a stratified random design: that is, (1) we chose plots only in semi-natural patches, and (2) a minimum of five to a maximum of 15 plots were sampled in each vegetation type identified during a preliminary field survey. In each 2 × 2 m sample plot the vascular plant species were identified and their percentage cover was visually estimated. We characterized the productivity of the plots by their values of Normalized Difference Vegetation Index (NDVI) (Rouse *et al.* 1974; Sellers 1985). NDVI is sensitive to differences between reflectance values of red and near-infrared radiation, which is caused by the absorption of red radiation by chlorophyll (Tucker & Sellers 1986). Thus, NDVI is a frequently used proxy for above-ground live biomass in temperate perennial grasslands (Paruelo *et al.* 1997). The amount of above-ground live biomass in the peak of the growing season correlates with annual net primary production in temperate steppe grasslands (Scurlock, Johnson & Olson 2002). We measured red (660 nm) and near-infrared (810 nm) radiation (irradiation and reflected radiation) using a portable Cropscan MSR87 multispectral radiometer (Cropscan, Inc., Rochester, MN, USA). For each plot, four subplots of one-by-one metre were sampled. NDVI was calculated from the radiation measurements for each subplot individually, and then, these values were averaged. NDVI ranged from 0.208 to 0.894, which corresponds to 1–529 g m^{-2} above-ground dry material, according to calibration made in the same study site (M. Kertész & G. Ónodi, unpublished data).

In the more arid habitats the peak of the biomass is in early June, while in the more productive habitats in July–August. Therefore, fieldwork was carried out in June in the dry grassland plots and in July in the meadows and marshes.

TRAIT SELECTION AND SAMPLING

We chose 11 traits considered to reflect plant strategies along environmental gradients (Weiher *et al.* 1999; Westoby *et al.* 2002). We used only relatively easily and quickly measurable 'soft traits' that are often good proxies of the more accurate but hard-to-quantify indicators of plant function (so-called hard traits; Weiher *et al.* 1999; Cornelissen *et al.* 2003).

We used both numerical and categorical traits in this study since categorical traits have previously been considered useful in addition to numerical traits (Schellberg *et al.* 1999). Five numerical traits: canopy height, leaf size, specific leaf area (SLA), leaf dry matter content (LDMC), and seed weight and six categorical traits: plant growth form, ability to reflower, shoot growth form, leaf distribution, age at first flowering and lateral spread were used in the analysis (see details in Table 1).

The numerical trait values of the 278 species found in the 137 plots are partly from trait data-bases and literature review, and partly from field sampling and measurements carried out in the study area. We used the LEDA Traitbase (Knevel *et al.* 2003; Kleyer *et al.* 2008) and CLO-PLA – data-base of clonal growth of plants (Klimeš & Klimešová 1999; Klimešová & De Bello 2009). Seed weight values were taken from the data set of Török *et al.* (2013) and from the Royal Botanic Gardens Kew Seed Information Database (Royal Botanic Gardens Kew 2014). During field sampling and measurement we followed the standard protocols suggested by Cornelissen *et al.* (2003) and the standards of the LEDA Traitbase (Knevel *et al.* 2003; Kleyer *et al.* 2008). The categorical trait values were assembled from the data-bases mentioned above and from the FLÓRA data-base (Horváth *et al.* 1995). For the species not covered by the data-bases, we used field expert's estimation. The proportion of the data-base-originated and field-collected data and the per cent of species with missing data are shown in Table 1. Based on previous studies (Pakeman &

Table 1. List of functional plant traits used. For each trait, only the categories used to categorize the 278 species found in the 137 sampling plots are listed

Trait	Type*	Unit or category	Definition	Missing data (% of species)	Data from field measurements (% of species)	Data-base sources used[†]
Plant growth form	C	Chamaephyte Hemicryptophyte Geophyte Liana Summer annuals Winter annuals	Combination of Raunkiaer's life-form, plant morphology and living conditions	1.44	0	FLORA LEDA
Ability to reflower	C	Monocarp Polycarp	The plant's ability to flower repeatedly	1.80	0	LEDA
Leaf distribution	C	Rosette Semi-rosette Leaves distributed regularly along the stem Shoot scarcely foliated	Distribution of leaves along the stem	2.16	0	LEDA
Shoot growth form	C	Liana Stem erect Stem ascending to prostrate Stem prostrate Emergent	Canopy structure of shoots	0.72	0	LEDA
Age at first flowering	O	Flowering in the first year flowering between 1 and 5 years flowering after 5 years	The earliest age at which a plant can flower in the field	1.08	0	LEDA
Lateral spread	O	1: < 0.01 m 2: 0.01-0.25 m 3: > 0.25 m	Distance of lateral spread of the plant in 1 year	1.80	0	LEDA Clo-Pla
Canopy height	N	m	Height of the highest photosynthetic issue	3.24	42.10	LEDA
Leaf size	N	mm^2	Projected surface area of a leaf	5.76	41.37	LEDA
SLA: specific leaf area	N	$mm^2\ mg^{-1}$	Leaf area/dry leaf mass	5.76	41.37	LEDA
LDMC: leaf dry matter content	N	$mg\ g^{-1}$	Dry leaf mass/fresh leaf mass	6.83	41.01	LEDA
Seed weight	N	g	Thousand-seed weight	7.19	0	Török SID

*N = numerical; C = unordered categories; O = ordered categories.
[†]FLÓRA = FLÓRA data-base (Horváth *et al.* 1995); LEDA = LEDA data-base (Knevel *et al.* 2003; Kleyer *et al.* 2008); CLO-PLA = CLO-PLA – data-base of clonal growth of plants (Klimeš & Klimešová 1999; Klimešová & De Bello 2009); Török = data set of Török *et al.* (2013); SID = Royal Botanic Gardens Kew Seed Information Database (Royal Botanic Gardens Kew 2014).

Quested 2007; Pakeman 2014) the 3% missing data does not cause considerable difference between the estimated and the actual community level trait indices.

Along our extremely long environmental gradient there are continuous changes in species composition and at the two ends of the gradient there are no common species. Thus, in this study we did not take intraspecific trait variability into account, accepting 'a central assumption of plant comparative ecology', which implies that variation within species is smaller than the differences between species (Westoby *et al.* 2002; Shipley 2007), and which was demonstrated in previous studies (Pontes *et al.* 2010; Kattge *et al.* 2011). The preliminary study of the inter- and intraspecific trait variability of the species we sampled supported this assumption (Fig. S2, Supporting Information).

STATISTICAL ANALYSIS

Thirty-four plots, where (i) the total cover of species with missing trait data exceeded 5% or (ii) the number of species with trait data was < 10, were excluded, and therefore, we used only 103 plots in the statistical analysis.

Information of categorical traits was converted into quantitative variables using metric multidimensional scaling (Podani 2000). Dissimilarity matrix of species was calculated by the Gower formula developed for handling binary and nominal variables (Podani 2000), and this dissimilarity matrix was used in the ordination. Axes were interpreted by visual inspection of spider plots of categorical variables (Fig. S3, Supporting Information). The first ordination axis (abbreviated as Axis1), which relates to life span explains 9.83% of the variation. Negative values indicate short life span (correlating with annual life-form, flowering in the first year, monocarpy, inability to spread laterally), while positive values are associated with long life span (perennial life-forms, polycarpy, flowering after the first year, ability to lateral spread). The second axis relates to shoot form: negative values indicate erect stem with semi-rosette forming leaves, while positive values are associated with regular distribution of leaves on stems ascending to prostrate. This axis explains 6.88% of the total variance. Hereafter, these two principal components were called 'life span' and

'shoot form' and were used in the further analyses instead of the correlating categorical values.

Following Ricotta & Moretti's (2011) recommendation, we quantified the mean and the dispersion of the trait values of the plots by community-weighted mean (Garnier *et al.* 2004) and Rao's quadratic entropy (Botta-Dukát 2005; Lepš *et al.* 2006), respectively. Community-weighted mean (CWM) expresses the mean trait value in the community weighted by the relative abundances of the species. Rao's quadratic entropy (RaoQ) is the mean dissimilarity between two species weighted by the product of their relative abundances. Note that community-weighted variance (Sonnier, Shipley & Navas 2010; Bernard-Verdier *et al.* 2012), the mean quadratic difference of species' trait values from the CWM weighted by their relative abundances equals RaoQ if half of the squared Euclidean distance is applied in its calculation (Champely & Chessel 2002). For details of the formulas, see Ricotta & Moretti (2011). CWM and RaoQ were calculated for each continuous trait and for the first two PCoA axes of categorical traits (see above) separately.

Trait convergence and divergence values were tested by a randomization test reshuffling trait values among species (Stubbs & Wilson 2004). Our simulation studies (Botta-Dukát & Czúcz 2015) proved that this test can detect the existing trait convergence due to environmental filtering if the data set covers a wide range of environmental variables, and can also detect the existing divergence due to competition if there is no direct or indirect effect of environmental filtering on that trait. Probabilities of type I error (*P*-values) were estimated for each plot separately from 9999 random communities. To improve the statistical power, plot-level p-values were combined using Fisher's omnibus test (Sokal & Rohlf 1981). If the null hypothesis is valid for each plot-level test, the calculated test statistics follow chi-square distribution with 2*number of tests degree of freedom (in our analysis, d.f. = 206). Since distribution of the Rao's quadratic entropy in the randomized communities was often highly right-skewed (see Fig. S4, Supporting Information), standardized effect sizes (Gotelli & McCabe 2002) are inappropriate to measure the strength of convergence/divergence (Ulrich & Gotelli 2010; Bernard-Verdier *et al.* 2012). Therefore, Chase *et al.* (2011) and Bernard-Verdier *et al.* (2012) applied linearly transformed p-values as effect size (ES). We improved this approach by replacing linear transformation with probit transformation. Probit transformation is used as alternative of logit transformation in generalized linear models to transform probabilities into minus infinity to infinity range (Dobson 2002). The advantage of probit transformation over linear or logit transformation is twofold: (i) if null distribution is Gaussian, the calculated effect size is asymptotically equal to Gotelli's standardized effect size (SES); and (ii) if the null hypothesis is true, both SES and ES follow standard normal distribution. Effect sizes were plotted against the NDVI values, and their trends were tested by fitting generalized additive models (GAM) that allow the fitting of a nonlinear curve without *a priori* specification of its functional form (Wood 2000; Zuur *et al.* 2009). If the homoscedasticity of residuals does not hold, a generalized additive mixed model was fitted choosing the most appropriate variance structure by the minimum AIC criteria (Zuur *et al.* 2009).

Comparing trait dispersion with random expectation cannot show which species and which trait values were preferred and filtered out. The trend of the community-weighted mean values shows the change of preferred values incorporating information of abundance. Since it does not inform us on the filtered out trait values, 5 and 95 percentiles of trait values (hereafter called lower and upper boundary) were also calculated for each plot, without weighting by abundance. These percentiles were chosen instead of minimum and maximum values because they were less influenced by outliers. We used binary data without weighting with abundance, because we were interested in which trait values were excluded by the local conditions. Changes of CWM (mean, upper and lower boundaries) along the productivity gradient were tested by fitting linear trend lines. If the homoscedasticity of residuals did not hold for ordinary least square regression, generalized least squares were used choosing the most appropriate variance structure by the minimum AIC criteria (Zuur *et al.* 2009).

All calculations were performed using the 'mgcv' (Wood 2011), 'nlme' (Pinheiro *et al.* 2014) and 'FD' (Laliberté & Legendre 2010; Laliberté, Legendre & Shipley 2014) add-on packages implemented in R statistical environment (R Core Team 2014).

Results

In the 103 plots used in the analysis we recorded 239 species and the number of species in the plots varied between 11 and 30.

Fisher's omnibus test found strong evidence for trait convergence when all traits were pooled (Table 2). If traits were analysed independently, there was strong evidence for convergence, that is for the existence of environmental filtering in the case of canopy height, leaf size, SLA and 'life span'. We found evidence of trait divergence and therefore of the existence of limiting similarity only in the case of LDMC and seed weight.

The average effect of trait convergence was stronger under harsher conditions and became weaker with growing productivity in the case of canopy height, leaf size and SLA (Fig. 1). There was an opposite trend for 'life span' and no significant changes in the case of 'shoot form' or if all traits were pooled. Trait divergence became weaker with growing productivity for seed weight, but there was a strong convergence for some plots with high NDVI. The strength of trait divergence for LDMC did not change significantly along the productivity gradient (Fig. 1).

We found changes in the optimal (mean) and filtered out trait values along the productivity gradient. The community-weighted mean of canopy height responded to the productivity gradient as expected: it increased with increasing productivity (Fig. 2). Both the upper and lower boundaries increased, although the former's increase was steeper

Table 2. Results of Fisher's omnibus test. It combines the plot-level p-values of randomization test into an overall test statistic that approximately follows a chi-square distribution

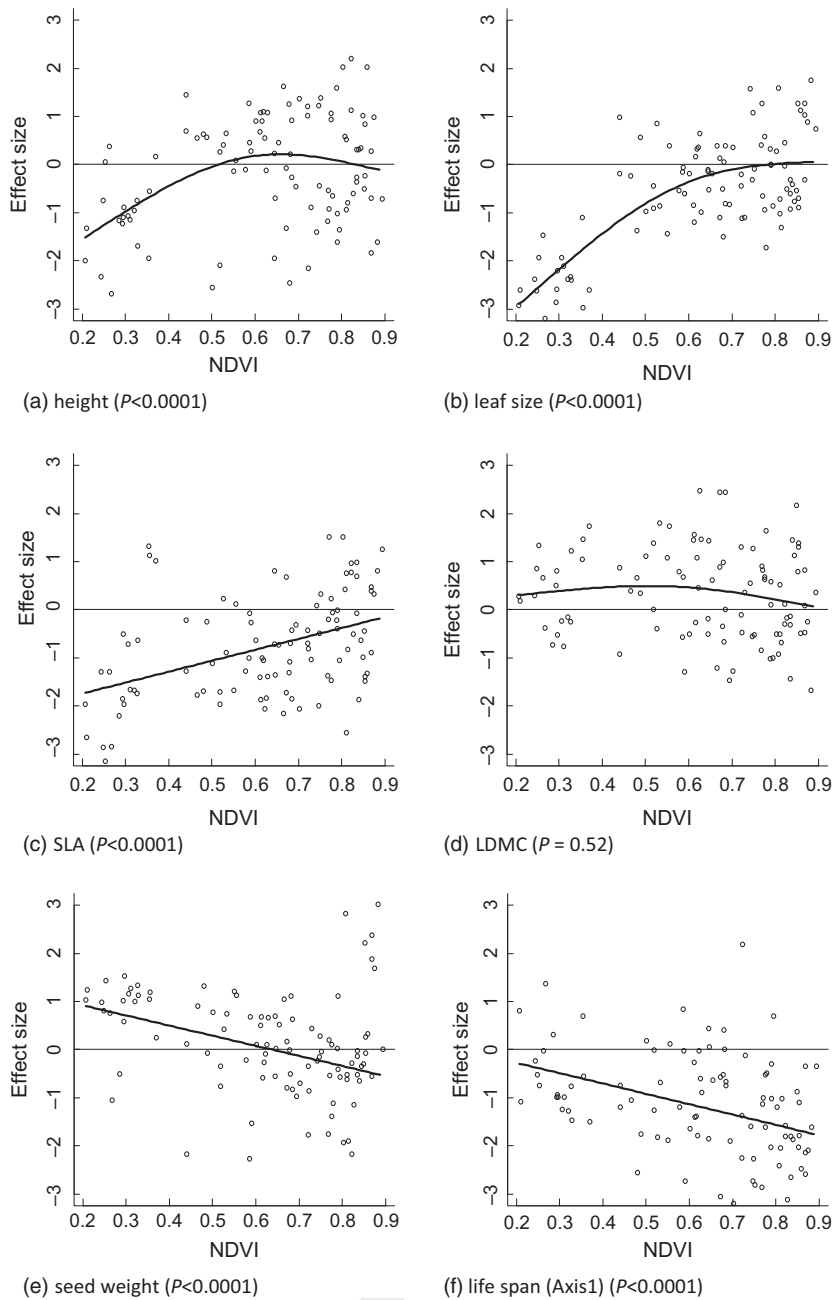|	Trait convergence		Trait divergence	
	Chi-square statistic	*P*-value	Chi-square statistic	*P*-value
All traits	**384.42**	**< 0.001**	81.81	> 0.999
Canopy height	**251.15**	**0.017**	197.97	0.644
Leaf size	**363.8**	**< 0.001**	129.23	0.999
SLA	**394.6**	**< 0.001**	103.17	> 0.999
LDMC	145.06	0.999	**272.95**	**0.001**
Seed weight	183.5	0.868	**241.35**	**0.046**
Axis1 (life span)	**550.89**	**< 0.001**	67.52	> 0.999
Axis2 (shoot form)	196.45	0.672	180.68	0.898

Significant results are highlighted in bold.

Fig. 1. Effect sizes in plot-level tests of trait convergence/divergence along the NDVI (a proxy of productivity) gradient. Positive values indicate divergence, negative ones convergence. Absolute values higher than 1.95 mean that the plot-level test is significant at the 5% level. Lines are trends fitted by GAM; departure of the fitted trend from the horizontal line was tested, and the resulting *P*-values can be seen below the figures in brackets.

(Table 3). We can thus say that tall plants are filtered out in habitats with low productivity, while short ones in habitats with high productivity. Similar trends were observed for the CWM of leaf size, SLA and 'life span' (Fig. 2). The upper boundary of leaf size increased steeply, while the lower boundary grew more moderately. The upper and lower boundaries for SLA run parallel with CWM; filtering is therefore mainly caused by the shift of the preferred value.

Discussion

EVIDENCE FOR COMMUNITY ASSEMBLY PROCESSES

We found evidence for both trait convergence and trait divergence. Convergence was seen in the case of canopy height, leaf size, SLA and 'life span', while divergence was shown in the case of LDMC and seed weight (Table 2). These results indicate that – as expected – both environmental filtering and limiting similarity play a role in forming the community. The higher number of converging traits cannot be interpreted as evidence for environmental filtering being generally more important than limiting similarity, since the number of significant results for both types of traits is influenced by the detectability of effects that depend on environmental heterogeneity and the randomization method. Weiher & Keddy (1995) predicted that trait convergence becomes the main trend if the 'scale of investigation' is high; that is, there is high environmental heterogeneity, while trait divergence can be easily detected only if environmental heterogeneity is low. The simulation study by Münkemüller *et al.* (2014) supported
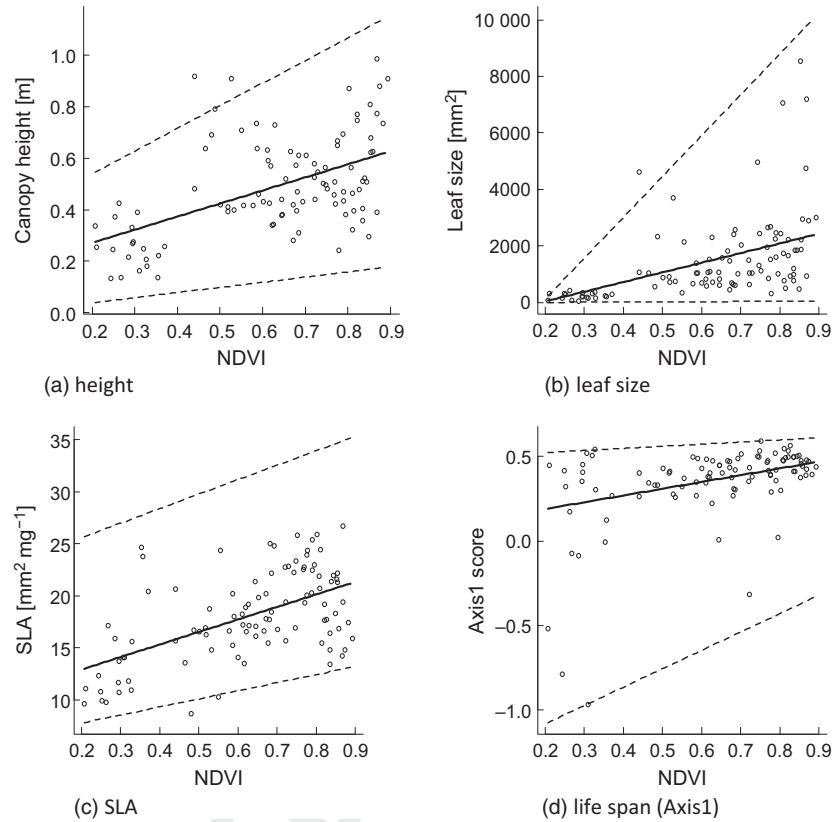
Fig. 2. Community-weighted trait values in the sampled plots (points), their trend (solid line) and the trend of lower and upper boundaries (dashed lines) along the NDVI (a proxy of productivity) gradient. Slopes of the trend lines (estimates and 95% confidence intervals) are summarized in Table 3.

Table 3. Slopes of the regression lines of lower/upper boundaries and community-weighted means against NDVI values (the proxy of productivity gradients). Numbers in brackets are the 95% confidence interval values. Since none of the intervals contains the zero, all slopes are significantly positive

	Lower boundary	CWM	Upper boundary
Canopy height	0.199 (0.153; 0.245)	0.507 (0.339; 0.675)	0.876 (0.676; 1.077)
Leaf size	63.926 (39.11; 88.743)	3412.189 (2533.966; 4290.412)	14 454.33 (10418.97; 18489.69)
SLA	7.763 (6.371; 9.156)	12.009 (8.367; 15.65)	13.866 (9.099; 18.632)
Axis1 (life span)	1.087 (0.784; 1.390)	0.400 (0.177; 0.623)	0.123 (0.073; 0.174)

this prediction: higher environmental heterogeneity makes it easier to detect environmental filtering, but on the other hand may mask the effect of limiting similarity. As a consequence, divergence is to be expected within a community, while among communities of different environments, convergence is the general pattern (Weiher & Keddy 1995; Grime 2006; Swenson *et al.* 2007). Since our study was carried out along a gradient extending from open sand grassland through meadows to marshes, with extreme heterogeneity in soil moisture availability and involving several plant community types, the sampling design is more suitable for detecting environmental filtering than limiting similarity.

The randomization method applied can also influence which effect can be detected. The method we used can detect trait divergence due to limiting similarity only if the effect of habitat filtering is negligible for the studied traits (Botta-Dukát & Czúcz, in press). Therefore, the fact that the number of cases for significant convergence was twice the number of

cases for divergence could be the consequence of the applied methods. We can be sure only in that both assembly rules are operating. In spite of this limitation, we prefer this conservative approach where the type I error rate is not higher than the predefined significance level. Moreover, it gives unbiased estimation on the occurrence and strength of environmental filtering.

Analysing the traits individually, canopy height, leaf size, SLA and 'life span' showed convergence (Table 2). This is in line with previous studies predicting the predominance of convergence in the case of traits associated with habitat conditions (Grime 2006). Though LDMC is generally thought to indicate similar plant ecological strategy to SLA and they are often correlated with each other (Cornelissen *et al.* 2003; Wright *et al.* 2004), in our study LDMC, the indicator of leaf tissue density (Wilson, Thompson & Hodgson 1999) showed a different pattern: we observed divergence (Table 2). Mason *et al.* (2011) also found that LDMC and SLA showed

evidence for contrasting assembly processes. They explained this contradiction by the difference in the light capture strategies of the species. A further issue that we have to consider is the comparability of trait values from the literature and from our field sampling. LDMC, which measures the fresh weight/dry weight of the leaf, strongly depends on the sampling methods, that is measured on rehydrated or not rehydrated leaves, and in the latter case on the weather conditions at the time of sampling. SLA, which measures leaf surface/ dry weight, is less sensitive to these factors.

While vegetative traits generally converged in our experiment, indicating the presence of environmental filtering, we found divergence in the case of seed weight, the only clearly generative trait in our analysis (Table 2). This supports Grime's (2006) concept that divergence should be common for reproductive traits, while convergence is predominant for vegetative traits, which are associated with the adaptation to environmental conditions (incl. the productivity of the habitat). It is also in line with several previous studies, where seed size diverged within local communities (Diaz, Cabido & Casanoves 1998; Swenson & Enquist 2009), although examples of convergence were also observed (May *et al.* 2013). Since seed size is an indicator of reproductive strategy (Tilman 1988), its divergence can help reduce competitive pressure when habitat filtering constrains the possible range of traits related to resource use and acquisition.

Life span, the combined trait composed of categorical traits showed a convergent pattern (Table 2). This variable is created from traits not purely vegetative or reproductive. Thus, the convergence we found here can be caused by the weaker divergence of the reproductive 'component' of the trait being outweighed by the strong environmental constrains causing convergence on the vegetative 'component' of the trait.

CHANGES ALONG THE PRODUCTIVITY GRADIENT

Several previous studies predicted and found changes in the strength and the relative importance of environmental filtering and limiting similarity along environmental gradients as shown in the introduction. There is, however, strong inconsistency regarding the size and even the direction of this effect. Individual traits can show different patterns, increasing this inconsistency even further. A possible reason for this inconsistency is that most of the studies where the role of propagule limitation could be excluded were carried out along relatively short range of a possible environmental gradient, often within one habitat type (e.g. in wet meadows (Mason *et al.* 2011; Carboni *et al.* 2014), mesic grasslands (Maire *et al.* 2012), dolomite rangeland (Bernard-Verdier *et al.* 2012)). Another explanation can be that different variables were used as proxy of productivity [soil properties (Bernard-Verdier *et al.* 2012; Mason *et al.* 2012), biomass (Mason *et al.* 2011)] and that in some papers productivity was combined with other factors [with disturbance (Mason *et al.* 2011; Bernard-Verdier *et al.* 2012; Maire *et al.* 2012), land-use (Pakeman 2011)]; thus, they may jointly result in the observed pattern. In cases like this, where the effects are

idiosyncratic, general trends can be detected by meta-analysis, but it would require more case studies than have been published. Thus, our results obtained along our extremely long gradient, where only productivity changed, can help reveal the general pattern.

Our findings pertaining to vegetative traits are in line with the stress-dominance hypothesis (Coyle *et al.* 2014), which predicts the dominance of environmental filtering under harsh conditions and the dominance of limiting similarity in more favourable habitats. Although we did not detect a shift from convergence to divergence, we observed a similar pattern: decreasing convergence with increasing productivity in the case of canopy height, leaf size and SLA (Fig. 1). To understand the biological background of this changing strength of trait convergence, we have to study which values are filtered out and how the optimal value (the mean) changes along the gradient. We found that the CWM of canopy height, SLA, leaf size and 'life span' increased as conditions became more favourable (Fig. 2). Therefore, tall plants with large and soft leaves are filtered out at low productivity, while under more benign conditions short plants 'disappear', but there is no strong selection on small-leaved plants. In the case of SLA the optimal value is increasing along the gradient, and values strongly differing from the optimum (mean) are filtered out. The CWM of 'life span' also changed, indicating that at high productivity short-lived species are filtered out.

Our productivity gradient extended from extremely dry open grasslands to highly productive marshes with closed vegetation. Adler *et al.* (2013) argued that along such long productivity gradients there is a shift in the importance of the environmental factors: while at the harsh end abiotic constrains (mainly shortage of nutrient or water) limit plant growth, at the more productive end competition for light is the strongest constraining factor, selecting for high relative growth rate (Tilman 1988). SLA is a good indicator of relative growth rate, especially when analysing a broad range of functional types (Reich, Walters & Ellsworth 1992). This explains that species selected in harsher environments usually produce smaller, photosynthetically less active leaves (lower SLA) with a higher content of structural carbohydrates (higher LDMC), which protects them against herbivory and physical damages (Poorter & Bergkotte 1992). As productivity increases, nutrient limitation decreases, while competition for light becomes more intense (Wilson & Tilman 1993). This results in higher SLA and lower LDMC values and allows more diverse resource-use strategies, reducing the convergence in leaf traits. An alternative explanation for the weaker convergence in the more productive plots could be that more intensive spatial niche segregation is present here. Although we have no measured data on within-plot environmental heterogeneity, according to our field experience, more productive plots are not more heterogeneous.

In grasslands, tall growth is generally thought to be associated with strong competitive ability (Gaudet & Keddy 1988). It expresses the ability to capture light; therefore, it indicates the plant's capacity for competitive dominance (Keddy 2010). If taller species have a disproportionate advantage over short

ones when light is more limiting than soil nutrients, we could expect convergence at both ends of the productivity gradient: due to the limited productivity at the harsh end and due to the exclusion of smaller plants at the productive end. But along our gradient, convergence became weaker as productivity increased (Fig. 1), and small species were not excluded (Fig. 2). This can be explained by hypothesizing a trade-off between canopy height and other traits that allows the coexistence (Kohyama & Takada 2009).

The clearly reproductive trait, seed weight showed a pattern different from that of vegetative traits: its divergence became weaker as conditions became more favourable; in some plots with high NDVI we even found convergence (Fig. 1). This contradicts Coyle's hypothesis, and is more in line with the findings and predictions of Pakeman (2011), Mason *et al.* (2012), Carboni *et al.* (2014), and supports Grime's (2006) prediction that higher productivity leads to trait convergence. The divergence in reproductive strategy can help reduce competitive pressure where habitat conditions limit the possible range of traits related to resource use. Since there is a trade-off between seed size and seed number (Turnbull, Rees & Crawley 1999; Jakobsson & Eriksson 2000), under severe conditions some species produce numerous small seeds, which can stay longer in the seed bank (Moles, Hodson & Webb 2000) waiting for the suitable conditions, and at least some of which will find a suitable place to germinate, while other species produce fewer but larger seeds with more nutrient reserve, which can help seedlings survive abiotic stress. These differences in seed characteristics contribute to the coexistence due to storage effect (Chesson 2000) in fluctuating environment. As productivity increases, the amplitude of fluctuations decreases; therefore, the importance of divergence in seed size decreases too. Since under more favourable conditions various resource-use strategies can be adaptable, the diversity of reproductive strategy is not essential for reducing competitive pressure. Furthermore, with growing productivity the role of seeds in regeneration becomes smaller, while the role of vegetative spread is growing (see Fig. S5, Supporting Information), further decreasing the importance of seed weight divergence.

The decreasing fluctuation of resources can also explain the increasing convergence of 'life span' (Fig. 2). In strongly fluctuating environments both annuals living their life span in the favourable periods and surviving the stressed season in the form of seeds, and perennials with better resource retention strategies are adaptable (Evenari *et al.* 1975). As productivity grows and stressed periods becomes more moderate and shorter, persisting in the occupied space is more adaptable; thus, short-lived species are filtered out, and longer life span becomes dominant, which corresponds with previous studies (Philips 1982).

Conclusions and implications

Our findings support the hypothesis that both environmental filtering and limiting similarity play a role in forming plant assemblages along our extremely long productivity gradient.

When all traits were pooled, strong convergence was found, but the analysis of individual traits showed that even traits associated with similar functions (SLA and LDMC) can show a different pattern. For vegetative traits related to resource use, convergence was predominant, indicating the presence of environmental filtering. On the other hand, traits related to regeneration showed divergence, indicating limiting similarity. The strength of the assembly forming processes changed along the gradient: the filtering effect of the habitat was stronger under harsher environments, which supports the stress-dominance hypothesis (Coyle *et al.* 2014). As productivity increased, environmental constraints on the traits related to resource use became weaker and the coexistence of various water and nutrient use strategies became possible. Due to this larger diversity in traits related to resource acquisition, the importance of differing in reproductive strategy become less important in maintaining stable coexistence.

Understanding the processes that create and stabilize local plant assemblages and finding out how these processes change along ecological gradients are endeavours of more than academic relevance. Human activity alters environmental conditions directly and indirectly (e.g. through climate change), causing shifts in the composition and abundance of species within communities. The trait-based understanding of the community-forming processes along environmental gradients could therefore be a valuable tool in predicting the possible effects of the changing environment and may help optimize human responses or restoration attempts.

Author contribution

The study was planned by Z. B.-D.; fieldwork (incl. new trait measurements) was organized and performed mostly by B. L., A. Cs. and B. K. (with all authors contributing to the collection of vegetation plot data); NDVI measurements were carried out by G. Ó.; statistical analyses were performed by Z. B.-D. and B. K.; and the manuscript was written by B. L. and Z. B.-D. (with the help of all of the other authors).

Data accessibility

Data used in the analyses are deposited in the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.5r62f

Conflict of interest

The authors have no conflict of interests to declare.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Location of the Orgovány grassland site.

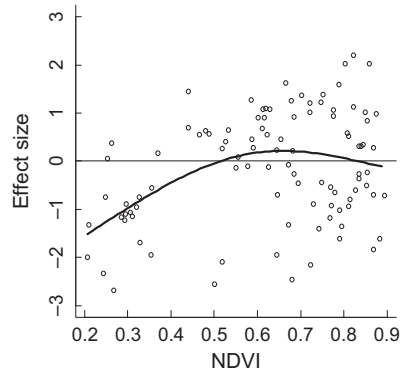**Figure S2.** Comparison of intra- and interspecific trait variation.

Figure S3. Metric multidimensional scaling of species based on their categorical traits and its interpretation by spider plots.

Figure S4. Illustration of the strong right skewness in the distribution of the random values.
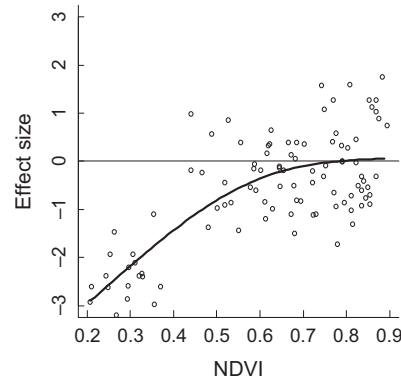
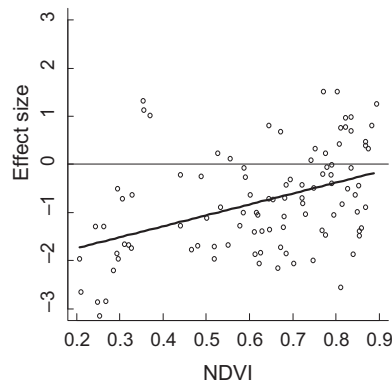**Figure S5.** Changes in lateral spread along the gradient.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract
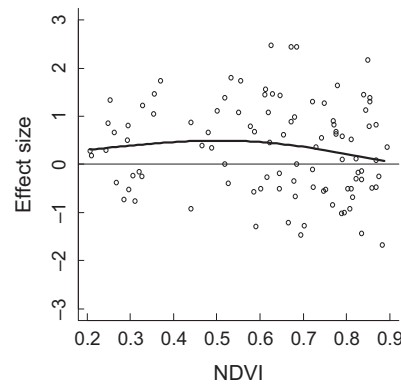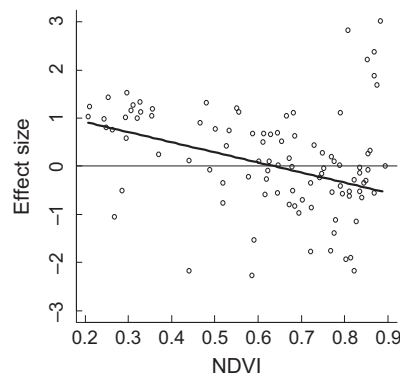of html only. It will not be published as part of main.
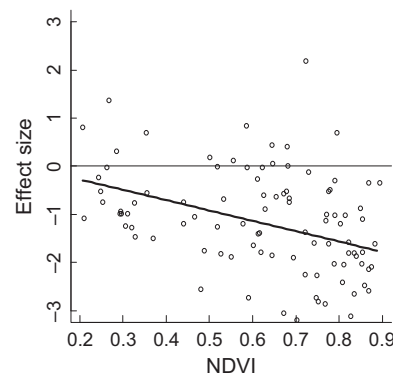

(a) height (*P*<0.0001)

(b) leaf size (*P*<0.0001)

(c) SLA (*P*<0.0001)

(d) LDMC (*P* = 0.52)

(e) seed weight (*P*<0.0001)

(f) life span (Axis1) (*P*<0.0001)

Effect sizes in plot-level tests of trait convergence/divergence along the NDVI (a proxy of productivity) gradient. Positive values indicate divergence and negative ones convergence. Absolute values higher than 1.95 mean that the plot-level test is significant at the 5% level. Lines are trends fitted by GAM; departure of the fitted trend from the horizontal line was tested, and the resulting P-values can be seen below the figures in brackets.

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