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SPECIAL FEATURE: ECOLOGICAL RESTORATION

Impact of mid-successional dominant species on the diversity and progress of succession in regenerating temperate grasslands

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Abstract

Questions: (i) Which species dominate mid-successional old-fields in Hungary? How does the identity of these species relate to local (patch-scale) diversity and to the progress of succession? (ii) Which species have the strongest negative impact on diversity in spontaneous old-field succession and what generalizations are possible about traits of these species? (iii) Are these species dominant or subordinate components in mature target communities? (iv) Do native or alien species have stronger effects on the diversity and progress of succession?

Location: Abandoned agricultural fields (abandoned croplands, orchards and vineyards) at various locations throughout Hungary.

Methods: Vegetation patterns on 112 old-fields, in 25 sites varying in soil and climatic conditions, topography, landscape contexts and land-use histories were sampled. Most old-fields had appropriate seed sources in the immediate vicinity, i.e. natural or semi-natural grasslands (meadows steppes, closed and open sand steppes) as source and target habitats. Age of abandoned fields ranged from 1 to 69 yr, but most sites were between 15 and 60 yr. The cover of vascular plant species (%) was estimated in 2 × 2-m plots. Relationships between diversity, progress of succession (similarity to target communities) and identity of dominants were tested.

Results: A small portion of successional dominants (eight species) had strong negative impacts on diversity. These species belonged to Poaceae, Asteraceae and Fabaceae. Most of these species were wind-pollinated, and capable of lateral vegetative spread. Dominant species varied in size and had, on average, a low requirement for *N* but a high requirement for light. With one exception, *Solidago gigantea*, they were native to the Hungarian flora. Significant differences were found among the impact of successional dominants when dominant species were grouped according to their original role (dominants or subordinates) in natural communities. The overall effect of species identity was also significant. *Bothriochloa ischaemum* was identified as the species with the strongest negative effect on species diversity.

Conclusions: Our results suggest that mid-successional dominant species differ in their impact on diversity and progress of succession. Mid-successional plots dominated by alien species, or by native species that were originally subordinate in natural communities, regenerate less successfully and may temporarily arrest succession. Therefore, early colonization of native dominants should be enhanced with restoration measures.

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Introduction

Mid-successional grasslands developing after the abandonment of agricultural fields are important components of many human-affected cultural landscapes (Prach & Řehouňková 2006; Cramer & Hobbs 2007; Jírová et al. 2012; Knappová et al. 2012). These grasslands provide habitats for many threatened species and contribute to landscape-scale ecosystem services (Prach et al. 2001; Cramer & Hobbs 2007; Török et al. 2011; Molnár et al. 2012). Studies on spontaneous succession in these habitats have supplied important data for theoretical ecology and for restoration (Pickett et al. 1987, 2001; Luken 1990; Prach et al. 2001; Cramer & Hobbs 2007; Török et al. 2011). Broad-scale comparative studies are particularly important for generalizations and for establishing databases for practical decisions (Prach & Pyšek 2001; Török et al. 2011). Several attempts have been made to explain the landscape-scale variability in the rate and direction of spontaneous succession, revealing effects of abiotic factors and climate (Prach & Řehouňková 2006; Prach et al. 2007; Jírová et al. 2012). Other studies have emphasized the role of surrounding vegetation and dispersal limitation (Novák & Konvička 2006; Prach & Řehouňková 2006; Kiehl 2010; Knappová et al. 2012). These studies showed that spontaneous succession is a good alternative to technical restoration if no strong abiotic or biotic limitations exist (Prach & Hobbs 2008; Török et al. 2011; Hölzel et al. 2012).

In addition to abiotic constraints and dispersal limitation, biotic filters limiting local plant establishment are also important in community reassembly and in regeneration of diversity (Hölzel 2005; Moore & Elmendorf 2006; Wilsey 2010; Házi et al. 2011; Szentes et al. 2012). Biotic filters can be particularly important in mid-successional grasslands, where the vegetation is often very heterogeneous within fields, and this heterogeneity may persist for a considerable time (Pickett et al. 1987, 2001; Bartha 2007; Házi et al. 2011; Szentes et al. 2012). Heterogeneity of mid-successional old-fields develops in the form of a patchwork of dominant species with variable degrees of local dominance, diversity and rate of succession (Bartha et al. 2008).

The mean rate of species turnover decreases over time, and a considerable proportion of species (ca. 50%) colonize as early as the first 5 yr of regeneration dynamics

(Bartha et al. 2003). The similarity to the target community is low at the beginning of succession and increases in later stages of succession (Ruprecht 2006). Consequently, the majority of target species are expected to enter the community in mid-to late-successional stages – when grasslands have a closed canopy and available microsites for establishment are limited. Different species have significantly different effects on the local rate of colonization and extinction and the magnitude of these species-specific effects changes during succession (Virágh & Bartha 2003). Many studies report the adverse effects of dominant species on diversity (e.g. Hölzel 2005; MacCain et al. 2010; Wilsey 2010; Deák et al. 2011; Házi et al. 2011; Szentes et al. 2012; Concilio & Loik 2013); however no comparative studies are available on the relative importance of dominant species controlling local diversity during succession.

According to Grime's theory (Grime 1979), there are essential differences between the traits of ruderal, competitive and stress-tolerant dominants, with important implications for diversity (Grime 1987, 1998). Grime suggested that dominant species with competitive and ruderal strategies have stronger negative impacts on diversity than stress-tolerant species. Fast growing species with the capacity for clonal expansion and dynamic foraging have the highest chance to monopolize resources and to reduce the opportunity of other subordinate species. In a survey of the Central European flora, Prach & Pyšek (1999) demonstrated that the most successful species appearing as dominants in man-made successional habitats have the traits predicted by Grime. Olf & Bakker (1998) distinguished global and local dominants and species that are intrinsically subordinate. However, their study did not analyse the relationship between dominance and diversity.

In our study, we compiled data from 25 individual surveys of old-field successions (Dancza 2000; Pál 2007; Margóczy et al. 2009; Házi et al. 2011; Szentes et al. 2012; and unpublished data) assessed in various parts of Hungary. These surveys used the same methods for data collection and represent various regions with different abiotic conditions, landscape contexts and land-use histories. Abandoned fields with target communities (seed sources) in the immediate vicinity were chosen in order to decrease the effect of dispersal limitation on diversity.

In the context of this study, an abandoned field was regarded as mid-successional if (i) some species from the target communities were already present, and (ii) some of them had become locally dominant (i.e. they formed distinct vegetation patches). At the same time, the species composition, abundance and distribution in these communities differed from the target communities. The aim of our national-scale survey was to explore the most important mid-successional dominant species with adverse effects on local diversity. We focused on mid-successional stages where biotic filters operate on late-successional (target) species of great conservation value. Species found in our survey should potentially be the subject of some restoration activity in the future.

This study examines the following questions: how is the identity of mid-successional dominant species related to local (patch-scale) diversity; which species have the strongest negative impacts on diversity in spontaneous old-field succession; and what generalizations are possible about the traits of these species?

First, we hypothesize (H1) that the results and conclusions of a previous Central European survey (Prach & Pyšek 1999) are general and can be extended to Hungary. We expect to find a small number of dominant species with common traits (tall, wind-pollinated plants, often capable of intensive lateral spread and requiring high nutrient supply and sufficient site moisture) described in Prach & Pyšek. We also explore whether species, which are dominants or subordinates in the natural (target) communities, have different impacts on diversity in succession (H2). We assume that most species who are subordinate in target communities are relatively weak competitors (Tilman 1988; Olf & Bakker 1998). Therefore, we hypothesize (H2a) that these species will reduce diversity less in succession compared to species that are dominant matrix species in target communities. Our reasoning contradicts to the proposal of Grime (1987), who argued that subordinate species with a ruderal competitor strategy, growing rapidly, are able to monopolize resources in relatively open, successional habitats and will strongly reduce diversity. Therefore we also set an alternative hypothesis (H2b) expecting stronger negative impacts from species that are subordinate in target communities. There is a consensus about the negative role of invasive alien species suppressing local diversity. This expectation has been recently tested and proven for selected invasive species in various habitats in the Czech Republic (Hejda et al. 2009). Based on this study, we hypothesize (H3) that alien species reduce local diversity in succession to the largest extent.

Methods

Study sites

We studied abandoned agricultural fields at various locations throughout Hungary. Data were compiled from 25 individual surveys of old-field successions (i.e. using chronosequences from 25 sites; see Supplement 1). A total of 112 old-fields – from different parts of the country – representing various ages (1–69 yr) since abandonment, varying climatic conditions, different topography, soils, landscape contexts and land-use histories were sampled (Table S1a, Fig. S1). The climate is sub-continental, sub-mediterranean, with mean annual temperatures around 9.0–10.5 °C. Annual precipitation ranges from ca. 500 to 700 mm. Sites have the typical bedrock types of the middle Carpathian basin: loess, loam, clay, sand and sandstone. Elevation ranges from 90 to 380 m, with various exposures (Table S1a). The old-fields (abandoned croplands, orchards and vineyards) varied in size from 0.1 to 20.0 ha, representing both productive and unproductive habitats. Most fields were situated in extensively used traditional landscapes with a rich species pool (good seed sources) in the neighbourhood. With two exceptions, target habitats (i.e. seed sources) were within 100 m, and at six areas, the target habitat (natural grassland) was adjacent to the abandoned field. In addition, target habitats (meadows steppes, closed and open sand steppes) around the old-fields were sampled. Target grasslands close to the abandoned fields with the same or similar abiotic conditions were selected carefully using local vegetation experts, based on local knowledge of vegetation differentiation, land-use history and succession. These grasslands are typical components of the remnants of the forest steppe biome reaching the Carpathian basin from the east. Their present species composition and landscape surroundings were shaped by long-term human influence, mostly grazing, deforestation and fragmentation by arable areas (Molnár et al. 2012). The vegetation of old-fields developed in spontaneous succession. With few exceptions (sheep grazing at three sites and mulching at two sites), the old-fields had no management. However, some older abandoned fields had occasional mowing, sheep or cattle grazing, and burning in the past. The length of local series (i.e. chronosequences) varied, but 13 out of the 25 study sites had a length of at least 22 yr. Most fields were mid-successional old-fields (aged between 15 and 60-yr).

Field sampling

Percentage cover of all vascular plant species was estimated in 2 × 2 m plots. Three plots were located randomly in each field, avoiding edge effects, and also considering spa-

tial heterogeneity (patches) in some older fields, where stratified random sampling was performed. In few cases, in homogenous vegetation, only one plot was sampled, and in contrast, there were very heterogeneous fields where larger sample sizes were used (between nine and 32 plots). Reference data (71 plots, 2×2 m) were also sampled from target communities from the close neighbourhood of particular abandoned fields. A total of 590 plots were sampled in old-fields (a subset: 366 from mid-successional fields (aged between 15 and 60 yr). A total of 322 mid-successional plots (a subset of 366 where the propagule sources were within 100 m or adjacent to the fields) were used for surveying mid-successional dominant species with potential biotic filter effects. The ages of the fields were determined using local experts, based on old military maps, air photos and interviews with local people. Surveys of particular fields were performed between 1995 and 2012 (for details on particular sampling dates see Table S1a). Table S1b and S1c provide detailed information on the distribution of sample plots between sites, fields and ages.

Data analyses

At plot scale (i.e. for each 2×2 -m plot) the total cover, Shannon and Simpson diversity, equitability and average coenological similarity (based on Bray–Curtis index and Sørensen index) between the given old-field plot and the related reference data on target community were calculated (Podani 1993; Tóthmérész 1997). The abundance-based Bray–Curtis similarity is high if a species is dominant in both successional and target plots. This index is lower if the successional dominant species is subordinate in the target community. To avoid this trivial result, dominant species were removed from samples before calculating Bray–Curtis similarities. Species in a plot were ranked according to absolute cover values, and dominant species were identified as the species with the first rank in the abundance hierarchy.

Correlations between community variables (e.g. number of species, equitability, quadratic diversity, similarity to target community) and age of site were analysed with Spearman rank order correlation coefficients and fitting linear regressions. Non-parametric tests were performed to analyse differences between effects of different dominant species on community variables (equitability, quadratic diversity, similarity to target community). Kruskal–Wallis test were used to analyse significant differences, considering all dominant species and species groups, while Mann–Whitney *U*-tests were calculated for each pair of species and species groups (Bonferroni adjustments were applied in that case). Multiple linear regression with standard stepwise regression was applied to analyse whether other factors (see Table S1a, Supplement 5) might have some

influence on the diversity or similarity to target communities. The analyses were computed with the STATISTICA program package (StatSoft, Inc., Tulsa, OK, USA).

Because one of our aims was to survey and provide basic information for decision-making in conservation and restoration management, our stratified sampling design followed the recommendations of Knollová et al. (2005), to maximize both the probability of finding plots dominated with different species and the variation in our sample. However, this sampling design may not be appropriate for estimating statistical populations and performing related tests. To avoid potential biases due to imbalanced subsample sizes and pseudo-replications, we performed a secondary sampling using three randomly chosen plots from each field (if more than three plots were available in the original sample). We also applied an abundance threshold (30%) for the cover of dominant species, for selecting plots with potential biotic effects of dominants. The whole data set ($N = 590$) was used to explore the temporal variability of data. A reduced data set (only mid-successional fields of ages between 15 and 60 yr with good seed sources, $N = 322$) was used for exploring the most important dominant species in succession, and a further reduced data set (with 30% abundance threshold and with a balanced number of plots per field) was used in the statistical tests. This reduced data set ($N = 108$ plots) was tested for potential auto-correlations. Spatial analysis was performed using models of GS⁺ (Gamma Design Software, Plainwell, MI, USA). However, we did not find significant spatial dependence in this data set (see Supplement 2).

Results

High variations in community attributes were found when community characteristics were depicted as a function of field age. Only species richness and the similarity of old-field sample plots to target communities showed slight positive correlation with field age (Fig. 1). These patterns show clearly that field age is a poor predictor of the progress of succession when assessed at regional scale. For example, there were 62-yr-old plots with high (ca. 80%) percentage similarity to target communities, while similarity to a target community was very low (<20%) in some other plots of the same age, suggesting the existence of factors arresting succession in these plots. High (close to maximum) diversity and equitability appeared in some mid-successional plots, while diversity and equitability were close to a minimum in others.

In total, 77 species were recorded as dominant in at least one sample plot representing mid-successional old-fields. Dominant species accounted for 19% of total mid-successional species richness (412 species). A total of 12 species (3% of the total mid-successional species richness) were

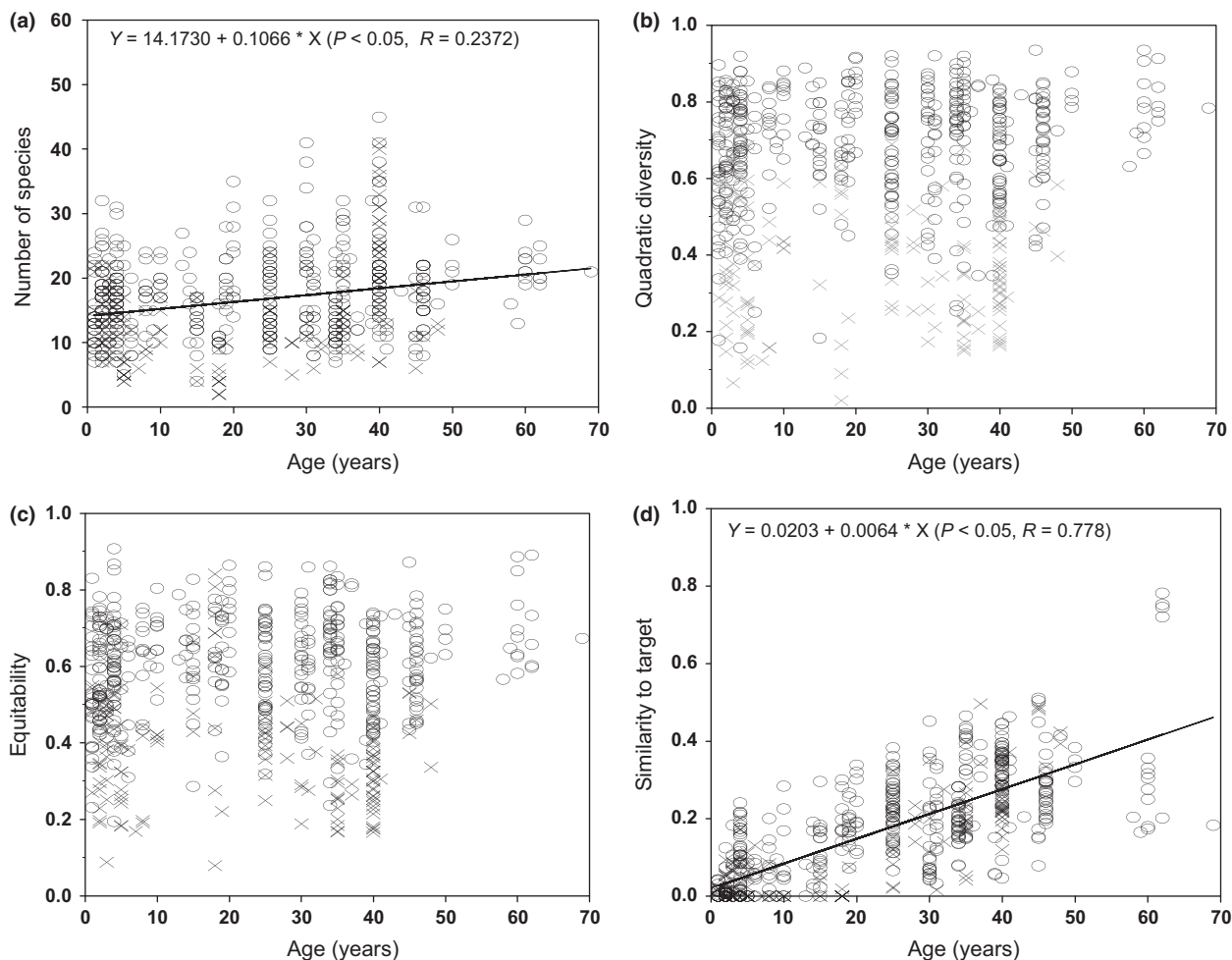


Fig. 1. The progress of old-field succession at a regional scale. Linear regression lines are shown if the correlation between x (age) and y (number of species, quadratic diversity, equitability and Sørensen index) were significant. X depicts plots with >60% cover of dominant species. (a) Number of species. (b) Quadratic diversity (Simpson index). (c) Equitability (estimated from Shannon diversity). (d) Similarity to target community (estimated with Sørensen index).

frequent (present in at least five plots; Supplement 3). Those 12 important dominant species were all perennials and had the capacity for lateral vegetative spread. Eight species belonged to Poaceae, while Asteraceae and Fabaceae both had two representatives. The competitor life strategy (according to Grime) was the most typical (but with various transitions to S and R strategy). These species had, on average, low requirement for N and high requirement for light, while their moisture demands were variable. Most of them were wind-pollinated species, and with one exception (*Solidago gigantea*) they were native to the Hungarian flora.

Diversity of mid-successional plots varied greatly, reflecting high variability of the local impact of dominant species. Almost the full range of possible diversity values were represented (Fig. 1b). The lowest 10% of diversity values were selected as representing plots with the

strongest suppressive impact of dominant species. The lowest diversity appeared in plots dominated by eight species (*Bothriochloa ischaemum*, *S. gigantea*, *Bromus erectus*, *Calamagrostis epigeios*, *Festuca vaginata*, *Inula ensifolia*, *Festuca rupicola* group and *Inula britannica*); these eight species accounted for 2% of the mid-successional species pool (Table 1).

The Kruskal–Wallis test showed significant differences among the impact of successional dominants on community characteristics (diversity, equitability and similarity to target community) when successional dominant species were grouped according to their role in natural (target) communities (Fig. 2, Table 2). Plots dominated by dominant species that are dominant also in semi-natural communities (group D) (*F. rupicola*, *F. vaginata*, *Brachypodium pinnatum*) showed the highest similarity to target communities (Fig. 2). In contrast, plots dominated by species that

Table 1. Mid-successional dominant species with the strongest negative effect on diversity found in a country-scale survey of abandoned fields in Hungary.

	Abundance			Position in succession		Characteristic vital attributes of species										
	Frequency% (N = 33)	Absolute cover	Relative cover	Age (yrs)	Effect	Quadratic diversity	Origin	Life form	N demand	Moisture demand	Light demand	Lateral spread (m yr ⁻¹)	Height	Pollination mode	Grime's life strategy	Family
<i>Batrachia ischaemum</i>	54.55	50–90	0.85–0.92	15–40	0.16–0.28	0.16–0.28	Native	H	2	3	9	0.01–0.25	2	Wind	CSR	Poaceae
<i>Solidago gigantea</i>	12.12	100–110	0.86–0.99	18–25	0.09–0.26	0.09–0.26	Alien	H	2–3	8	7	0.01–0.25	3–4	Insect	C	Asteraceae
<i>Bromus erectus</i>	9.09	75–90	0.84–0.92	35–40	0.15–0.28	0.15–0.28	Native	H	2	3	8	<0.01	3	Wind	CS	Poaceae
<i>Calamagrostis epigeios</i>	6.06	80–85	0.86–0.91	28–30	0.17–0.25	0.17–0.25	Native	H	3	5	7	0.01–0.25	3–4	Wind	C/SC	Poaceae
<i>Festuca vaginata</i>	6.06	65–70	0.86–0.89	37	0.21–0.25	0.21–0.25	Native	H	1	2	9	<0.01	2	Wind	CS	Poaceae
<i>Inula ensifolia</i>	6.06	40–70	0.86–0.87	19–34	0.24–0.25	0.24–0.25	Native	H	1–2	3	8	<0.01	2	Insect	CS	Asteraceae
<i>Festuca rupicola</i> group	3.03	70	0.85	25	0.27	0.27	Native	H	1–2	3	9	<0.01	2	Wind	CS	Poaceae
<i>Inula britannica</i>	3.03	60	0.85	34	0.27	0.27	Native	TH-H	3	7	8	>0.25	2	Insect	CS	Asteraceae

Origin of species is according to the Hungarian Flora Database 1.2. (Horváth et al. 1995). Life forms are according to Raunkiaer's system (Raunkiaer 1934). Ecological indicator values are from Borhidi's system (modified from Ellenberg's system; Borhidi 1995). The values of lateral spread were taken from the CLO-PLA trait database (Klimeš & Klimešová 1999). The height of species originate from the LEDA trait base (Kleyer et al. 2008). The type of pollination mode come from the BioFlor trait database (Kühn et al. 2004). The life strategies (CSR) are according to Grime's system (Grime 1979). For more details see Supplement 3.

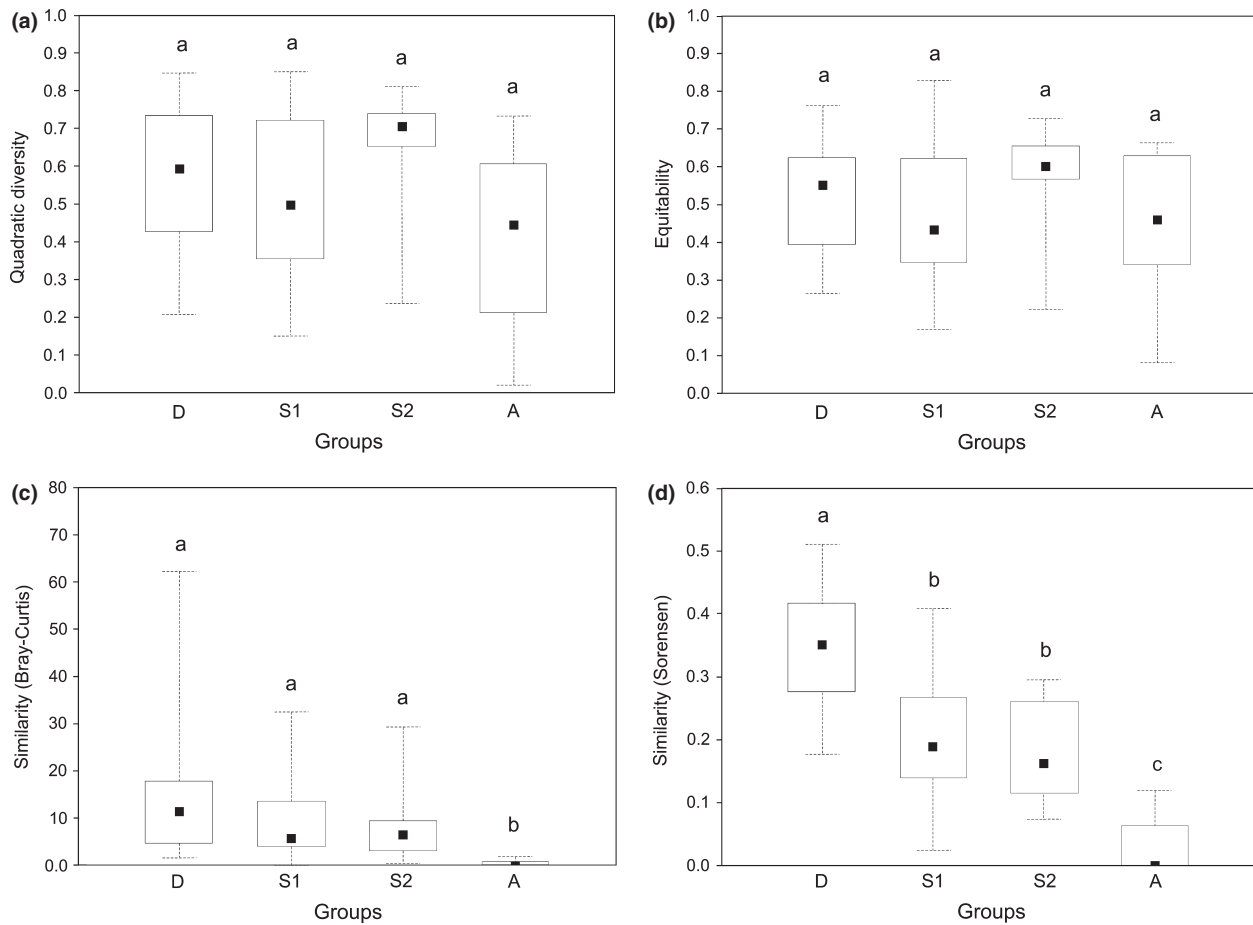


Fig. 2. The effect of mid-successional dominants classified according to their role in target communities. Box plots show the median, quartiles and range of data. Significant ($P < 0.05$) differences between species groups, assessed with Mann-Whitney *post-hoc* *U*-tests, are indicated by different letters. Species groups are: D = species that are dominants (matrix species) in target communities. S1 = subordinate grasses in target communities. S2 = subordinate dicots in target communities. A = alien (exotic) weeds. **(a)** Quadratic diversity (Simpson index); **(b)** Equitability (estimated from Shannon diversity); **(c)** Percentage similarity to target community (estimated with Bray-Curtis index); **(d)** Percentage similarity to target community (estimated with Sørensen index).

Table 2. Kruskal-Wallis test showing that the nine most important dominant species and the four species groups (D, S1, S2, A) in our survey were significantly different from each other regarding three of all calculated community indices.

Variable	df	N	H-value	P	
For dominant species					
Quadratic diversity	8	99	15.6864	0.0471	*
Equitability	8	99	11.7589	0.1623	n.s.
Sørensen similarity	8	99	47.0492	< 0.0010	***
Bray-Curtis similarity	8	99	38.9955	< 0.0010	***
For four species groups					
Quadratic diversity	3	108	8.029	0.0454	*
Equitability	3	108	5.1866	0.1586	n.s.
Sørensen similarity	3	108	46.5315	< 0.0010	***
Bray-Curtis similarity	3	108	23.3214	< 0.0010	***

* $P < 0.05$; *** $P < 0.001$.

are subordinate grasses in semi-natural communities (group S1; e.g. *B. ischaemum*, *B. erectus*, *C. epigeios*, *Poa pratensis*, *Arrhenatherum elatius*) showed lower similarity to target communities. Plots dominated by dicot subordinates in semi-natural communities (group S2) had relatively high diversity and equitability, but low similarity to target communities. The lowest similarity to target communities appeared in mid-successional plots dominated by alien species (group A).

The overall effect of species identity was also significant on community characteristics when dominant species were treated separately (Table 2, Fig. 3, Supplement 4). Considering pair-wise differences between impacts of dominant species on diversity, Mann-Whitney *U*-tests revealed significant differences between *F. vaginata* and

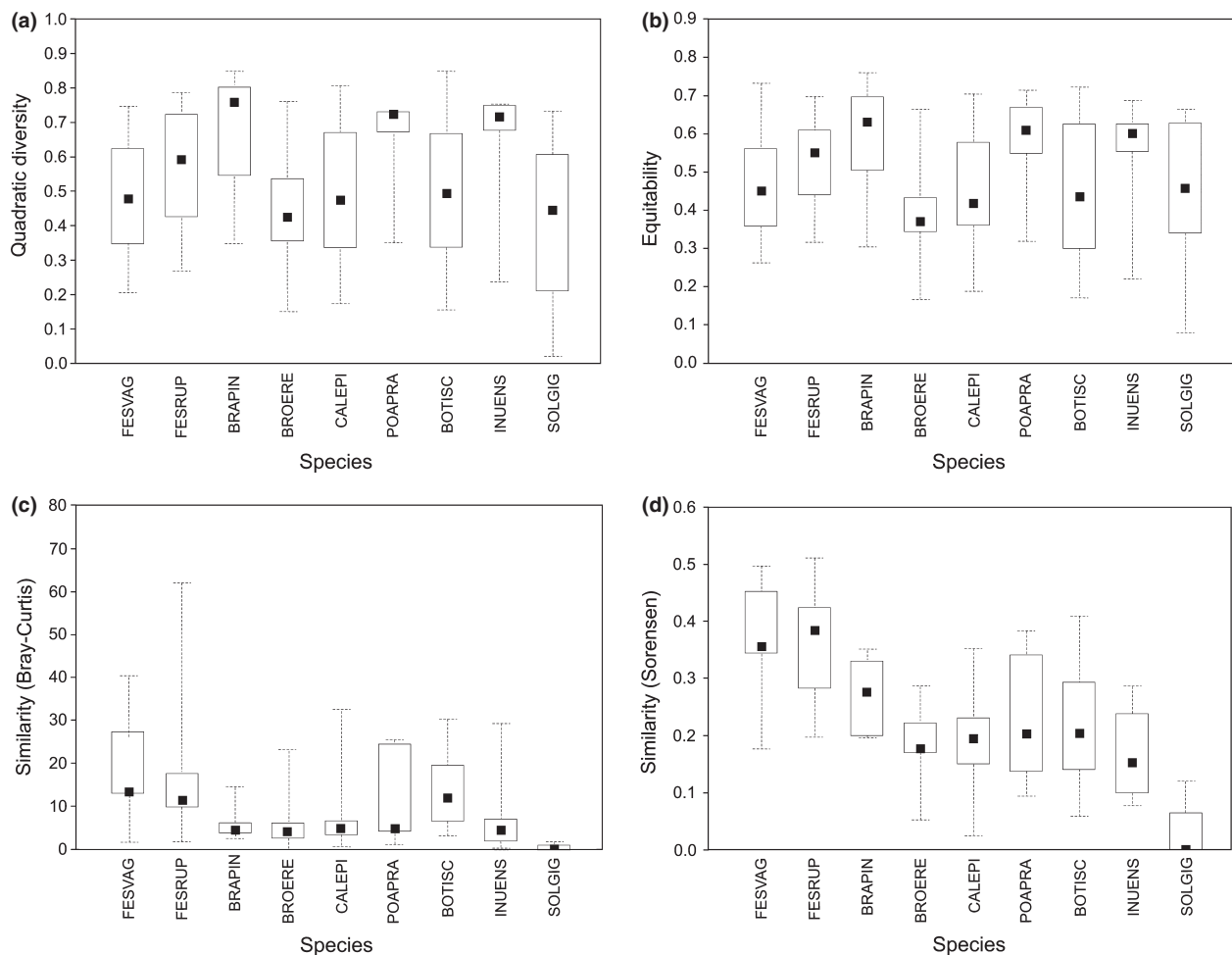


Fig. 3. The effect of the identity of dominant species in mid-successional old-fields on. **(a)** Quadratic diversity (Simpson index); **(b)** Equitability (estimated from Shannon diversity); **(c)** Percentage similarity to target community (estimated with Bray-Curtis index); **(d)** Percentage similarity to target community (estimated with Sørensen index). (Box plots show the median, quartiles and range of data (for statistical tests see Table 2 and Supplement 4). FESVAG = *Festuca vaginata*; FESRUP = *Festuca rupicola*; BRAPIN = *Brachypodium pinnatum*; BROERE = *Bromus erectus*; CALEPI = *Calamagrostis epigeios*; POAPRA = *Poa pratensis*; BOTISC = *Bothriochloa ischaemum*; INJUENS = *Inula ensifolia*; SOLGIG = *Solidago gigantea*.

B. erectus, and between *F. rupicola* and several other grasses (*B. erectus*, *P. pratensis*, *B. ischaemum*). The similarity to target communities (estimated with the Sørensen index) also differed between species pairs. Plots dominated by *S. gigantea* had lower similarity to target communities than plots dominated by other species (Supplement 4).

Data used in these analyses represent old-fields with varying climatic conditions, different topography, soils, landscape contexts and land-use histories (Table S1a). To reveal the contribution of these factors, multiple linear regressions with standard step-wise regression was applied. Besides the cover of dominant species, the total cover of the plots, age of old-fields, mean annual temperature and mean annual precipitation of sites, elevation, slope and aspect of fields, the last cultivation before abandonment, landscape type and type of recent management were tested

as independent variables. Results showed that quadratic diversity depended mainly on the cover of dominant species (with a smaller contribution of total cover and a minimal correlation with landscape type; Supplement 5). Similarity to the target community was effected mainly by field age, cover of dominant species and the mean annual precipitation. The low number of other significant factors found with multiple linear regression emphasizes the importance of the biotic filter effects of dominants on diversity and on the progress of succession. To further illustrate the importance of dominant species on local community characteristics, an example is presented depicting the variability of plot-level estimates within the same fields (Fig. 4). The within-field spatial variability of plot-scale community characteristics is considerable. For example, the spatial variability of quadratic diversity in a 31-yr-old

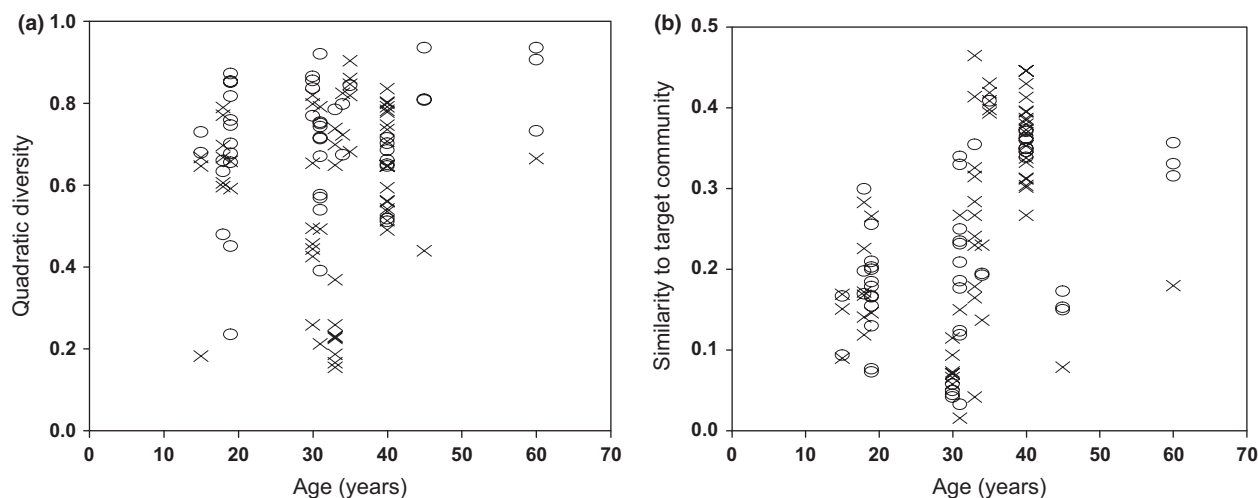


Fig. 4. Within-field variability of local (patch-scale) community characteristics in mid-successional old-fields. Plots within a particular field (see vertical series of points on graphs) experience the same abiotic environment (climate, soil, land-use history etc.) still express very large spatial variability. The large differences between plots suggest the importance of within-community biotic interactions (e.g. filter effects of locally dominant species). (a) Quadratic diversity (Simpson index) and (b) Similarity to target community (Sørensen index). X = plots dominated by *Bothriochloa ischaemum*, O = plots dominated by other species.

abandoned field accounted for the 65% of the total variation found in the whole data set, while 41% of the total variability of the Sørensen index appeared within this 31-yr-old abandoned field (Fig. 4). Replicated plots from the same field had similar abiotic constraints and species pool, therefore, the high within-field variation in diversity can be attributed to the biotic filter effect of dominant species (i.e. to the effect of identity and cover of dominants).

Discussion

Dominant species in mid-successional abandoned fields with a strong negative impact on succession

We identified 77 species, 19% of the mid-successional species pool (and ca. 10% of the whole species pool including data from target communities) as dominants in 2 × 2-m plots. This magnitude corresponds with the number of dominants (56 species) reported in the only other similar comparative study in Europe (Prach & Pyšek 1999). Our country-scale survey found eight species (*B. ischaemum*, *S. gigantea*, *B. erectus*, *C. epigeios*, *F. vaginata*, *I. ensifolia*, *F. rupicola* group and *I. britannica*) with the strongest negative impacts on local patch-scale diversity. Their relative cover ranged between 84% and 99%, corresponding well with the threshold (80% cover) used by Prach & Pyšek (1999). Contrary to our expectation, our first hypothesis (H1), related to generalizations about traits of these dominant species, was only partially supported by these results. While the number of the most successful dominants were similar (nine in the Czech survey and eight in the Hungarian survey), there were

remarkable differences in the traits of the most successful species. Ideal successional dominants in the western part of the Czech Republic were tall, wind-pollinated plants, often capable of intensive lateral spread and requiring high nutrient supply and sufficient site moisture. In Hungary, most successional dominants were also wind-pollinated species and had the capacity for lateral vegetative spread. However, the most successful dominant species in our study varied in size and had, on average, low requirement for N, but high requirement for light. These differences can be partly explained by the drier climate in Hungary and the fact that our survey was restricted to mid-successional old-fields. Among the most important successional dominants recorded in the Czech survey, *Artemisia vulgaris*, *Chenopodium album* and *Elymus repens* were also important in Hungary. However, they appear in the early stages of succession and in ruderal (often eutrophic) habitats (Bartha 2007; Bartha et al. 2008).

In contrast to the results of Prach & Pyšek (1999), our survey revealed that many mid-successional old-fields in Hungary are dominated by species typical of dry grasslands and prefer secondary habitats with dry conditions, nutrient-poor soils and eroded surfaces. *Bothriochloa ischaemum* was identified as the species with the strongest negative effect. This C₄ perennial bunchgrass is native to Hungary, and appears in small gaps or eroded surfaces with drier and warmer microhabitats in slope steppe grasslands (Bartha 2007; Szentes et al. 2012). *Bothriochloa ischaemum* is indicated as an invasive species in several parts of the world (Gabbard & Fowler 2007; Schmidt et al. 2008). The importance of this species is likely to

increase in the future due to global warming (Auerswald et al. 2012).

Dominance does not necessarily mean that a species is having a filter effect. Other factors potentially limit diversity and the progress of succession, including dispersal limitation, disturbances, herbivory, adverse soil or climatic conditions and stochastic factors. Our data represented varying climatic conditions, different topography, soils, landscape contexts and land-use histories. However, these factors did not show significant correlations or showed only minimal correlations with quadratic diversity and similarity to the target community. Other studies that found significant effects of abiotic constraints (e.g. effects of low soil pH and low temperature; Prach & Řehouňková 2006; Prach et al. 2007; Jírová et al. 2012) worked in a broader range of habitats, including more adverse environmental conditions. In contrast to other studies (Novák & Konvička 2006; Prach & Řehouňková 2006; Kiehl 2010; Knappová et al. 2012), dispersal was not an important limiting factor in our case, because we selected abandoned fields with good seed sources in the neighbourhood. We found extremely high within-field spatial variability of plot-scale community characteristics. The magnitude of plot-scale spatial variability within some abandoned fields reached 40–60% of total regional-scale variation of data. Because replicated plots from the same field had similar abiotic constraints and species pool, therefore, the high within-field variation of diversity and progress of succession can be attributed to the local biotic effect of dominant species. Our results and interpretation are in accordance with many previous studies (Pickett et al. 2001; Virágh & Bartha 2003; Hölzel 2005; Moore & Elmendorf 2006; MacCain et al. 2010; Wilsey 2010; Deák et al. 2011; Házi et al. 2011; Szentes et al. 2012) reporting the adverse effects of dominant species on diversity. Although some abiotic limitation, stochastic and historical factors are always present, our study emphasizes the importance of biotic filter effects in succession.

Does the dominance rank in mature communities predict biotic filter effects in succession?

Our results supported the hypotheses (H2 and H3), that different dominant species have different impacts on succession. Mid-successional plots dominated by species that are dominant in natural grasslands (*F. rupicola*, *F. vaginata*, *B. pinmatum*) showed higher similarity to target communities than plots dominated by species that are subordinate in mature communities (e.g. *B. ischaemum*, *B. erectus*, *C. epigeios*, *P. pratensis*). This result suggests that the impacts of species dominant in transitional habitats are related to their role in mature (near-equilibrium) communities, supporting Grime's theory (Grime 1987, 1998) and

our H2b hypothesis. Ruderal competitors that are subordinate in mature communities grow fast and monopolize resources in open successional habitats where they are released from the control of dominant matrix species. Studying secondary succession on abandoned meadows, Falińska (1991) described similar patterns, distinguishing 'dominants' (species able to co-exist with others, cf. group D in our study) and 'monopolists' (fast-growing clonal species tending to eliminate other species, cf. group S1 and S2 in our classification). In our study, species that are matrix species in mature communities correspond to 'global dominants' according to the classification of Olf & Bakker (1998), while species that are subordinate in mature communities correspond to 'local dominants'. We suggest that local dominants have a stronger impact in the intermediate stages of community reassembly than global dominants. Using similar reasoning, alien species should have even stronger suppressive effect on local diversity. In accordance with this expectation (cf. our third hypothesis, H3) and the results of another survey from Hejda et al. (2009), we found that *S. gigantea* (an alien species) had the strongest negative impact.

Understanding the patterns of successional dominant species at landscape scale

A national-scale survey of Hungary identified 12 species, a small proportion (3%) of the mid-successional species pool, as important successional dominants in human-affected cultural landscapes. Our results suggest that these mid-successional dominant species differ in their impacts on the diversity and progress of succession. How do the relative importance and dynamic relationships (successional states) of these dominant species vary in different regions? What kind of patterns theory could predict, and how can we understand, the present and future variability of successional pathways? In accordance with other studies (Pickett et al. 2001; Prach & Řehouňková 2006; Prach et al. 2007; Jírová et al. 2012), our survey presents additional evidence of the high spatio-temporal variability in vegetation succession. Part of this variability can be explained by abiotic differences between regions. However, we argue that biotic interactions (local assembly processes) modulated by human influences (by generating different sizes and frequencies of disturbances, and by changing the sizes of disturbed areas and the availability of propagule sources) have significant effects on successional pathways. We present here a conceptual model to explain the complexity of spontaneous succession in this context, assuming that abiotic parameters (climate, soil, topography) are more or less constant in the region, while human influences vary.

How many different regeneration and degradation pathways can be distinguished within a landscape where

the abiotic conditions are homogenous? How will these successional pathways change in the future due to increasing human influence? The answer to these fundamental questions depends on the intensity of disturbance and the size and composition of the species pool of a given landscape. Fine-scale disturbances in natural communities induce stochastic micro-successions without visible changes at stand level (Herben et al. 1993). Slightly bigger disturbances (e.g. mounds of burrowing animals) induce some directional changes in community composition (Bartha 2007). Large disturbances (e.g. cultivated fields) need more time to recover after abandonment and will produce a distinct series of successional phases (Bartha 2007). We suggest that the larger the extent and intensity of a disturbance, the larger the number of potential species attaining local dominance with some biotic filter effects on local plant assembly. We also suggest that at the same degree of disturbances, the number of potential dominant species and the length of successional pathways increases by the increasing dispersal limitation of natural matrix-forming species (Fig. 5). Species that are subordinate in natural communities might be able to colonize and grow faster than the corresponding dominant matrix species (cf. colonization–competition trade-off; Tilman 1988). Below a certain threshold (when disturbances are moderate and there are good propagule sources), all species that become local dominants in succession originate from the local natural communities. In our survey, most abandoned fields were situated in extensively used traditional landscapes with a relatively rich species pool, high naturalness and good regeneration potential. As a consequence, most successional dominant species were dominants (D) or subordinates (S1, S2) in natural reference communities.

After crossing a threshold, ruderal species will have more and more chances of establishing large persistent populations and forming distinct successional stages (Prach & Pyšek 2001). Similar to our results, Prach & Pyšek (1999) only found a few alien species that became dominant in successional communities. However, other more ruderal landscapes might have different successional pathways with a larger contribution of weeds (native and alien weeds) as successional dominants (Szegi et al. 1988; Prach & Pyšek 2001). Due to increasing disturbances and decreasing natural species pools, we expect an increasing role for alien species in the future. Our results suggest that mid-successional dominant species differ in their impact on the diversity and progress of succession. There is a challenge to increase future restoration success through influencing the establishment and growth of potential successional dominant species. During grassland restoration, field managers should enhance the colonization of native dominant grasses and suppress other grasses that are aliens

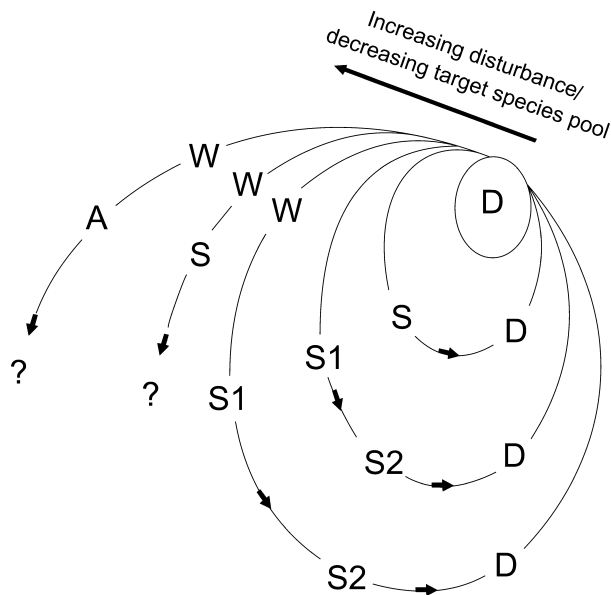


Fig. 5. A conceptual model explaining the variability of temporal patterns of dominant species in different old-field successions in a theoretical landscape where the abiotic conditions (climate, soil, topography) are homogenous. The reference state is a natural community dominated by species D (the natural matrix-forming dominant). Disturbances of various kinds (from the smallest such as small mammal burrowing, to the largest such as ploughing or surface mining) generate regeneration cycles of various lengths. The bigger the extent and intensity of a disturbance, the longer is the successional pathway and the larger the number of potential species (S1, S2, W and A in our example) attaining local dominance with some biotic filter effects on local plant assembly. At the same degree of disturbances, the number of potential dominant species increases through the increasing dispersal limitation of natural matrix-forming species. Successional dominants (D, S, A, W) are classified according to their origin and role in target communities. D = dominants (matrix species) in target communities. S = subordinate species in target communities (S1, S2 denote different subordinate species). W = native weeds. A = alien weeds.

or subordinates in local natural grasslands. The small number of important dominants found in the broad-scale survey of Prach & Pyšek (1999) and in our present study suggests that similar surveys in other countries would also identify only eight to ten important species. Due to the low number of potential key species, understanding their traits and developing successful restoration measures seems to be a feasible and operational task for the future.

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Supporting information

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

Appendix S1.

Table S1a. Site characteristics.

Table S1b. Detailed distribution of old-field plots.

Table S1c. Detailed distribution of old-field plots after resampling (N=108).

Fig. S1. The locations of study sites in Hungary.

Appendix S2. Spatial analyses for potential autocorrelations based on the spatial coordinates of sites.

Appendix S3. Survey of dominant species in 25 successional old-field series.

Appendix S4. Detailed statistical tests: Mann–Whitney U-test for each species pair.

Appendix S5. Multiple regression model of quadratic diversity and Sørensen similarity (as dependent variables) in relation to different independent variables.