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

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4

1 **Abstract**

2 **Questions:** (1) Which species dominate mid-successional old-fields in Hungary? How does
3 the identity of these species relate to local (patch-scale) diversity and to the progress of
4 succession? (2) Which species have the strongest negative impact on diversity in spontaneous
5 old-field succession and what generalizations are possible about the traits of these species?
6 (3) Are these species dominant or subordinate components in mature target communities? (4)
7 Do native or alien species have stronger effects on the diversity and progress of succession?

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

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

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

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

1 **Keywords:** biotic filters; community assembly; old-field succession; plant traits; regional
2 survey; restoration; species diversity.

3
4 **Nomenclature:** Király (2009)

5
6 **Running head:** Filter effects of mid-successional dominants
7

8 9 **Introduction**

10
11 Mid-successional grasslands developing after the abandonment of agricultural fields are
12 important components of many human affected cultural landscapes (Prach & Řehouňková
13 2006; Cramer & Hobbs 2007; Jírová et al. 2012; Knappová et al. 2012). These grasslands
14 provide habitats for many threatened species and contribute to landscape-scale ecosystem
15 services (Prach et al. 2001; Cramer & Hobbs 2007; Török et al. 2011; Molnár et al. 2012).
16 Studies on spontaneous succession in these habitats have supplied important data for
17 theoretical ecology and for restoration (Pickett et al. 1987; Luken 1990; Prach et al. 2001;
18 Pickett et al. 2001; Cramer & Hobbs 2007; Török et al. 2011). Broad-scale comparative
19 studies are particularly important for generalizations and for establishing databases for
20 practical decisions (Prach & Pyšek 2001; Török et al. 2011). Several attempts have been
21 made to explain the landscape-scale variability in the rate and direction of spontaneous
22 succession, revealing effects of abiotic factors and climate (Prach & Řehouňková 2006; Prach
23 et al. 2007; Jírová et al. 2012). Other studies have emphasized the role of surrounding
24 vegetation and dispersal limitation (Novák & Konvička 2006; Prach & Řehouňková 2006;
25 Kiehl 2010; Knappová et al. 2012). These studies showed that spontaneous succession is a
26 good alternative to technical restoration if no strong abiotic or biotic limitations exist (Prach
27 & Hobbs 2008; Török et al. 2011; Hölzel et al. 2012).

28 In addition to abiotic constraints and dispersal limitation, biotic filters limiting local plant
29 establishment are also important in community reassembly and in regeneration of diversity
30 (Hölzel 2005; Moore & Elmendorf 2006; Wilsey 2010; Házi et al. 2011; Szentes et al. 2012).
31 Biotic filters can be particularly important in mid-successional grasslands, where the
32 vegetation is often very heterogenous within fields, and this heterogeneity may persist for a
33 considerable time (Pickett et al. 1987, 2001; Bartha 2007; Házi et al. 2011; Szentes et al.
34 2012). Heterogeneity of mid-successional old-fields develops in the form of patchwork of

1 dominant species with variable degree of local dominance, diversity and rate of succession
2 (Bartha et al. 2008).

3 The mean rate of species turnover decreases over time and considerable proportion of species
4 (ca. 50%) that colonise as early as the first 5 years of regeneration dynamics. (Bartha et al.
5 2003). The similarity to the target community is low at the beginning of succession and
6 increases in later stages of succession (Ruprecht 2006). Consequently, the majority of target
7 species are expected to enter the community in mid to late successional stages- when
8 grasslands have a closed canopy and available microsites for establishment are limited.
9 Different species have significantly different effects on the local rate of colonization and
10 extinction and the magnitude of these species-specific effects changes during succession
11 (Virágh & Bartha 2003). Many studies report the adverse effects of dominant species on
12 diversity (e.g. Hölzel 2005; Wilsey 2010; MacCain et al. 2010; Házi et al. 2011; Deák et al.
13 2011; Szentes et al. 2012; Concilio & Loik 2013). However, no comparative studies are
14 available on the relative importance of dominant species controlling local diversity in
15 succession.

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

27 In our study, we compiled data from 25 individual surveys of old-field successions (Dancza
28 2000; Margóczy 2009; Házi et al. 2011; Szentes et al. 2012; Pál 2012; and unpublished data)
29 assessed in various parts of Hungary. These surveys used the same methods for data
30 collection and represent various regions with different abiotic conditions, landscape contexts
31 and land use histories. Abandoned fields with target communities (seed sources) in the
32 immediate vicinity were chosen in order to decrease the effect of dispersal limitation on
33 diversity.

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

10

11 This study examines the following questions:

12

13 How is the identity of mid-successional dominant species related to local (patch-scale)
14 diversity? Which species have the strongest negative impacts on diversity in spontaneous old-
15 field succession? What generalizations are possible about the traits of these species?

16

17 First, we hypothesize (H1) that the results and conclusions of a previous Central European
18 survey (Prach & Pyšek 1999) are general and can be extended to Hungary. We expect to find
19 a small number of dominant species with common traits (tall, wind-pollinated plants, often
20 capable of intensive lateral spread and requiring high nutrient supply and sufficient site
21 moisture) described by Prach & Pyšek.

22

23 We also explore whether species, which are dominants or subordinates in the natural (target)
24 communities, have different impacts on diversity in succession (H2). We assume that most
25 species who are subordinate in target communities are relatively weak competitors (Tilman
26 1988, Olf & Bakker 1998). Therefore, we hypothesize (H2a) that these species will reduce
27 diversity less in succession compared to species which are dominant-matrix species in target
28 communities. Our reasoning contradicts to the proposal of Grime (1987) who argued that
29 subordinate species with ruderal competitor strategy, growing rapidly, are able to monopolize
30 resources in relatively open successional habitats and will strongly reduce diversity.
31 Therefore we also set an alternative hypothesis (H2b) expecting stronger negative impacts
32 from species which are subordinate in target communities.

33

1 There is a consensus about the negative role of invasive alien species suppressing local
2 diversity. This expectation has been recently tested and proven for selected invasive species
3 in various habitats in the Czech Republic (Hejda et al. 2009). Based on this study, we
4 hypothesize (H3) that alien species reduce local diversity in succession to greatest extent.

7 **Material and Methods**

9 *Study sites*

10 We studied abandoned agricultural fields at various locations scattered within Hungary. Data
11 were compiled from 25 individual surveys of old-field successions (i.e. using
12 chronosequences from 25 sites, see Supplement 1). 112 old-fields - from different parts of the
13 country - representing various ages (1-69) since abandonment, varying climatic conditions,
14 different topography, soils, landscape contexts and land use histories were sampled
15 (**Supplement Table S1a** and **Fig. S1**). The climate is sub-continental, sub-mediterranean,
16 with mean annual temperatures around 9-10.5 °Celsius. Annual precipitation ranges from ca.
17 500 to 700 mm. Sites have the typical bedrock types of the middle Carpathian basin: loess,
18 loam, clay, sand, and sandstone. Elevation ranges from 90 to 380 m, with various exposures
19 (**Supplement Table S1a**). The old-fields (abandoned croplands, orchards and vineyards)
20 varied in size between 0.1 and 20 hectares, representing both productive and unproductive
21 habitats. Most fields were situated in extensively used traditional landscapes with a rich
22 species pool (good seed sources) in the neighbourhood. With two exceptions, target habitats
23 (i.e. seed sources) were within 100 m, and at six areas, the target habitat (natural grassland)
24 was adjacent to the abandoned field. In addition, target habitats (meadows steppes, closed and
25 open sand steppes) around the old-fields were sampled. Target grasslands close to the
26 abandoned fields with the same or similar abiotic conditions were selected carefully by local
27 vegetation experts based on local knowledge of vegetation differentiation, land-use history
28 and succession. These grasslands are typical components of the remnants of the forest steppe
29 biome reaching the Carpathian basin from the east. Their present species composition and
30 landscape surroundings were shaped by long-term human influence, mostly grazing,
31 deforestation and fragmentation by arable areas (Molnár et al. 2012). The vegetation of old-
32 fields developed in spontaneous succession. With few exceptions (sheep grazing at three sites
33 and mulching at two sites) the old-fields had no management. However, some older
34 abandoned fields had occasional mowing, sheep or cattle grazing and burning in the past. The

1 length of local series (i.e., chronosequences) varied, but 13 out of the 25 study sites had a
2 length at least 22 years. Most fields were mid-successional old-fields (aged between 15 and
3 60 years).

4 *Field sampling*

6 Percentage cover of all vascular plant species was estimated in 2 x 2 m plots. 3 plots were
7 located randomly in each field, avoiding edge effects, and also considering spatial
8 heterogeneity (patches) in some older fields, where stratified random sampling was
9 performed. In few cases, in homogenous vegetation, only one plot was sampled, and in
10 contrast, there were very heterogeneous fields where larger sample sizes were used (between
11 9 and 32 plots). Reference data (71 plots, 2 x 2 m) were also sampled from target
12 communities from the close neighbourhood of particular abandoned fields. 590 plots were
13 sampled in old-fields (a subset: 366 from mid-successional fields (aged between 15 and 60
14 years). 322 mid-successional plots (a subset of 366 where the propagulum sources were
15 within 100 m or adjacent to the fields) were used for surveying mid-successional dominant
16 species with potential biotic filter effects. The age of the fields were determined by local
17 experts based on old military maps, air photos and interviews with local people. Surveys of
18 particular fields were performed between 1995 and 2012 (for details on particular sampling
19 dates see **Supplement Table S1a**). **Supplement Table S1b** and **Table S1c** provide detailed
20 information on the distribution of sample plots between sites, fields and ages.

21 *Data analyses*

23 At plot scale (i.e. for each 2 m x 2 m plots) the total cover, Shannon and Simpson diversity,
24 equitability and average coenological similarity (based on Bray-Curtis index and Sorensen
25 index) between the given old-field plot and the related reference data on target community
26 were calculated (Podani 1993; Tóthmérész 1997). The abundance-based Bray-Curtis
27 similarity is high if a species is dominant in both successional and target plots. This index is
28 lower if the successional dominant species is subordinate in the target community. To avoid
29 this trivial result, dominant species were removed from samples before calculating Bray-
30 Curtis similarities. Species in the plot were ranked according to absolute cover values and
31 dominant species were identified as the species with the first rank in the abundance hierarchy.
32 Correlations between community variables (e.g. number of species, equitability, quadratic
33 diversity, similarity to target community) and age of site were analyzed by Spearman rank
34 order correlations coefficient and fitting linear regression. Nonparametric tests were

1 performed to analyze differences between effects of different dominant species on
2 community variables (equitability, quadratic diversity, similarity to target community).
3 Kruskal-Wallis test were used to analyze significant differences considering all dominant
4 species and species groups, while Mann-Whitney U-test were calculated for each pair of
5 species and species groups (Bonferroni adjustment were applied in that case). Multiple linear
6 regression with standard step-wise regression was applied to analyse if other factors (see
7 **Supplement Table S1a** and **Supplement 5**) might have some influence on the diversity or
8 similarity to target communities. The analyses were computed by STATISTICA program-
9 package (StatSoft, Inc. 2001).

10 Because one of our aims was to survey and provide basic information for decision-making in
11 conservation and restoration management, our stratified sampling design followed the
12 recommendations of Knollová et al. (2005) to maximize both the probability of finding plots
13 dominated with different species, and the variation in our sample. However, this sampling
14 design may not be appropriate for estimating statistical populations and performing related
15 tests. To avoid potential biases due to imbalanced subsample sizes and pseudo-replications,
16 we performed a secondary sampling using 3 randomly chosen plots from each field (if more
17 than 3 plots were available in the original sample). We also applied an abundance threshold
18 (30%) for the cover of dominant species, for selecting plots with potential biotic effects of
19 dominants. The whole data set (N=590) was used to explore the temporal variability of data.
20 A reduced data set (only mid-successional fields of ages between 15 and 60 years with good
21 seed sources, N=322) was used for exploring the most important dominant species in
22 succession, and a further reduced data set (with 30% abundance threshold and with a
23 balanced number of plots per field) was used in the statistical tests. This reduced data set
24 (N=108 plots) was tested for potential auto-correlations. Spatial analysis was performed using
25 models of GS⁺ (Gamma Design Software, USA). However, we did not find significant spatial
26 dependence in this data set (see **Supplement 2**).

27

28

29 **Results**

30

31 High variation in community attributes were found when community characteristics were
32 depicted as a function of field age. Only species richness and the similarity of old-field
33 sample plots to target communities showed slight positive correlation with field age (**Fig. 1**).
34 These patterns show clearly that field age is a poor predictor of the progress of succession

1 when assessed at regional scale. For example, there were 62 years old plots with high (ca. 80
2 %) percentage similarity to target communities. In contrast, similarity to target community
3 was very low (< 20 %) in some other plots of the same age suggesting the existence of
4 factors arresting succession in these plots. High (close to maximum) diversity and equitability
5 appeared in some mid-successional plots while diversity and equitability were close to
6 minimum in others.

7 In total, 77 species were recorded as dominant in at least one sample plot representing mid-
8 successional old-fields. Dominant species accounted for 19% of total mid-successional
9 species richness (412 species). 12 species (3% of the total mid-successional species richness)
10 were frequent (present in at least 5 plots) (**Supplement 3**). Those 12 important dominant
11 species were all perennials and had capacity for lateral vegetative spread. Eight species
12 belonged to Poaceae family, while Asteraceae and Fabaceae families both had two
13 representatives. The competitor life strategy (according to Grime) was the most typical (but
14 with various transitions to S and R strategy). These species had, on average, low
15 requirements for nitrogen and a high requirement for light, while their moisture demands
16 were variable. Most of them were wind pollinated species, and with one exception, *Solidago*
17 *gigantea*, they were native to the Hungarian flora.

18 Diversity of mid-successional plots varied greatly reflecting high variability of the local
19 impact of dominant species. Almost the full range of possible diversity values were
20 represented (**Fig. 1b**). The lowest 10% of diversity values were selected representing plots
21 with the strongest suppressive impact of dominant species. The lowest diversity appeared in
22 plots dominated by 8 species (*Bothriochloa ischaemum*, *Solidago gigantea*, *Bromus erectus*,
23 *Calamagrostis epigeios*, *Festuca vaginata*, *Inula ensifolia*, *Festuca rupicola* group and *Inula*
24 *britannica*) These 8 species accounted for 2% of mid-successional species pool (**Table 1**).

25 Kruskal-Wallis test showed significant differences among the impact of successional
26 dominants on community characteristics (diversity, equitability and similarity to target
27 community) when successional dominant species were grouped according to their role in
28 natural (target) communities (**Fig. 2, Table 2**). Plots dominated by species dominant also in
29 semi-natural communities (group D) (*Festuca rupicola*, *Festuca vaginata*, and *Brachypodium*
30 *pinnatum*) showed the highest similarity to target communities (**Fig. 2**). In contrast, plots
31 dominated by species which are subordinate grasses in semi-natural communities (group S1)
32 (e.g. *Bothriochloa ischaemum*, *Bromus erectus*, *Calamagrostis epigeios*, *Poa pratensis* and
33 *Arrhenatherum elatius*) showed lower similarity to target communities. Plots dominated by
34 dicot subordinates in semi-natural communities (group S2) had relatively high diversity and

1 equitability, but low similarity to target communities. The lowest similarity to target
2 communities appeared in mid-successional plots dominated by alien species (group A).
3 The overall effect of species identity was also significant on community characteristics when
4 dominant species were treated separately (**Table 2, Fig. 3, Supplement 4**). Considering
5 pairwise differences between impacts of dominant species on diversity, Mann-Whitney U
6 tests revealed significant differences between *Festuca vaginata* and *Bromus erectus*, between
7 *Festuca rupicola* and several other grasses (*Bromus erectus*, *Poa pratensis* and *Bothriochloa*
8 *ischaemum*). The similarity to target communities (estimated by Sørensen index) also differed
9 between species pairs. Plots dominated by *Solidago gigantea* had lower similarity to target
10 communities than plots dominated by other species (**Supplement 4**).

11 Data used in these analyses represent old-fields of varying climatic conditions, different
12 topography, soils, landscape contexts and land use histories (**Supplement Table S1a**). To
13 reveal the contribution of these factors, multiple linear regression with standard step-wise
14 regression was applied. Besides the cover of dominant species, the total cover of the plots, the
15 age of old-fields, the mean annual temperature and the mean annual precipitation of sites, the
16 elevation, slope and aspect of fields, the last cultivation before abandonment, the landscape
17 type and the type of recent management were tested as independent variables. Results showed
18 that Quadratic diversity depended mainly on the cover of dominant species (with a smaller
19 contribution of total cover and a minimal correlation with the landscape type) (**Supplement**
20 **5**). Similarity to the target community was effected mainly by field age, cover of dominant
21 species, and the mean annual precipitation. The low number of other significant factors found
22 by multiple linear regression emphasizes the importance of the biotic filter effects of
23 dominants on diversity and on the progress of succession. To further illustrate the importance
24 of dominant species on local community characteristics, an example is presented depicting
25 the variability of plot level estimates within the same fields (**Fig. 4**). The within-field spatial
26 variability of plot-scale community characteristics is considerable. For example, the spatial
27 variability of Quadratic diversity in a 31-year-old abandoned field accounted for the 65% of
28 the total variation found in the whole data set while 41% of the total variability of Sorensen
29 index appeared within this 31-year-old abandoned field (**Fig. 4**). Replicated plots from the
30 same field had similar abiotic constraints and species pool, therefore, the high within-field
31 variation of diversity can be attributed to the biotic filter effect of dominant species (i.e. to the
32 effect of identity and cover of dominants).

33

34

1 Discussion

2 3 *Dominant species in mid-successional abandoned fields with strong negative impact on* 4 *succession*

5
6 We identified 77 species, 19 % of the mid-successional species pool (and ca. 10 % of the
7 whole species pool including data from target communities) as dominants in 2 m x 2 m plots.
8 This magnitude corresponds with the number of dominants (56 species) reported by the only
9 other similar comparative study in Europe (Prach & Pyšek 1999). Our country-scale survey
10 found 8 species (*Bothriochloa ischaemum*, *Solidago gigantea*, *Bromus erectus*, *Calamagrostis*
11 *epigeios*, *Festuca vaginata*, *Inula ensifolia*, *Festuca rupicola* group and *Inula britannica*)
12 with the strongest negative impacts on local patch-scale diversity. Their relative cover ranged
13 between 84% and 99% corresponding well with the threshold (80% cover) used by Prach &
14 Pyšek (1999). Contrary to our expectation, our first hypothesis (H1) related to the
15 generalizations about traits of these dominant species was only partially supported by these
16 results. While the number of the most successful dominants were similar (nine in the Czech
17 survey and eight in the Hungarian survey), there were remarkable differences in the traits of
18 the most successful species. Ideal successional dominants in the western part of Czech
19 Republic were tall, wind-pollinated plants, often capable of intensive lateral spread and
20 requiring high nutrient supply and sufficient site moisture. In Hungary, most successional
21 dominants were also wind pollinated species and had capacity for lateral vegetative spread.
22 However, the most successful dominant species in our study varied in size, and had, on
23 average, low requirements for nitrogen, but high requirements for light. These differences can
24 partly be explained by the drier climate in Hungary and the fact that our survey was restricted
25 to mid-successional old fields. Among the most important successional dominants recorded
26 in the Czech survey, *Artemisia vulgaris*, *Chenopodium album*, *Elymus repens* were also
27 important in Hungary. However, they appear in the early stages of succession and in ruderal
28 (often eutrophic) habitats (Bartha 2007; Bartha et al. 2008).

29 In contrast to the results of Prach & Pyšek (1999), our survey revealed that many mid-
30 successional old fields in Hungary are dominated by species typical to dry grasslands and
31 prefer secondary habitats with dry conditions, nutrient poor soils, and eroded surfaces.
32 *Bothriochloa ischaemum* was identified as the species with the strongest negative effect. This
33 C4 perennial bunchgrass is native to Hungary, and appears in small gaps or eroded surfaces
34 with drier and warmer microhabitats in slope steppe grasslands (Bartha 2007; Szentes et al.

1 2012). *Bothriochloa ischaemum* is indicated as an invasive species in several parts of the
2 world (Gabbard et al. 2007; Schmidt et al. 2008). The importance of *Bothriochloa ischaemum*
3 is likely to increase in the future, due to global warming (Auerswald et al. 2012).

4 Dominance doesn't necessarily mean that a species is having a filter effect. Other factors are
5 potentially limiting diversity and the progress of succession including dispersal limitation,
6 disturbances, herbivory, adverse soil or climatic conditions, and stochastic factors. Our data
7 represented varying climatic conditions, different topography, soils, landscape contexts and
8 land use histories. However, these factors did not show significant correlations or showed
9 only minimal correlations with Quadratic diversity and similarity to the target community.
10 Other studies which found significant effects of abiotic constraints (e.g. effects of low soil pH
11 and low temperature) (Prach & Řehouňková 2006; Prach et al. 2007; Jírová et al. 2012)
12 worked in a broader range of habitats including more adverse environmental conditions. In
13 contrast to other studies (Novák & Konvička 2006; Prach & Řehouňková 2006; Kiehl 2010;
14 Knappová et al. 2012), dispersal was not an important limiting factor in our case, because we
15 selected abandoned fields with good seed sources in the neighbourhood. We found extremely
16 high within-field spatial variability of plot-scale community characteristics. The magnitude of
17 plot-scale spatial variability within some abandoned fields reached the 40-60 % of total
18 regional scale variation of data. Because replicated plots from the same field had similar
19 abiotic constraints and species pool, therefore, the high within-field variation of diversity and
20 progress of succession can be attributed to the local biotic effect of dominant species. Our
21 results and interpretation are in accordance with many previous studies (Pickett et al. 2001;
22 Virágh & Bartha 2003; Hölzel 2005; Moore & Elmendorf 2006; MacCain et al. 2010; Wilsey
23 2010; Deák et al. 2011; Házi et al. 2011; Szentes et al. 2012) reporting about the adverse
24 effects of dominant species on diversity.

25 Although some abiotic limitation, stochastic and historical factors are always present, our study
26 emphasize the importance of biotic filter effects in succession.

27

28

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

30

31 Our results supported the hypotheses (H2 and H3) that different dominant species have
32 different impacts on succession. Mid-successional plots dominated by species which are
33 dominant in natural grasslands (*Festuca rupicola*, *Festuca vaginata* and *Brachypodium*
34 *pinnatum*) showed higher similarity to target communities than plots dominated by species

1 which are subordinate in mature communities (e.g. *Bothriochloa ischaemum*, *Bromus erectus*,
2 *Calamagrostis epigeios* and *Poa pratensis*). This result suggests that the impacts of species
3 dominant in transitional habitats are related to their role in mature (near-equilibrium)
4 communities, supporting Grime's theory (Grime 1987, 1998) and our H2b hypothesis.
5 Ruderal competitors who are subordinate in mature communities grow fast and monopolize
6 resources in open successional habitats where they are released from the control of dominant
7 matrix species. Studying secondary succession on abandoned meadows, Falińska (1987)
8 described similar patterns distinguishing 'dominants' (species able to coexist with others, cf.
9 group D in our study) and 'monopolists' (fast growing clonal species tending to eliminate
10 other species, cf. group S1 and S2 in our classification). In our study, species which are
11 matrix species in mature communities correspond to 'global dominants' according to the
12 classification of Olff & Bakker (1998) while species which are subordinate in mature
13 communities correspond to 'local dominants'. We suggest that local dominants have a
14 stronger impact in the intermediate stages of community reassembly than global dominants.
15 Using similar reasoning, alien species should have even stronger suppressive effect on local
16 diversity. In accordance with this expectation (c.f. our third hypothesis, H3) and the results of
17 another survey made by Hejda et al. (2009), we found that *Solidago gigantea* (an alien
18 species) had the strongest negative impact.

19

20 *Understanding the patterns of successional dominant species at landscape scale*

21

22 A national-scale survey of Hungary identified 12 species, a small proportion (3%) of mid-
23 successional species pool as important successional dominants in human affected cultural
24 landscapes. Our results suggest that these mid-successional dominant species differ in their
25 impacts on the diversity and progress of succession.

26 How do the relative importance and dynamic relationships (successional states) of these
27 dominant species vary in different regions? What kind of patterns theory could predict and
28 how can we understand the present and future variability of successional pathways?

29 In accordance with other studies (Pickett et al. 2001; Prach & Řehouňková 2006; Prach et al.
30 2007; Jírová et al. 2012), our survey presented additional evidence of the high spatiotemporal
31 variability in vegetation succession. Part of this variability can be explained by abiotic
32 differences between regions. However, we argue that biotic interactions (local assembly
33 processes) modulated by human influences (by generating different sizes and frequencies of

1 disturbances, and by changing the sizes of disturbed areas and the availability of propagulum
2 sources) have significant effects on successional pathways.

3 We present here a conceptual model to explain the complexity of spontaneous succession in
4 this context, assuming that abiotic parameters (climate, soil, topography) are more or less
5 constant in the region, but human influences vary.

6 How many different regeneration and degradation pathways can be distinguished within a
7 landscape where the abiotic conditions are homogenous? How will these successional
8 pathways change in the future due to increasing human influence? The answer to these
9 fundamental questions depends on the intensity of disturbance and the size and composition
10 of the species pool of a given landscape. Fine-scale disturbances in natural communities
11 induce stochastic micro-successions without visible changes at stand level (Herben et al.
12 1993). Slightly bigger disturbances (e.g. mounds of burrowing animals) induce some
13 directional changes in community composition (Bartha 2007). Large disturbances (e.g.
14 cultivated fields) need more time to recover after abandonment and will produce a distinct
15 series of successional phases (Bartha 2007). We suggest that the bigger the extent and
16 intensity of a disturbance, the larger the number of potential species attaining local
17 dominance with some biotic filter effects on local plant assembly. We also suggest that at the
18 same degree of disturbances, the number of potential dominant species and the length of
19 successional pathways increases by the increasing dispersal limitation of natural matrix
20 forming species (**Fig. 5**). Species which are subordinate in natural communities might be able
21 to colonize and grow faster than the corresponding dominant matrix species (cf. colonization-
22 competition trade off, Tilman 1988). Below a certain threshold, (when disturbances are
23 moderate and there are good propagulum sources), all species which become local dominants
24 in succession originate from the local natural communities. In our survey, most abandoned
25 fields were situated in extensively used traditional landscapes with relatively rich species
26 pool, high naturalness and good regeneration potential. As a consequence, most successional
27 dominant species were dominants (D) or subordinates (S1, S2) in natural reference
28 communities.

29 After crossing a threshold, ruderal species will have more and more chances to establish large
30 persistent populations and form distinct successional stages (Prach & Pyšek 2001). Similar to
31 our results, Prach and Pyšek (1999) found only a few alien species which became dominant
32 in successional communities. However, other more ruderal landscapes might have different
33 successional pathways with larger contribution of weeds (native and alien weeds) as
34 successional dominants (Szegi et al. 1987; Prach & Pyšek 2001). Due to increasing

1 disturbances and decreasing natural species pools, we expect an increasing role of alien
 2 species in the future. Our results suggest that mid-successional dominant species differ in
 3 their impact on the diversity and progress of succession. There is a challenge to increase
 4 future restoration success by influencing the establishment and growth of potential
 5 successional dominant species. During grassland restoration, field managers should enhance
 6 the colonization of native dominant grasses and suppress other grasses which are aliens or
 7 subordinates in local natural grasslands. The small number of important dominants found in
 8 the broad-scale survey of Prach & Pyšek (1999) and in our present study suggests that similar
 9 surveys in other countries would also identify only 8-10 important species. Due to the low
 10 number of potential key species, understanding their traits and developing successful
 11 restoration measures seems to be a feasible and operational task for the future.

12
 13

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15
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24

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1 **List of Appendices**

2 Appendix S1: The locations of study sites in Hungary.

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

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

6 Appendix S4: Detailed statistical tests: Mann-Whitney U Test for each species pair.

7 Appendix S5: Multiple regression model of Quadratic diversity and Sorensen similarity (as
8 dependent variables) in relation to different independent variables.

1 Table 1. Mid-successional dominant species with the strongest negative effect on diversity found in a country-scale survey of abandoned fields
 2 in Hungary.
 3

	Abundance			Position in succession	Effect	Characteristic vital attributes of species									
	Frequency% (N=33)	Absolute cover	Relative cover	Age (years)	Quadratic diversity	Origin	Life form	Nitrogen demand	Moisture demand	Light demand	Lateral spread (m/yr)	Height	Pollination mode	Grime's life strategy	Family
<i>Botriochloa ischaemum</i>	54.55	50-90	0.85-0.92	15-40	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	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	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	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	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	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	native	H	1-2	3	9	<0.01	2	wind	CS	Poaceae
<i>Inula britannica</i>	3.03	60	0.85	34	0.27	native	TH-H	3	7	8	>0.25	2	insect	CS	Asteraceae

4
 5 Origin of species is according to the Hungarian Flora Database 1.2. (Horváth et al. 1995). Life forms are according to Raunkiaer's system
 6 (Raunkiaer 1934). Ecological indicator values are from Borhidi's system (modified from Ellenberg's system) (Borhidi 1995). The values of the
 7 lateral spread were taken from the CLO-PLA trait database (Klimeš and Klimešová 1999). The height of the species originate from the LEDA

1 trait base (Kleyer et al. 2008) The types of the pollination mode come from the BioFlor trait database (Kühn et al. 2004). The life strategies
2 (CSR) are according to Grime's system (Grime 1979). For more details see Supplement 3.

1

2

3 Table 2. Kruskal-Wallis test showing that the 9 most important dominant
 4 species and the 4 species groups (D, S1, S2, A) in our survey were significantly
 5 different from each other regarding three of all calculated community index.

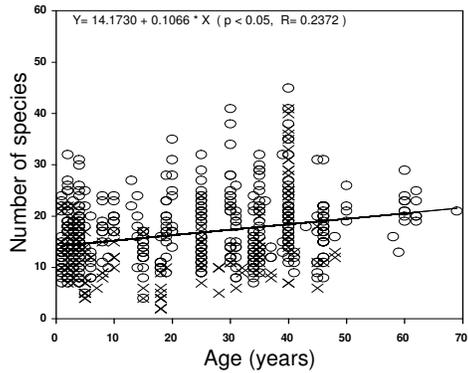
6

<u>Variable</u>	<u>d.f.</u>	<u>N</u>	<u>H-value</u>	<u>P</u>	
<i>for dominant species</i>					
Quadratic diversity	8	99	15.6864	0.0471	*
Equitability	8	99	11.7589	0.1623	n.s.
Sorensen similarity	8	99	47.0492	< 0.0010	***
Bray-Curtis similarity	8	99	38.9955	< 0.0010	***
<i>for 4 species groups</i>					
Quadratic diversity	3	108	8.0290	0.0454	*
Equitability	3	108	5.1866	0.1586	n.s.
Sorensen similarity	3	108	46.5315	< 0.0010	***
Bray-Curtis similarity	3	108	23.3214	< 0.0010	***

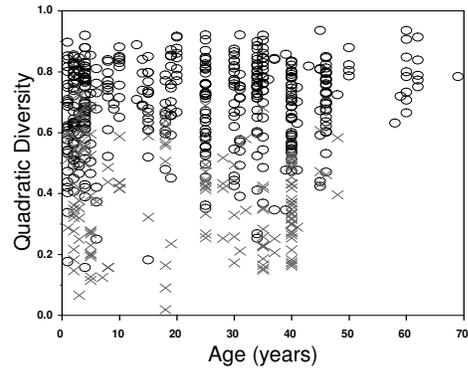
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2 A,



B,

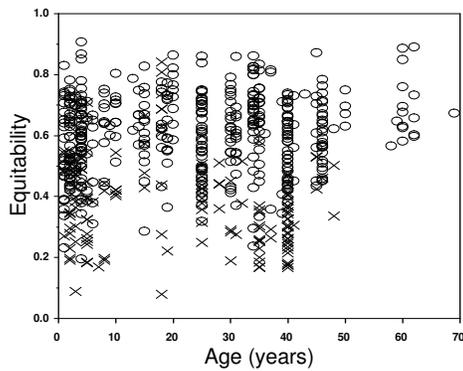


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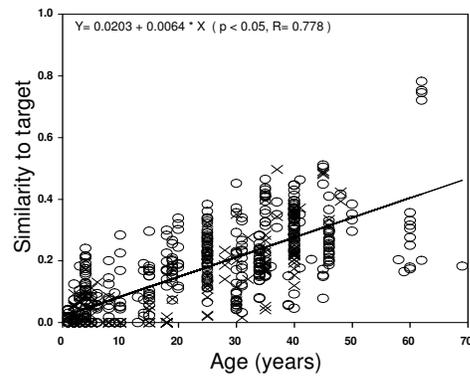
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C,



D,



6

7

8 Figure 1. The progress of old-field succession at regional scale. Linear regression line are
 9 shown if the correlation between x (age) and y (Number of species, Quadratic Diversity,
 10 Equitability and Sørensen index) were significant. X depicts plots with more than 60% cover
 11 of dominant species.

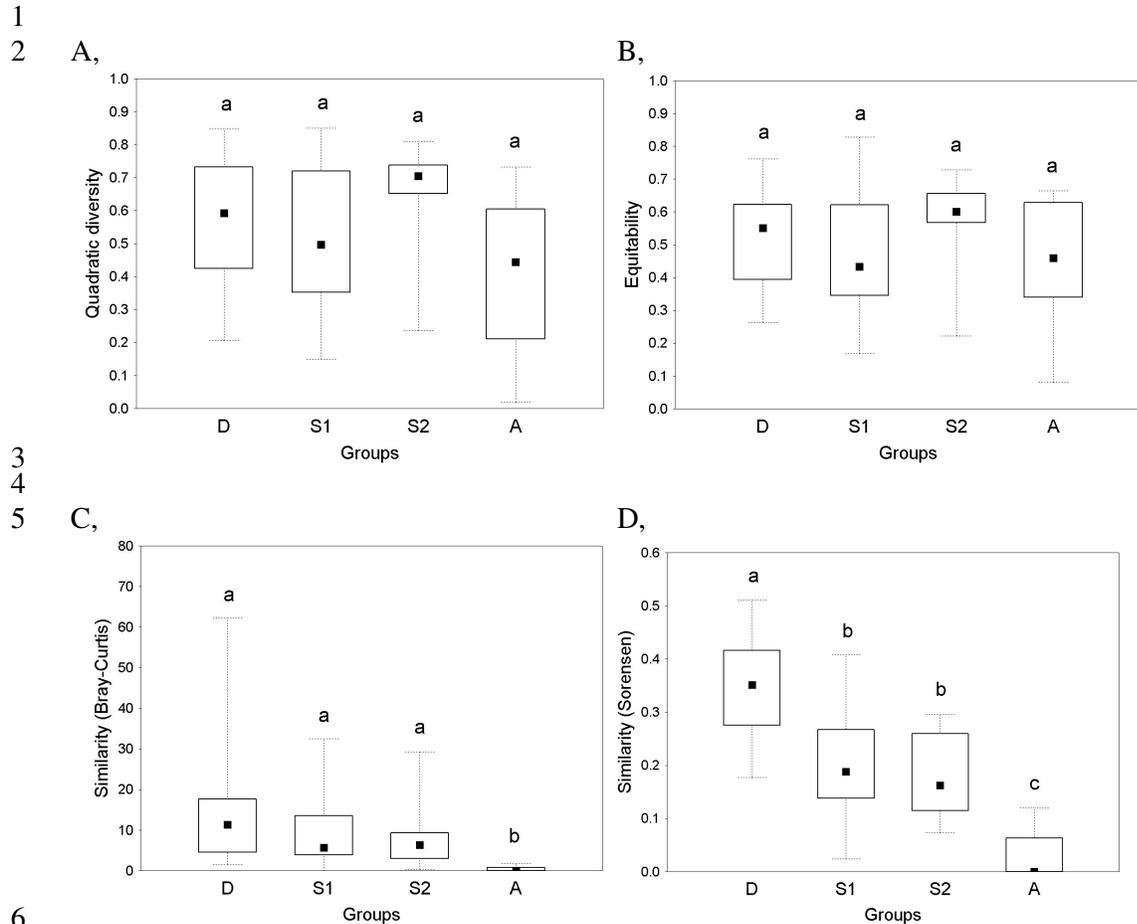
12 A, Number of species

13 B, Quadratic Diversity (Simpson index)

14 C, Equitability (estimated from Shannon diversity)

15 D, Similarity to target community (estimated by Sørensen index)

16



8 Figure 2. The effect of mid-successional dominants classified according to their role in target
9 communities. Box plots show the median, quartiles and range of data. Significant ($p < 0.05$)
10 differences between species groups, assessed with Mann-Whitney *post-hoc* U tests, are
11 indicated by different letters. Species groups are:

12 D = species which are dominants (matrix species) in target communities

13 S1 = subordinate grasses in target communities

14 S2 = subordinate dicots in target communities

15 A = alien (exotic) weeds

16 A, Quadratic Diversity (Simpson index); B, Equitability (estimated from Shannon diversity);

17 C, Percentage similarity to target community (estimated by Bray-Curtis index); D, Percentage
18 similarity to target community (estimated by Sørensen index);

19

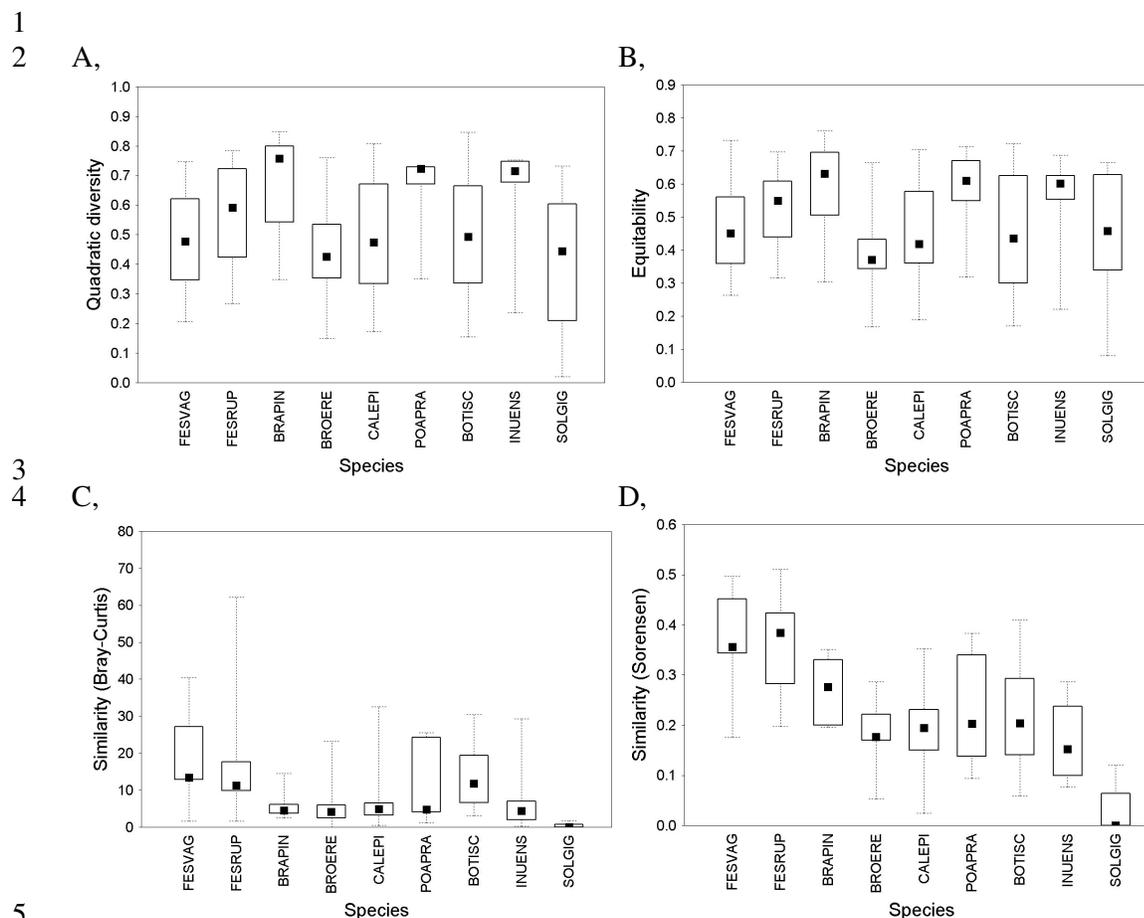


Figure 3. The effect of the identity of dominant species in mid-successional old-fields on
 A, Quadratic diversity (Simpson index); B, Equitability (estimated from Shannon diversity);
 C, Percentage similarity to target community (estimated by Bray-Curtis); D, Percentage
 similarity to target community (estimated by 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*; INUENS = *Inula ensifolia*; SOLGIG = *Solidago gigantea*

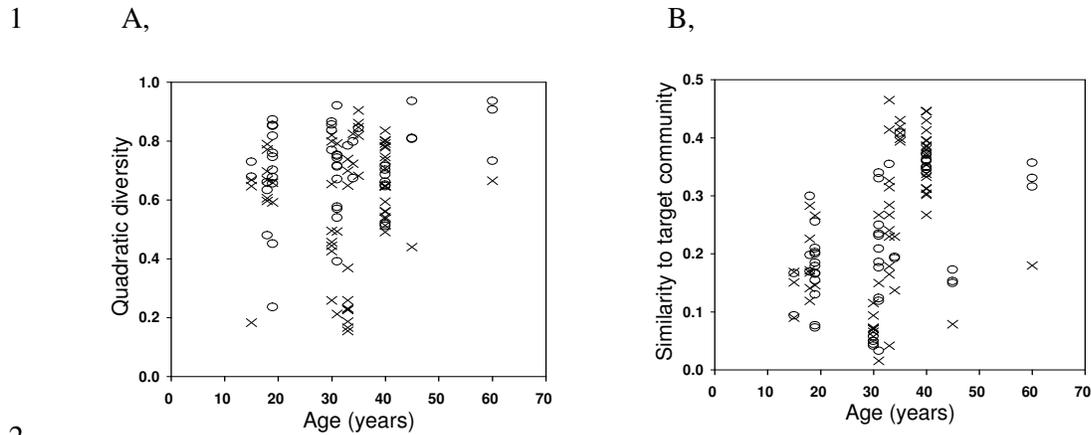
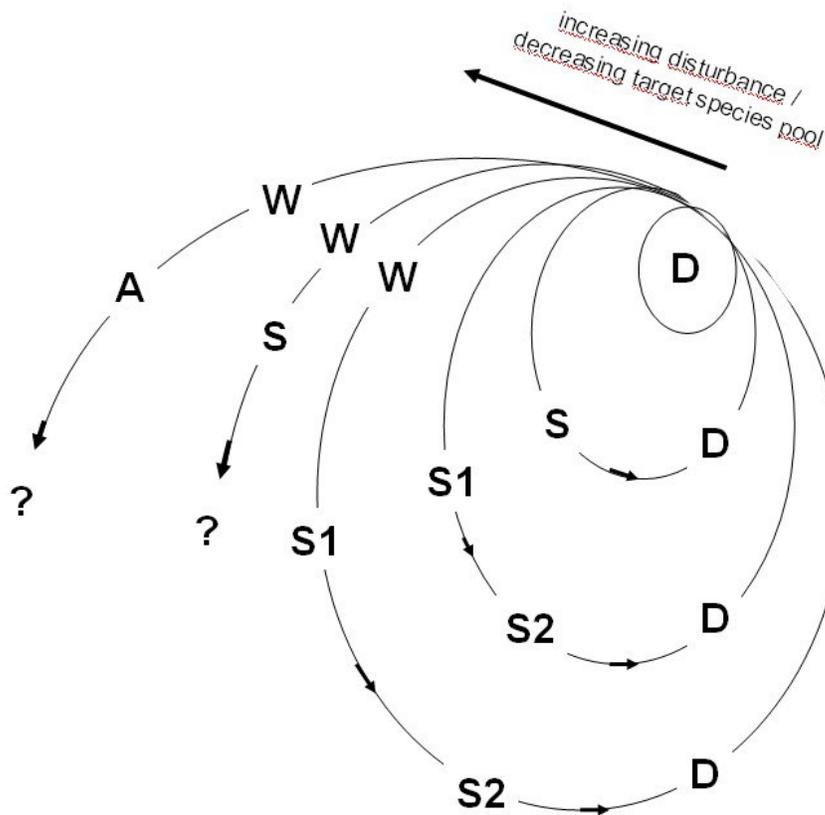


Figure 4. Within-field variability of local (patch-scale) community characteristics in mid-successional old-fields. Plots within a particular field (see the vertical series of points on the graphs) experience the same abiotic environment (climate, soil, landuse history etc..) still express very large spatial variability. The large differences between plots suggest the importance of within-community biotic interactions (e.g. the filter effects of locally dominant species).

A, Quadratic diversity (represented by Simpson index) and B, Similarity to target community (estimated by Sørensen index).

X = plots dominated *Bothriochloa ischamum*, O = plots dominated by other species.

1



- 2
3 Figure 5. A conceptual model explaining the variability of temporal patterns of dominant
4 species in different old-field successions in a theoretical landscape where the abiotic
5 conditions (climate, soil, topography) are homogenous.
6 The reference state is a natural community dominated by species D (the natural matrix
7 forming dominant). Disturbances of various kinds (from the smallest ones as small mammal
8 burrowing, to the largest ones as plowing or surface mining) generate regeneration cycles of
9 various lengths. The bigger the extent and intensity of a disturbance, the longer is the
10 successional pathway and the larger is the number of potential species (S1, S2, W and A in
11 our example) attaining local dominance with some biotic filter effects on local plant
12 assembly. At the same degree of disturbances the number of potential dominant species
13 increases by the increasing dispersal limitation of natural matrix forming species.
14
15 Successional dominants (D, S, A, W) are classified according to their origin and role in target
16 communities.
17 D = dominants (matrix species) in target communities
18 S = subordinate species in target communities (S1, S2 denotes different subordinate species)
19 W= native weeds
20 A = alien weeds