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The Association of Dispersal and Persistence Traits of Plants with Different Stages of Succession in Central European Man-Made Habitats

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Abstract Traits related to seed dispersal, clonality and bud bank affect the success or failure of plant species. Using data from 13 successional seres in various human-made habitats the spectra of traits associated with dispersal and persistence were compared to determine the traits that can be used to predict the occurrence of particular plant species at each stage in a succession and how the importance of these traits changes over time. Differences in the traits of species associated with primary and secondary successions were also studied. Species with seeds that are dispersed by water (hydrochory) decreased in abundance during the course of succession. Species with a splitting main root, monocyclic and dicyclic shoots also decreased in abundance. Species capable of forming a potential below-ground bud bank, hypogeogenous rhizome and retaining a long-term connection with clonal offspring increased in abundance. The results indicate that seed dispersal is more important in

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determining the species composition in the early stages of succession whereas bud banks and clonal traits are more important in the later stages and for colonizing a locality. Primary and secondary seres did not remarkably differ in the trait spectra of the species present indicating that these trends occur in both types of succession.

Keywords Bud bank · Clonality · Disturbance · Persistence · Plant traits
Seed dispersal · Succession

Plant nomenclature Kubát et al. (2002)

Introduction

The presence of plants at a locality depends on their ability to reach and persist at that site. Therefore, plants that produce propagules adapted for different modes of dispersal or develop into plants that can persist at a site because they can propagate vegetatively in several different ways are considered to be important colonizers of barren substrates (Bakker et al. 1996; Nathan and Muller-Landau 2000; Ozinga et al. 2005a,b, 2007, 2009; Ehrlén et al. 2006; Moore and Elmendorf 2006). Consequently, dispersal and persistence traits could, along with other factors like regional species pool or environmental characteristics, be important determinants of the changes in vegetation that occur during succession. While successional changes in vegetation based on floristic composition are usually divergent and not directly comparable among sites, similar changes in the incidence of the broader categories of plant traits occur during succession (Fukami et al. 2005). Therefore, analyzing trait spectra might be a more universal tool than species identity for describing and understanding plant assemblages (Simberloff 2004; McGill et al. 2006; Klimešová et al. 2008; Ricotta and Burrascano 2008).

This functional approach is used in studies on succession (Noble and Slatyer 1980; Prach et al. 1997), however it is usually applied to only one or a few seres or broad life-history categories rather than well-defined traits (Prach et al. 1997). Studies comparing functional traits over large geographical or time scales are rather scarce (Walker and del Moral 2003) and thus the potential of the functional approach in comparative studies seeking general trends in succession has not been fully explored.

Here previous comparative analyses of a number of different seres in central-European human-made habitats are extended (Prach and Pyšek 1994; Prach et al. 1997, 2001, 2007). The objective was to elaborate on a previous study (Prach and Pyšek 1994) that indicates that clonality increases in importance over a period of 10 years of succession. The present study was made on the same seres but for a longer (15 years) period, using more recent data on clonality, and including dispersal and bud-bank traits previously not analyzed. This extension is possible because of new databases that contain comprehensive information on the dispersal and clonal traits of central European species, i.e., BIOPOP (Poschlod et al. 2003; http://www.floraweb.de\proxy\biopop), LEDA (Kleyer et al. 2008; http://www.leda-traitbase.org) and CLO-PLA (Klimešová and Klimeš 2006; http://clopla.butbn.cas.cz).

In this analysis two methodological approaches were used: *i*) In the species-based approach the changes in species covers during the course of succession are explained in terms of the attributes of the plants. *ii*) At the community level, trait attributes are scaled up from the species level to the community level taking into account the covers of all the species with a particular trait. In the former approach the response of individual species are of similar importance, whereas in the later the dominant species outweigh the less common species. Thus, it is hypothesized that in the first approach the attributes are those important in colonization while in the second they are more important for spreading within the plot.

Using this approach the aim was to *i*) identify the most important dispersal and persistence traits associated with successional stages and *ii*) test the hypothesis that plant traits have a different role in primary and secondary succession. Primary succession occurs on new substrates that lack a soil profile and seed bank, while secondary succession occurs on substrates with a seed bank and which were previously covered with vegetation but was then denuded by disturbance (Glenn-Lewin et al. 1992). The expectation is that dispersal traits will be more important in the initial stages of primary succession and persistence traits in the initial stages of secondary succession.

Material and Methods

Study Sites

Data on species presence and covers from 13 successional seres were analyzed. Two sampling methods were used to record the changes in vegetation: *i*) Long-term monitoring (LTM). Permanent plots (5×5 m) were established after each site was created and sampled more or less annually, especially in the early stages of succession; *ii*) Space-for-time substitution (SFT; Pickett et al. 1987). Permanent plots were established at each site at comparable stages but of different ages and the course of succession was inferred by comparison (for details see Prach et al. 2007). Percentage values for species covers were estimated visually between July and September when the vegetation was most abundant. The period of time, for which the successional data were collected, ranged from 12 to 76 years. However, only the first 12–15 years of succession, for which data were available for all the seres monitored, were analyzed in this study. The seres included the following habitats (in parentheses is the number of samples and sampling method used at each locality):

Old Fields. Succession in abandoned fields in the Bohemian Karst near Prague (Osbornová et al. 1989; Prach et al. 2007). Three seres were distinguished based on soil moisture: xeric (5 – number of study sites; LTM, SFT) dominated by *Arrhenatherum elatius* (37.5%), closely followed by *Festuca rupicola* and *Poa angustifolia* after 15 years; mesic (3; LTM, SFT) dominated by *Arrhenatherum elatius* (87.5%) after 15 years; and wet (3; LTM, SFT) with *Phragmites australis* the dominant species (80%) after 15 years of succession.

Ruderal Urban Sites. Three seres based on the nature of the substrate were distinguished in the town of Plzeň: nutrient-poor, mineral (1; LTM) dominated by

Calamagrostis epigejos. (43.8%); moderate nutrient content, mineral (1; LTM) dominated by *Sambucus nigra* (37.5%); nutrient-rich with organic topsoil (1; LTM) also dominated by *Sambucus nigra* (68.8%). Data from Pyšek (1978).

Spoil Heaps. Two sub-seres were distinguished on spoil heaps that resulted from brown coal mining in NW Bohemia (Prach 1987), wet depressions (3; SFT) dominated by *Phragmites australis* (18%) and spoil heaps (5; LTM, SFT) dominated by *Holcus mollis* (37.6%).

Dumps of Soil Around a Fishpond. Succession on longitudinal piles of soil alongside a newly constructed fishpond in S Bohemia. The piles consist of autochthonous organic peaty topsoil (1; LTM), which is dominated by *Phalaris arundinacea* (30%) and mineral subsoil (1; LTM) dominated by *Betula pendula* (50%). Data provided by Prach (unpubl.).

Bulldozed Sites. Reclaimed sites in areas deforested due to air pollution. To facilitate the replanting of spruce, the sites were bulldozed to create plots covered with grass, which when the topsoil was removed (3; LTM, SFT) were dominated by *Deschampsia flexuosa* (56%) and the bulldozed mounds of soil (3; LTM, SFT) were dominated by *Calamagrostis villosa* (46%). Data from Pyšek (1992).

Exposed Bottom. Succession on an exposed bottom of an empty water reservoir at Dřínov (NW Bohemia) (1; LTM) was dominated by *Calamagrostis epigejos* (80%). Data provided by Prach et al. (unpubl.).

Phytosociological relevés for each year of each sere were used in a multivariate analysis. The dataset consisted of 123 samples and 189 species. Mean cover values of each species were calculated from relevés taken at the same stage in the same year. Each relevé was characterized by the age of the succession, which is the number of years since the beginning of that succession. Each sere was characterized by altitude and characteristics of the substrate at the beginning of the succession, determined using standard methods in the Chemical Laboratory of the Institute of Botany AS CR in Průhonice: pH, total nitrogen content, content of NH_4^+, NO_3^-, PO_4^{3-} soluble ions, and C:N ratio (data from Prach et al. 2007). The initial conditions of a site were characterized by using the direct measurements of soil chemistry along with Ellenberg indicator values for nitrogen and moisture (Ellenberg et al. 1991), based on the species present in the first five years of succession. All these characteristics are included as environmental variables in the ordination.

Plant Traits

Information on traits related to seed dispersal (dispersal traits) was obtained from the databases BIOPOP (Poschlod et al. 2003) and LEDA (Kleyer et al. 2008), which summarize literature data on Central-European species. The following modes of dispersal were considered: anemochory (dispersal by wind), hydrochory (by water), epizoochory (in the fur or on the claws of animals), endozoochory (after digestion by animals), dysochory (by seeds collected and stored by animals) and anthropochory (by man).

Information on traits related to persistence (persistence traits) was obtained from the CLO-PLA3 database (Klimešová and Klimeš 2006, 2008), which includes traits related to clonality and vegetative regeneration. This database integrates information on the presence and type of the bud bank of distinct parts of plants. The bud bank types are distinguished according to the mode of perennation of bud-bearing organs as perennial (bud bearing organs persist for two or more years), seasonal (plant organs persist for less than two years) and potential (ability to form adventitious buds on leaves or roots). This database also contains data on the type of the clonal growth organ (CGO) and its role in the life of the plants. Such organs are characterized as necessary (adult plants in all populations possess a CGO), additive (not needed for flowering and overwintering of a plant and absent in some plants or populations) or regenerative (develop after an injury). A species is considered as clonal if it has a necessary or additive CGO. This database also includes records of the persistence of the connection between clonally produced offspring (ramets), shoot cyclicity (life-span of a shoot) and the extent of the lateral spread of a species per year. There is usually more than one record for each species so all the records referring to different attributes of a clonal trait for each species were incorporated proportionally. For instance, for a species that has six records for the extent of lateral spread, three that are less than 0.01 m/year and three of 0.01–0.25 m/year, the approximate categorization for lateral spread is 0.5 for a spread of 0.01 m/year and 0.5 for 0.01–0.25 m/year. For the list of all traits recorded see Table **1**.

Data Analysis

Species Level

The species-based approach was adapted from de Bello et al. (2005). Species score (response) to successional age (dependent variable) was quantified first by using of canonical correspondence analysis (CCA) in CANOCO for Windows software (ter Braak and Šmilauer 2002). The unimodal method was chosen because the length of the longest gradient exceeded 3 (Lepš and Šmilauer 2003). Species covers were log transformed prior to analysis (for details see Lepš and Šmilauer 2003). In the first step, CCA was done for the whole dataset, different types of succession (primary *vs* secondary) and individual seres. Selection of significant environmental variables (successional age, altitude, substrate pH, total nitrogen content, content of NH_4^+, NO_3^-, PO_4^{3-} soluble ions and C:N ratio) was done using forward selection. The significance of environmental variables was tested using the Monte Carlo permutation test with 499 permutations. In the next step, only time (age) was considered as the explanatory variable and other previously selected significant environmental variables ($P<0.05$) and the type of locality were considered as covariates (partial CCA) in a given analysis (e.g., for the whole dataset or for primary/secondary succession or for individual seres). Consequently, the species scores to successional age obtained from the ordination axis constrained by age in CCA were predicted on the basis of species traits (independent variables, the trait included if $P<0.05$) using forward stepwise linear regression performed in STATISTICA 8 software package (StatSoft Inc. 2008).

Table 1 Results of species- and community-based approach analyses. + or −: a significant increase or decrease in the incidence of plants with a given attribute with the age of the succession. +− or −+: peak and valley-shaped dynamics of the attribute during succession

		Species-based approach			Community-based approach		
Trait	Trait type	All seres	Primary succession	Secondary succession	All seres	Primary succession	Secondary succession
Seed dispersal	Anemochory				+0.08**	+0.14**	+0.11*
	Hydrochory	−0.24***	−0.16**	−0.29***	−0.06**	−+0.39***	
	Epizoochory				+−0.13***	+−0.46***	+−0.11*
	Endozoochory				−0.12***	−0.25***	−0.06*
	Dysochory				+0.03[a]		+0.11**
	Anthropochory					+0.15**	−0.06*
Tap root persistence	Persistent				−0.08**	−0.33***	−+0.06*
	Not-persistent			+0.32**	+0.04*	+0.24***	
Clonality	Clonal			−0.29**	+−0.24***	+0.42***	+0.17**
	Nonclonal				−+0.24***	−0.42***	−0.17**
Bud bank in layer >10 cm	Perennial				+0.24***	+0.08*	+0.46***
	Seasonal		+0.40*		−0.31***	−+0.49***	−0.37***
Bud bank in layer 0 to 10 cm	Perennial				+0.12***	+0.11*	+0.18***
	Seasonal		−0.84***		−0.32***	−+0.55***	−0.39***
Bud bank in layer 0 cm	Perennial				+0.06**	+0.10*	+0.07*
	Seasonal				−0.18***		−0.05*
	Potential		−0.20**				
Bud bank in layer 0 cm to −10 cm	Perennial				+0.05*	+−0.56***	
	Seasonal				−0.04*		−0.16***
	Potential				+0.15***		+0.28***
Bud bank in layer <−10 cm	Perennial				+0.15***	+0.31***	+−0.37***
	Potential	+0.25***		+0.44***	+−0.29***	+−0.34***	+0.38***
Necessary CGO	Horizontal above-ground rhizome						−0.07*
	Epigeogenous rhizome						
	Hypogeogenous rhizome	+0.19**		+0.25**	+−0.09*	+0.27***	+−0.13**
	Stem tuber						

Table 1 (continued)

	Root-splitter	−0.17**			−+0.08**	−+0.29***	−0.07*
	Roots with adventitious buds						
Additive CGO	Horizontal aboveground rhizome				+−0.07*		+−0.07*
	Epigeogenous rhizome						
	Roots with adventitious buds			−0.18*	+−0.13***	+−0.35***	
	Offspring tuber				+0.06**	+0.11*	
	Plantlet (pseudovivipary)						
	Root-splitter						
Regenerative CGO	Fragment of stem						+−0.04*
	Roots with adventitious buds				+0.18***	+0.10*	+0.35***
	Root-splitter	−0.13*					
Shoot cyclicity in CGO	1	−0.47***	−0.22**	−0.30***	−0.24***	−0.33***	−0.26***
	2	−0.22*			+−0.05*	+0.25***	+−0.06*
	>2				+0.26***	+0.09*	+0.51***
Persistence of connection to CGO (years)	1				−0.05*		−0.17***
	2						−0.08*
	>2	+0.22***	+0.26**		+−0.14**	+0.35***	+−0.14**
Nr. offspring shoots/ parent shoot/ year in CGO	<1				−0.09***		−0.17***
	1		+0.26***		+0.06**	+0.25***	
	2–10				+−0.13***	+−0.44***	+−0.21***
	>10					+0.12*	−0.08*
Lateral spread (m/yr) in CGO	<0.01		−0.35***		+0.05**	+0.15**	+0.03*
	0.01–0.25				+−0.19***	+−0.62***	+−0.13**
	>0.25					+0.11*	−0.06*
Offspring size	Small				+0.04*		+0.05*
	Same				+−0.02*	+0.37***	−0.10**

In the species-based approach the traits that significantly ($P<0.05$) predict species' response to the course of succession revealed by *forward stepwise linear regression* are presented. In the community-based approach, the significantly ($P<0.1$) changing incidence of traits during the course of succession revealed by comparing weighted trait values with the abundance of species over time in the different communities are presented. Presented are correlation coefficients β and significance tests. Statistical significance for the species-based approach: * − $0.05>P>0.01$; ** − $0.01>P>0.001$; *** − $0.001>P$.

Community Level

In the community-based approach, aggregated trait values are calculated for each sample as mean values for each particular trait weighted according to the abundance of species with given trait values (as all traits were categorical, the value represents the relative proportion of species possessing a given trait, weighted by their cover). The age of the succession was used as a predictor (explanatory variable) to test for temporal trends (increase, decrease, hump or valley-shaped) in particular traits using a generalized linear model and considered as significant if $P<0.1$ (McCullagh and Nelder 1989). If not significant, a second-order polynomial was fitted. Relative proportions of aggregated traits were used after angular transformation to linearize sigmoid distributions and equalize variances of proportions.

Primary* vs *Secondary Succession

Redundancy analysis (RDA) was used to test differences in trait composition (in the 1st year and after 15 years of succession) and environmental conditions from the onset of succession between primary and secondary seres. The type of succession was chosen as the environmental variable and its significance was tested using the Monte Carlo permutation test with 499 permutations. Linear methods were chosen rather than unimodal because the length of the longest gradient was shorter than 3 (Lepš and Šmilauer 2003).

Results

All Seres – Cumulative Data

In the species-based approach hydrochory was selected as the most important dispersal attribute across seres because species with this trait decreased in abundance during the course of succession (see Table 1). Species with a splitting main root, monocyclic and dicyclic shoots also decreased during succession (see Table 1). In contrast, species with a potential below-ground bud bank, hypogeogenous rhizome and long-term connection between clonal offspring increased during succession (Table 1). The abundance of species with other traits did not appear to change significantly during succession.

In the community-based approach the importance of many attributes changed during the course of succession across seres (Table 1). The proportion of species dispersed by means of endozoochory significantly decreased during succession, whereas those dispersed by anemochory and dysochory increased. Those species with splitting main roots, monocyclic and dicyclic shoots, a seasonal bud bank, stolons (horizontal above-ground rhizome characterized as necessary), connections between clonal offspring persisting for one year or those that produce less than one offspring shoot per mother shoot per year thrived in the early stages of succession. Plants of following characteristics increased in cover during succession: those that form a below-ground bud bank, have long-persisting connections among clonal offspring, regenerate from roots, possess polycyclic shoots, produce one offspring shoot per parent or their lateral spread is up to 1 cm/year.

Primary vs *Secondary Succession*

In the species-based approach hydrochory was the dispersal attribute selected as significantly predicting the species that are present at each stage in a succession in both types of seres. Hydrochory was important at the beginning of the succession and then plants with the attribute decreased in the course of succession (Table 1).

In primary succession, species forming a seasonal and potential bud bank in layers near the soil surface, species with monocyclic shoots and of short lateral spread decreased during the course of succession. Species forming a seasonal bud bank in the upper layers (more than 10 cm above soil surface) and with long-term connection between ramets producing one offspring shoot per year increased throughout succession (Table 1).

In secondary succession, the clonal species and species forming adventitious buds on roots decreased over the succession whereas species with transient main roots, potential below-ground bud banks and hypogeogenous rhizomes increased during the course of succession (Table 1). Individual seres' results are available in the Electronic Supplementary Material **1.**

In the community-based approach the RDA did not reveal differences in trait composition between primary and secondary seres both at the beginning and after 15 years of succession (1st year – dispersal mode: P=0.6840, F=0.527, clonal traits: P=0.9980, F=0.131, all traits: P=0.99, F=0.154; after 15 years – dispersal mode: P=0.9780, F=0.123, clonal traits: P=0.9080, F=0.373, all traits: P=0.9340, F=0.353). Nonetheless, some changes in the proportional covers of species with certain traits in the course of succession were detected. The proportion of species that are dispersed by man increased in primary seres but decreased in secondary seres (Table 1). The proportion of species producing many offspring shoots increased during succession in primary seres but decreased in secondary seres. The same pattern was observed also for the size of offspring (Table 1). Other traits showed consistent changes in both types of seres or were significant only in one sere.

Individual seres' results are available in the Electronic Supplementary Material **2.**

Discussion

By using data from 13 seres in different habitats, some dispersal and persistence traits important in community dynamics in a Central-European context were identified, which complete some earlier findings (Prach and Pyšek 1994; Prach et al. 1997). Seed dispersal by water is the most important mode of dispersal at the beginning of succession. In terms of persistence traits, species with monocyclic and dicyclic shoots and a splitting main root were gradually replaced by species with potential below-ground bud banks, hypogeogenous rhizome and long-persisting connections between ramets. Seed dispersal played the same role in seres with a seed bank (secondary succession) and lacking a seed bank (primary succession).We found, however, some persistence traits important either in primary or secondary successional seres.

Dispersal Traits

The contribution of hydrochory at the onset of succession in all seres is surprising because many seres were located at dry sites distant from water courses. Nonetheless, dispersal of seeds adapted to hydrochory in areas distant from wetlands is reported by Ozinga et al. (2004, 2009). Species possessing seeds with an impermeable seed coat may be present in a community because they survived in the seed bank rather than because of their good floating ability (Ozinga et al. 2004). Alternatively, seeds with various appendages may be spread not only by animals or wind but also by water. Concerning hydrochory, it should also be mentioned that it includes, according to the definition of Poschlod et al. (2003), seeds spread by rain and runoff, which may occur in the open early stages of succession. However, this type of water dispersal refers only to a few species and cannot explain the observed pattern.

The prevalence of anemochory increased slightly during succession, which seems surprisingly, because wind dispersal is often interpreted as a strategy of pioneers. However, this common assumption may not necessarily be true, as measurements of terminal velocities of alpine and lowland species suggest (cf. Tackenberg and Stöcklin 2008).

Persistence Traits

The increase in species that have both an above-ground and below-ground bud bank of perennial type during the course of succession indicates a replacement of short-lived herbs by perennial herbs or by herbs with long-lived below-ground plant organs. Additionally, it can be explained by the increasing abundance of shrubs and trees, i.e., species that have a long life. Also increasing and/or increasing and consequently decreasing proportions of species with potential bud banks in the course of succession was probably due to the increase in root sprouting woody species (mainly shrubs like *Rubus* species). Although all seres were of human-made habitats, disturbance events were probably rare and this facilitated the dominance of persistence over regenerative strategies (Kleyer 1999; Kahmen and Poschlod 2004).

The incidence of clonality did not increase during the course of succession if particular species are considered. Nonetheless, the importance of clonal species decreased in secondary successional seres if the species level is considered but increased if the community level is applied. This indicates that clonality is not an essential attribute for species to colonize a locality but is important for further persistence and local spread or for attaining high dominance. Clonal trait types also changed during succession. As the effect was consistent at both species and community levels the decreasing importance of short lifespan of shoots (shoot cyclicity 1 year) and increasing importance of persistent connection among ramets should be mentioned. This indicates that fast turnover of biomass and shoots was replaced by the strategy of occupying space and conserving nutrients. At the community level, some clonal traits showed increasing importance from the beginning of succession but their importance decreased in later successional stages. This pattern indicates that the 15 years of succession covered by this study does not reflect unidirectional changes. This might have resulted from the increasing cover of trees, which changed the conditions for herbaceous plants later in the succession, for example, increasing and then decreasing lateral spread, rate of vegetative multiplication and persistence of connection among ramets.

Primary vs *Secondary Succession*

As the importance of seed dispersal is similar in both successional types, it is concluded that seeds originating from the surroundings rather than the seed bank played an important role in the community dynamics of secondary seres. The greater role of seed dispersal in secondary succession is also reported by Bischoff et al. (2009). However, species with small, easily spread seeds usually have more abundant seed banks than those with large seeds (Bekker et al. 1998; Thompson et al. 2001). This co-variation could mask the importance of a seed bank in secondary seres in the current study.

The importance of persistence traits differ between primary and secondary seres if the species based approach is considered, nonetheless no important differences are observable if the community-based approach is applied. Such discrepancy illustrates that trends are masked by dominance of a species with distinct characters (see **Discussion** below) in the community based approach in which plants covers are considered. The significant role of clonality and regeneration from roots at the beginning of succession on secondary seres indicates that the initial vegetative re-establishment of plants could be important in secondary seres as suggested by Prach and Pyšek (1994).

Species vs *Community-Based Approach*

Some dispersal and persistence traits play a significant role in community dynamics and determining a species' presence at a particular stage of succession. The use of different statistical approaches revealed that in the species-based approach, dispersal attributes are more closely associated with succession, whereas in the community based approach it is persistence attributes. Such discrepancy could be explained by strong dominance of some species in studied communities. In the case that a community was dominated by one species (e.g., *Calamagrostis epigeos*), the importance of trait attributes typical for this species was higher in the community-based approach than in the species-based approach. Consequently, subordinate species co-occurring with this dominant affected output of analysis more in the species-based than in the community-based approach. Cingolani et al. (2007) suggest that dominant species have trait values better fitted to the environment than minor species and including minor species into analyses may therefore obscure trait-environment relationships. The results of our study indicate that the simultaneous use of both a species-based and community-based approach is desirable. The different outputs of these approaches showed that the ability to reach the site is the most limiting factor in succession if individual species are considered. Persistence and spread during succession, however, are important attributes of plants at the community level. Therefore, each approach may answer a different question and thus the two approaches are complementary.

Conclusion

Overall there are no differences in the trait composition of plants in primary and secondary seres, which accords with the results of a previous study by Prach et al. (1997). Therefore, even though primary succession starts on undeveloped soils that do not have seed and bud banks, dispersal and persistence traits are of similar importance and show similar dynamics during the course of succession in both types of seres. In addition to the environmental characteristics that differed significantly between the seres (see Prach et al. 2007) there are traits with consistent predictability/importance during succession in all seres. Dispersal traits are more important at the beginning and persistence traits later on in the succession. The traits enabling persistence at the population level (e.g., clonal multiplication) together with traits providing persistence at the individual level (e.g., polycyclic shoots and perennial organs) increased in significance over the time scale of this study.

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