Functional traits during succession: is plant community assembly trait-driven?

Funkční vlastnosti rostlin během sukcese: je formování společenstva řízeno vlastnostmi rostlin?

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D e d i c a t e d   t o   t h e   m e m o r y   o f   L e o š   K l i m e š

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Little is known about changes in the significance of environmental filtering and neutral processes during the succession of plant communities. Generally, a succession is expected to be trait-driven and a shift is predicted from high importance of seed dispersal ability in initial phases to importance of strong competitive ability in later stages. In this study, we consider a community assembly trait-driven in the case of a shift in functional traits during succession and randomly assembled in the case there is no shift in functional traits during succession. We therefore tested whether urban plant communities show trait convergence or trait divergence in relation of successional stage, water and nutrient availability. At two scales (100 × 100 cm and 10 × 10 cm), we analysed traits relevant to seed dispersal, stress tolerance and competitive ability and compared real data with null models. We subsequently used regression trees to associate convergence and divergence to plot age and stress due to low water and soil nutrient availability. Most traits were neither significantly convergent nor divergent and the variance explained by the regression trees was often lower than 20%. We found divergence in seed number instead of the expected convergence towards high seed number. In accord with expectations we found low seed terminal velocity and annual life span in early succession. Convergence in seed bank longevity occurred at intermediate plot age, and convergence in the combination of life span and lateral spread showed the relevance of competition filtering in the most fertile plots. On the other hand, competition-induced convergence in canopy height or specific leaf area was not supported by our results. We concluded that, based on the traits considered in this study, the overwhelming evidence was that community assembly during the first 40 years of succession was driven by trait-neutral mechanisms.

K e y w o r d s : assembly rules, coexistence mechanisms, dispersal limitation, limiting similarity, outlying mean analysis; urban biodiversity

Introduction

The question of how plant communities are assembled has resulted in nearly a century of unresolved debate on the predictive value of assembly rules (Clements 1916, Weiher & Keddy 1999, Hubbell 2001). On the one hand, community assembly is assumed to be a result of a filtering process, which can be predicted from species functional traits. In this deterministic model, species are selected from a regionally available pool if species capacities for dispersal, stress and competitive tolerance meet the local requirements of spatiotemporal isolation, environmental conditions and community invasibility (Keddy 1992). On the other hand, concepts of trait-neutral assembly have challenged this view by

emphasizing the importance of arrival sequence, priority effects or demographic stochasticity (see Robinson & Dickerson 1987, Hubbell 2001). In such a framework, community composition is a consequence of stochastic processes rather than predictable functional filtering.

Currently, the ecological consensus is that filter and neutral mechanisms simultaneously affect community assembly (Hubbell 2001, Leibold & McPeek 2006). However, the relative importance of either mechanism is hypothesized to vary among ecosystems and even at different stages of community formation (Leibold et al. 2004, Cottenie 2005). During the course of succession, a change in the nature of the filters determining local plant diversity is expected. While neutral or trait-driven dispersal processes prevail primarily in the initial phase of succession, competition filtering elicits stronger responses as succession advances and dense canopies develop (Peet 1992, Weiher & Keddy 1999, Navas & Violle 2009).

Direct tests of neutrality require detailed species and (meta-)community information, which is often difficult to obtain (Nee & Stone 2003, Gotelli & McGill 2006). Alternatively, trait-neutral processes may be indirectly inferred if plants are organized randomly with respect to traits perceived as important, whereas non-random distributions designate filtering processes that shape functional community composition in a characteristic way (Grime 2006, Mason et al. 2007). Consequently, comparing observed patterns with random expectations may allow the evaluation of trait-driven versus trait-neutral assembly mechanisms (Gotelli & McGill 2006).

How do dispersal, stress and competition filters shape community assembly during succession? Functional convergence and divergence may be considered the most likely non-random patterns (e.g. MacArthur & Levins 1967, Losos 2000, Grime 2006). Convergence and divergence denote that the functional similarity of species forming a community will be respectively greater and smaller than the corresponding similarity of a random assembly. This can be explained by strong selective pressure for a particular trait(s) by each filter, which sieves only small subsets of plants with particular trait expressions from the total range available in the geographical species pool (Keddy 1992, Díaz et al. 1999). In contrast, random samples of plants from the species pool are expected if trait-neutral processes prevail.

Filtering by dispersal is assumed to be greater if a locality is exposed to strong spatial or temporal isolation, generating convergence towards increased dispersal ability. Divergence may be induced if alternative dispersal strategies are equally successful and manifest themselves in contrasting trait expressions. However, a single dispersal strategy is often favoured. For example, wind dispersal is considered the main dispersal vector in early stages of succession (Fenner 1987, Prach & Pyšek 1999), whereas dispersal by birds plays a major role in shrub communities (Miles 1987, Ozinga et al. 2004). If only the dispersal filter is operative, trait values associated with stress tolerance and competitive ability should not be convergent or divergent, but a random sample from the geographical species pool of plants with a particular trait composition.

Similar to filtering by dispersal, environmental stress may induce convergence (Weiher & Keddy 1995). Yet, filtering by tolerance of stress is not restricted to early stages of succession, and involves tolerance traits rather than dispersal traits. Convergence towards non-phanerophytic life forms at alpine tree lines is one prominent example (Tranquillini 1979, Wielgolaski & Karlsen 2007). On the other hand, alternative adaptive strategies for

surviving environmental stress are reported for many communities (Larcher 1984, Grime 2002), which increases the expectation that divergence will occur. In dry grasslands, for example, co-occurrence of ephemerals and scleromorphic perennials may yield strong divergence in traits associated with growth and reproductive rates.

Predictions of functional patterns induced by the filter by competition are probably the most controversial (recently summarized by Schamp et al. 2008, Navas & Violle 2009). Functional divergence in competition-related traits is predicted by theories of niche differentiation and character displacement (Brown & Wilson 1956, Hutchinson 1959). Based on the assumption that competition is most intense among species with similar resource exploitation and associated trait expressions, coexistence should require a minimum dissimilarity in resource use and an upper limit to the functional similarity of interacting species (i.e. limiting similarity: MacArthur & Levins 1967, Pacala & Tilman 1994). In contrast, functional convergence is considered to be the result of competition if strongly competitive species exclude less competitive species from a community (Tilman 1990, Grime 2006). The competition filter differs from the dispersal and the stress filters as it only affects neighbouring plants and therefore requires a consideration of scale (Huston 1999, Murrell & Law 2003, Stubbs & Wilson 2004). Competitive effects may only be detected over very small distances, typically not exceeding a few centimeters in the case of herbaceous plants (Wilson & Whittaker 1995, Holdaway & Sparrow 2006). In late succession only, when competitive exclusion has already resulted in a community-wide absence of less competitive species, the community as a whole may be characterized by convergent trait values (e.g. tall canopy, large leaves) and the competition filter elevated to the community level.

The necessity to consider functional patterns at the community and neighbourhood scale is often regarded as adding unwanted complexity to the investigation of assembly rules (Lawton 1999, Weiher & Keddy 1999). However, it provides an opportunity to separate filtering by competition from filtering by dispersal and stress. We assume that functional convergence or divergence displayed at the community scale indicates filtering by stress, whereas filtering by competition should be observable at the neighbourhood scale, unless convergence toward traits associated with strongly competitive plants results from exclusion of less competitive species.

Empirical evidence for functional convergence and divergence along gradients in succession is rare as most studies only deal with late stages of succession and the results are inconsistent. While some find no evidence for significant functional filtering (e.g. Schamp et al. 2008, Thompson et al. 2009) others confirm that functional divergence (e.g. Stubbs & Wilson 2004) or convergence occurs (e.g. Franzén 2004). Significant convergence and divergence are even observed within a single community (e.g. Weiher et al. 1998, Watkins & Wilson 2003). Functional convergence and divergence has also been related to the availability of resources for both animal (Mouillot et al. 2007, Schamp et al. 2010) and plant communities (Schamp & Aarssen 2009). Increasing relevance of limiting similarity is demonstrated by Holdaway & Sparrow (2006) but not compared with neutral expectations. From a species, but not a functional perspective, Ruprecht et al. (2007) find no support for increased levels of deterministic community organization late in succession compared to less mature formations.

In this study, we explored the importance of trait-driven relative to trait-neutral community assembly by investigating functional patterns, i.e. convergence and divergence in

a series of stages in a succession. We judged the importance of trait-driven filter processes by the presence of functional convergence and divergence at the community and neighbourhood scales. The absence of non-random functional patterns was considered to be evidence for trait-neutral mechanisms (see Table 1). Based on the assumption mentioned above, our hypotheses were as follows: (i) Convergence in traits favouring long-distance dispersal during the initial phase of succession at the community scale. (ii) Convergence or divergence in stress tolerance traits during the entire course of succession. Divergence indicates alternative plant strategies for surviving environmental stress. (iii) Convergence or divergence in traits related to competitive ability at the neighbourhood scale in later stages of succession. Convergence is predicted to result from the presence of a group of strongly competitive plants, whereas divergence points to limiting similarity. At later stages in succession, competitive exclusion should result in community-wide convergence towards traits indicating a strong competitive effect. These patterns eventually elevate to the community scale. (iv) Communities with trait values indistinguishable from a random sample of the geographical species pool indicates trait-neutral assembly.

To evaluate these hypotheses we compared observed estimates of functional diversity with estimates of random assemblies generated by unconstrained null models. These models produce species and trait value distributions with equal occurrence probabilities. In addition, we calculated constrained null models in order to distinguish between filtering by competition and by stress and spatial isolation. Constrained null models generate random communities by constraining randomization according to species positions on abiotic gradients (Peres-Neto et al. 2001). The functional patterns were subsequently related to the ages of the succession and stress level to determine the importance of assembly filters at different times during the succession and in different environments. This allowed us to determine the importance of trait-driven relative to trait-neutral mechanisms during the course of succession.

Table 1. – Overview of hypothesized functional patterns generated by trait-driven and trait-neutral assembly mechanisms at the community and neighbourhood scales. Abbreviations denote convergence (CON), divergence (DIV) and random samples of trait values (RAN).

Scale	Trait-driven assembly			Trait-neutral assembly
	Dispersal filter	Stress filter	Competition filter	
Community	CON in dispersal traits	CON in stress tolerance traits: a single strategy to cope with stress[1] DIV: alternative strategies	RAN CON in competitive effect traits: competitive exclusion has already taken place	RAN
Neighbourhood	RAN	RAN	CON in competitive effect traits: one superior functional group DIV: limiting similarity[1]	RAN

[1] following Weiher & Keddy (1995)

Material and methods

Study area

The study was conducted in an industrial park in the city of Bremen, Germany (53°05'N, 8°44'E, mean annual temperature 8.8 °C, mean annual precipitation 694 mm: Deutscher Wetterdienst 2006–2007), which is an artificial island habitat. The area was created by raising the level of the original marshland by approximately 2 m by adding sand in a step-by-step procedure beginning in the 1970s. By 2007, this process had generated an area of about 4.0 km^2 with an age gradient spanning nearly 40 years. Consequently, the area differed from the surrounding landscape in edaphic conditions and altitude, which induced sharp contrasts in water and soil resource availability and species pools.

The majority of the area was used for development, including buildings and infrastructure. However, a substantial fraction was not utilized and colonized by ruderal communities. Seed bank analyses indicated that the foreign fill material was almost free of diaspores (data not shown). Therefore, we are confident that the area was colonized by dispersal rather than regeneration from a soil seed bank.

We applied a stratified random sampling method using the range in patch ages from 0 to nearly 40 years as estimates of the progress in the succession. Patch age was determined from aerial photographs taken at 5 to 10-year intervals since 1972. Patch age was processed in GIS (ESRI 2006) and patches subsequently assigned to one of eight age classes for the analysis. Finally, we placed equal numbers of plots per age class at random coordinates.

Soil data

To determine available soil water and nutrients as indicators of environmental stress, we collected soil samples from each soil layer down to a depth of 0.8 m at each plot, below which no plant roots were noted. The following soil parameters were determined in the laboratory: available potassium (flame photometer, Egnér et al. 1960), phosphorus (Continuous Flow Analyser, Murphy & Riley 1962), pH (gauged in a CaCl$_2$-solution), calcium carbonate (CaCO$_3$) and bulk density (all according to Schlichting et al. 1995). Soil texture, moisture and organic content were measured in the field according to the Ad-hoc-AG Boden (2005) standards. Soil aeration was derived from bulk density and soil texture using empirical functions in Ad-hoc-AG Boden (2005).

Vegetation data

Ruderal plant communities dominated the study area in 2007, with the following most abundant species (in decreasing order): *Senecio inaequidens*, *Holcus lanatus*, *Rumex acetosella*, *Arenaria serpyllifolia*, *Poa pratensis*, *Vulpia myuros*, *P. trivialis* and *Agrostis capillaris* (nomenclature following Jäger & Werner 2002).

Vegetation composition data was collected at the local community and neighbourhood scales. We sampled 92 plots and counted presences of each vascular plant species in 100 subplots of 0.1×0.1 m totalling 1 m^2. We subsequently used species frequencies from the 1 m^2 plot for the local community-scale analysis and species composition per subplot for the neighbourhood-scale analysis. As we were interested in plant coexistence and competition we recorded species presence/absence in the subplots based on the vertical projection of its above-ground parts relative to the ground surface rather than the rooting point.

Trait selection

In studies dealing with functional diversity the selection of traits should be linked to the function(s) of interest (Lepš et al. 2006 and references therein). Here, we were interested in dispersal capacity, tolerance to abiotic stress and competitive ability and selected seven traits associated with these functions: canopy height measured as the distance between the highest photosynthetic tissue and the base of the plant, specific leaf area (SLA), life span, lateral spread, seed bank longevity, seed number and first month of flowering (Table 2). Values for the first six traits were extracted from the LEDA Traitbase (Kleyer et al. 2008), and first month of flowering from Jäger & Werner (2002). Lateral spread indicated either the mere absence of clonal organs (lateral spread = 0) or, in case of presence of a clonal growth organ, its annual increment in horizontal growth (lateral spread per year > 0).

Often, functional divergence is explored either by using a single a priori selected trait (e.g. Kraft et al. 2008, Cornwell & Ackerly 2009) or by all available traits, without referring to particular functions (e.g. Thompson et al. 2009). Extending the conclusions of Lepš et al. (2006), we assumed that using a few well-targeted suites of traits would be ecologically more meaningful. For instance, divergence in the combination of flowering month and life span may be interpreted as evidence for temporal niche differentiation between spring annuals and long-lived perennials. In addition to the seven single traits, we therefore calculated functional dispersion for five trait combinations associated with dispersal ability, tolerance to abiotic stress and competitive ability (Table 2).

Dispersal ability was described by a combination of (i) the quotient of seed number and terminal velocity, and (ii) seed number, specific leaf area (SLA) and life span. High capacity for anemochorous dispersal is associated with high seed number (Kolb & Diekmann 2005) and its additive effect with terminal velocity (Grashof-Bokdam & Geertsema 1998, Tackenberg et al. 2003, Schleicher et al. 2011). The combination of seed number, SLA and life span served to distinguish two groups of pioneer species. Long-lived species are often characterized by moderate growth rates, whereas short-lived species require increased growth rates in order to rapidly generate many seeds (Grubb 1987, Vitousek & Walker 1987, Grime 2002). SLA was used as an indicator of plant growth rate (Garnier 1992, Reich et al. 1999).

Depending on the limiting resource and its temporal variability, stress tolerance may involve a variety of traits. These include reduced SLA (Fonseca et al. 2000, Wright et al. 2004), annual life form (Weiher et al. 1999, Bossuyt & Honnay 2006), production of persistent seed banks or the generation of clonal organs to store or translocate resources (Warner & Chesson 1985, Klimeš et al. 1997). Additionally, the combination of seed bank and clonal organs may show a trade-off between generative and vegetative regeneration in order to survive periods when the availability of resources is reduced in time or space (Eriksson 1996, Ehrlén & van Groenendael 1998).

Competitive ability describes a species capacity to capture resources in the presence of neighbours. Depending on whether competition is for soil resources or light, increased competitive ability is attributed to high SLA values (Garnier 1992, Reich et al. 1992) or canopy height (Anten & Hirose 1999, Gross et al. 2007). Moreover, increased life span or high lateral spread have both been associated with space acquisition (Grime 2002, Gross et al. 2007) and may therefore be considered alternative strategies. Finally, plants that have a long life span and flower late are more competitive (Grime 2002). We used a combination of life span and flowering month, and life span and lateral spread, to investigate interactive effects.

Table 2. – Overview of plant traits and trait combinations, functional importance and data availability. Trait combinations were selected following the literature on the additive effects between traits (see Materials and methods for more details). Letters indicate that the trait (combination) is relevant for dispersal capacity (D), competitive capacity (C), or stress tolerance (S). % Data availability denotes the percentage of species of the species pool for which trait information was available. Trait combinations are denoted by an "&" between involved traits.

Functional trait	Unit	Minimum	Median	Maximum	Functional importance	% Data availability
Terminal velocity	m/sec	0.07	1.87	5.00	D	79
Seed number	Counts	3	735	12410000	D	90
Canopy height	m	0.03	0.36	40.00	C	100
Month of flowering	no. of months	1	6	8	C	100
SLA	mm^2/mg	4.90	23.35	60.09	C/S	89
Lateral spread	ordinal				C/S	80
	(0: no clonal organ; 1: < 1 cm; 2: 1–25 cm; 3: > 25 cm)					
Life span	ordinal (1: annual; 2: biennial; 3: perennial)				C/S	100
Seed bank longevity	categorical (0: transient; 1: short-term persistent)				S	91
Log (seed number) / terminal velocity					D	79
Seed number & SLA & life span					D	89
Month of flowering & life span					C	100
Life span & lateral spread					C/S	100
Lateral spread & seed bank longevity					S	80

Statistical analysis

A s s e s s m e n t   o f   t h e   e n v i r o n m e n t a l   n i c h e

An outlying mean index analysis (OMI; Dolédec et al. 2000) of the soil nutrient and water variables was used to assess species responses to environmental stress (see also Choler & Michalet 2002, Matejusová et al. 2003, Thuiller et al. 2005). OMI determines the niche of each species by calculating the mean position along environmental gradients from the distance of the mean habitat conditions of the plots occupied by the species and the mean conditions at the study area (Dolédec et al. 2000). Niche breadth is based on the variability in habitat conditions used by a species. OMI, unlike constrained correspondence analysis, makes no assumptions about the length of gradients and assigns equal weight to species-poor and species-rich sites.

As ordination techniques are often sensitive to data with skewed distributions (Legendre & Legendre 2006) we applied power transformations to soil aeration, pH and available potassium and phosphorous to yield a skewness between –1 and 1 (McCune & Grace 2002). Nearly 50% of the plots lacked calcium carbonate. Therefore, calcium carbonate was coded as a binary variable.

A s s e s s m e n t   o f   f u n c t i o n a l   c o n v e r g e n c e   a n d   d i v e r g e n c e

The choice of index can be crucial when exploring the distribution of coexisting species in functional space (Stubbs & Wilson 2004). Recent studies suggest that functional diversity should be broken down into functional richness, evenness, divergence and dispersion (Villéger et al. 2008, Laliberté & Legendre 2010). These statistics make it possible to deal with any number of traits, different data types (i.e. quantitative, semi-quantitative and qualitative) and weighting of species and traits.

Our interest was in the distribution of trait values and therefore we evaluated functional dispersion (Laliberté & Legendre 2010). Functional dispersion (FDis) describes dispersion of a trait within the functional volume of the community (also see Mouchet et al. 2010 for a thorough discussion of index properties). In contrast to functional divergence as defined by Villéger et al. (2008), FDis incorporates information on the volume (Laliberté & Legendre 2010), which is also relevant when comparing communities. FDis may therefore be regarded as a surrogate of Villéger et al.'s measures of functional richness and functional divergence, which combine the advantages of both statistics. Preliminary analyses indicate that it is not necessary to include functional richness in FDis and functional evenness and divergence have little meaning when dealing with low species numbers (n < 6), which were recorded at the neighbourhood scale (0.1 × 0.1 m). Therefore, functional evenness and divergence data are not presented here.

Standardization to zero mean and unit variance is often recommended for the calculation of functional diversity (e.g. Petchey & Gaston 2002, Villéger et al. 2008). However, it is not applicable when combining continuous, ordinal and categorical traits (Laliberté & Legendre 2010). Therefore, traits were standardized to range between zero and one. Seed number and canopy height were log-transformed to reduce the effects of species with extreme trait values.

Null models

The comparison of observed values with corresponding values for a random assembly, using a null model approach, was applied to assess the significance of functional patterns. We compared unconstrained with constrained null models. The unconstrained model considers that all species – and also all trait values – have an equal probability of occurring throughout the study area. The constrained model recommended by Peres-Neto et al. (2001) aims at incorporating species habitat preferences, i.e. during the generation of random communities traits are assigned to species whose occurrence in the random communities is constrained by habitat suitability in terms of soil water and nutrients. If constrained and unconstrained null models provide similar results, environmental stress has little significance for the occurrence of species (Peres-Neto et al. 2001).

For the unconstrained null model, we followed Watkins & Wilson (2003) and Stubbs & Wilson (2004) and randomized the rows of the species × trait matrix rather than species × plot matrix to generate null model communities. That is, species were randomly assigned the functional characteristics of another species in the species pool without replacement. This procedure helped to maintain the trait-correlation structure as observed in the field in the randomized communities and preserve biological realism within the randomized communities. Our species pool included all vascular plant species noted in the plots during our survey. FDis for all single traits and trait combinations was calculated for all observations, and for 1000 randomizations of each plot (local community scale) as well as each subplot (neighbourhood scale; Fig. 1). The proportion of randomizations with a test statistic equal to that observed, or more extreme, gave the probability of the observed FDis predicted by the null model (Mason et al. 2007, Mason et al. 2008). If the observed FDis was lower or higher than expected based on a random association and using a threshold of $P < 0.05$, this indicated that competition had induced significant functional convergence or divergence, respectively. At the community scale, FDis was weighted by species frequencies in each plot.
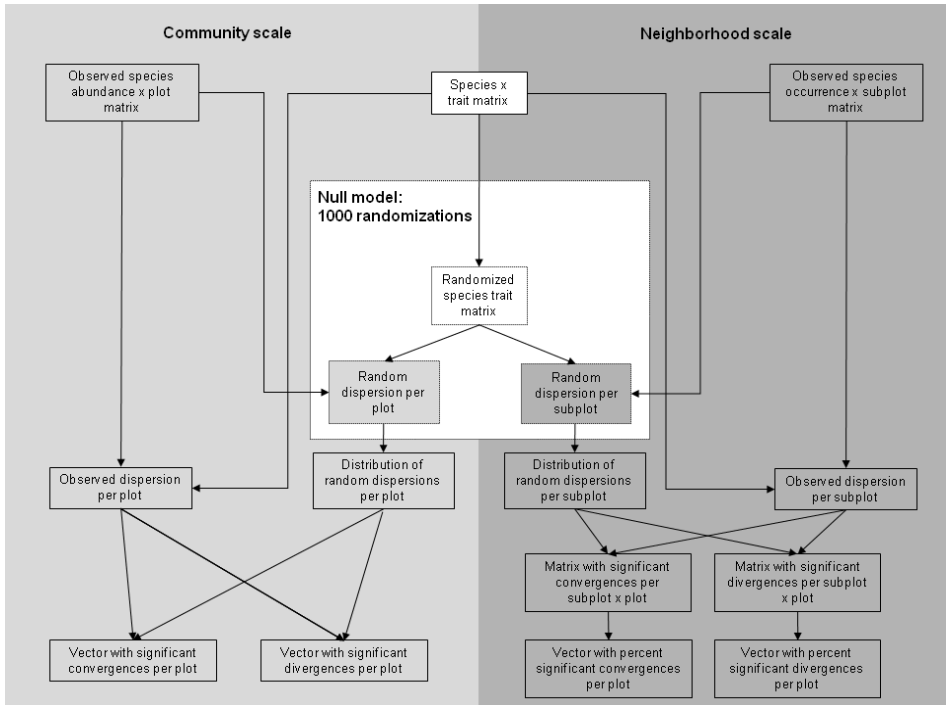
Fig. 1. – Flow chart of the computational steps performed for each trait and trait combination in assessing significant functional convergence and divergence at the community (plot: pale grey area) and neighbourhood (subplot: dark grey area) scales. Significance is derived from the percentage of random dispersions greater (convergence) or smaller (divergence) than the observed dispersion (P < 0.05). Random dispersions were generated by swapping the rows in a species × trait matrix in a null model algorithm with 1000 randomizations (white rectangle).

For the null model constrained by habitat suitability, we used information on niche position and niche breadth, as obtained by OMI, to assess the suitability of each plot for each species. Habitat suitability of a plot increased with niche breadth of the species and with decreasing deviation of the species niche center from the abiotic conditions of the plot. During generation of random communities the probability of sampling particular traits increased with predicted habitat suitability.

The use of constrained null models is based on the assumption that observed species distributions represent fundamental niches. If the absence of species is, however, not related to abiotic stress but to competition the constrained model may remove any community pattern resulting from competition. For instance, the underrepresentation of species that occur early in succession in the late stages of succession may falsely be attributed to filtering by abiotic factors instead of competition. Therefore, the question of how and when to use constrained null models to define local species pools is subject to debate (e.g. Fox & Brown 1993, 1995, Wilson 1995, Stone et al. 1996, 2000, Brown et al. 2000, 2002, Pither & Aarssen 2005). We assumed that competition increased with succession indicated by plot age. Therefore, we refrained from including plot age in the constrained null model and only used soil parameters. As none of the soil parameters measured showed

strong relationships with plot age (maximum Spearman correlation coefficient: $r_s = 0.37$, P < 0.001, organic content) we are confident that our approach did not eliminate any competition-driven community patterns in the data set.

Like environmental stress, filtering by dispersal can reduce the pool of locally available species. Indeed, Schleicher et al. (2011) show that a significant fraction of species in the study area is affected by habitat isolation. We therefore calculated a second constrained null model in which the likelihood of a species belonging to the local species pool corresponded to the degree of local habitat isolation (see Schleicher et al. 2011 for more details). The determination of species-specific isolation measures required complete surveys of the study area for each species (Moilanen 2002). Therefore we could only calculate isolation constrained null models for a subset of 58 species. The isolation constrained null model was compared to an unconstrained null model calculated for the same reduced species pool.

Analyses of the relationships between functional patterns along gradients in succession and stress

Significant functional patterns (trait convergence/divergence) may be limited to particular stages of the succession or certain levels of resource depletion. This requires a technique that can detect nonlinear relationships, as well as those sections along the environmental gradient with trait convergence or divergence. We used regression tree analysis (Breiman et al. 1984) to uncover the relationship, if any, between (i) presence/absence of functional patterns at the community scale, and (ii) percentage of subplots with significant functional convergence or divergence per plot relative to plot age and soil aeration (Fig. 1). Regression trees were built with a minimum bucket size of three and cross-validated using 100 randomizations.

Relationships among functional traits were assessed by Spearman correlations for continuous traits and Wilcoxon–Mann-Whitney tests for categorical variables. All statistical analyses were performed using software R (R Development Core Team 2005) and the packages "ADE4" (OMI analysis, Thioulouse et al. 1997) and "rpart" (Regression Tree Analysis, Therneau et al. 2009). Null models were generated using an adapted version of the command "oecosimu" in the package "vegan" (Oksanen et al. 2009) and functional dispersions using the function "dbFD" (Laliberté & Legendre 2010).

Results

Taxonomic and functional diversity

Across all plots we identified 134 vascular plant species as representative of the geographical species pool. These species are highly variable in their expression of functional traits. For instance, seed number and canopy height varied by eight and three orders of magnitude, respectively (Table 2). This variability was also reflected in a substantial variation in FDis among plots (Fig. 2).

Correlations among traits were generally weak and only correlations with Spearman coefficients > 0.3 are discussed. The strongest correlations were observed between canopy height and seed number, and life span and lateral spread ($r_s = 0.47$ and $r_s = 0.38$, respectively).
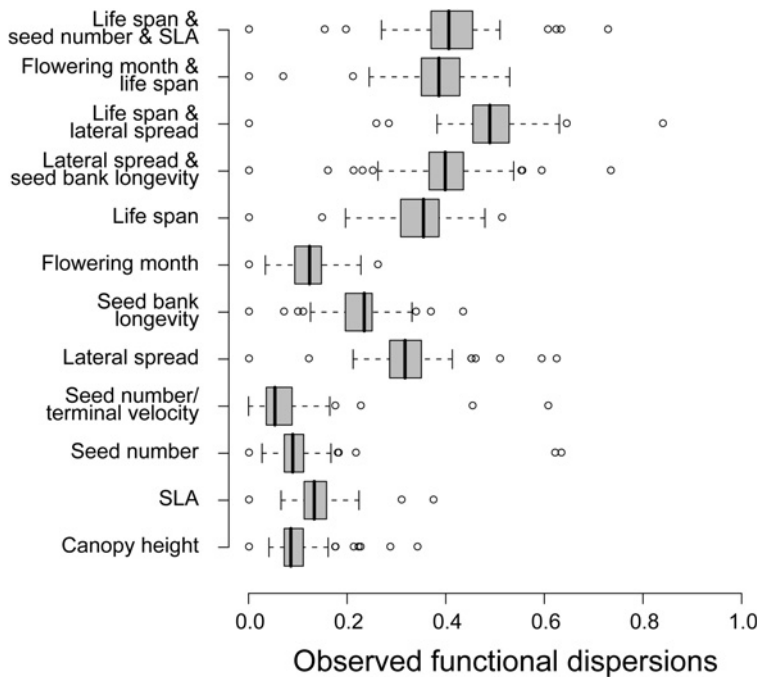
Fig. 2. – Boxplots of observed functional dispersions (FDis) for single functional traits and trait combinations observed at the community scale. Boxplots show median, 25% and 75% quartils, minimum and maximum, respectively.

Taller species were also characterized by a lower SLA ($r_s = -0.31$), and seed number was inversely correlated with terminal velocity ($r_s = -0.34$). Moreover, species with short-term seed banks produced more seed and flowered later than species forming transient seed banks (Wilcoxon–Mann-Whitney test: P = 0.04, and P = 0.03).

Results of the outlying mean analysis

The first two axes of the OMI analysis accounted for 42% and 22% of the total variation in marginality, i.e. the variation in distances between (i) the mean habitat conditions used by a species, and (ii) the mean habitat conditions in all plots. The first axis was primarily related to a gradient in soil resource availability as explained by soil aeration (Table 3). The second axis was primarily explained by soil pH. The Monte-Carlo randomization test was significant at P < 0.001 for mean marginality. However, only 14 out of 134 species differed significantly in their niche requirements from the average soil conditions, suggesting that soil parameters influenced only a minority of the species (Fig. 3). Consequently, in the environmentally constrained null models only the relative occurrence probabilities of the 14 species varied among plots, whereas equal probabilities were assigned to the remaining 120 species. The results of the OMI analysis supported the absence of a strong environmental filter in this system. Indeed, the null models constrained by habitat suitability provided no qualitative departure from the results of the unconstrained model. Similarly, the

Table 3. – Summary of soil variables measured at the plot level, with units, means, standard deviations where applicable, and correlation coefficients with the 1st axis of the outlying mean index analysis (OMI correlation). NA denotes not applicable.

Soil variable	Unit	Minimum	Median	Maximum	OMI correlation
Soil aeration	volume %	15.19	32.00	38.00	0.58
Phosphorous	kg/ha	0.00	181.10	2876.00	–0.34
Potassium	kg/ha	0.00	189.90	895.30	–0.33
pH		4.48	6.39	7.70	–0.23
Organic content[1]	Ordinal [mass-%]	0	1	4	–0.48
Soil moisture[1]	Ordinal [lg hPa]	0	2	5	–0.04
CaCO$_3$[2]	Categorical	NA	NA	NA	0.41

[1]Levels following Ad-hoc-AG Boden (2005): organic content: 0: 0%; 1: < 1%; 2: 1–2%; 3: 2–4%; 4: 4–8%. Soil moisture: 0: > 4.0 lg hPa; 1: 4.0–2.7 lg hPa; 2: 2.7–2.1 lg hPa; 3: 2.1–1.4 lg hPa; 4: ≥ 1.4 lg hPa; 5: 0 lg hPa.
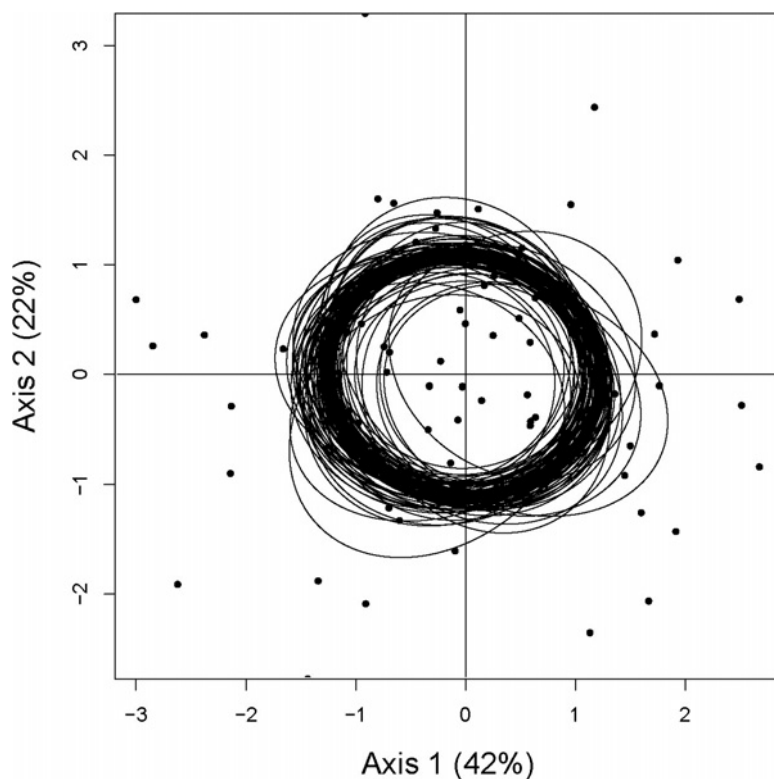[2]Two levels: free of CaCO$_3$; contains CaCO$_3$.

Fig. 3. – Outlying mean index analysis (OMI) of 134 plant species observed in the study area based on local environmental variables. Inertia of axes is given in parentheses. Interpretations of axes are provided in the Methods. Dots represent plots and ellipses are a graphical summary of the cloud of points generated by each species and represent each species environmental niche. The center of each ellipse is anchored on a mean, and its width and height are determined by the variance and the slope of the main axis of the ellipse by the covariance.
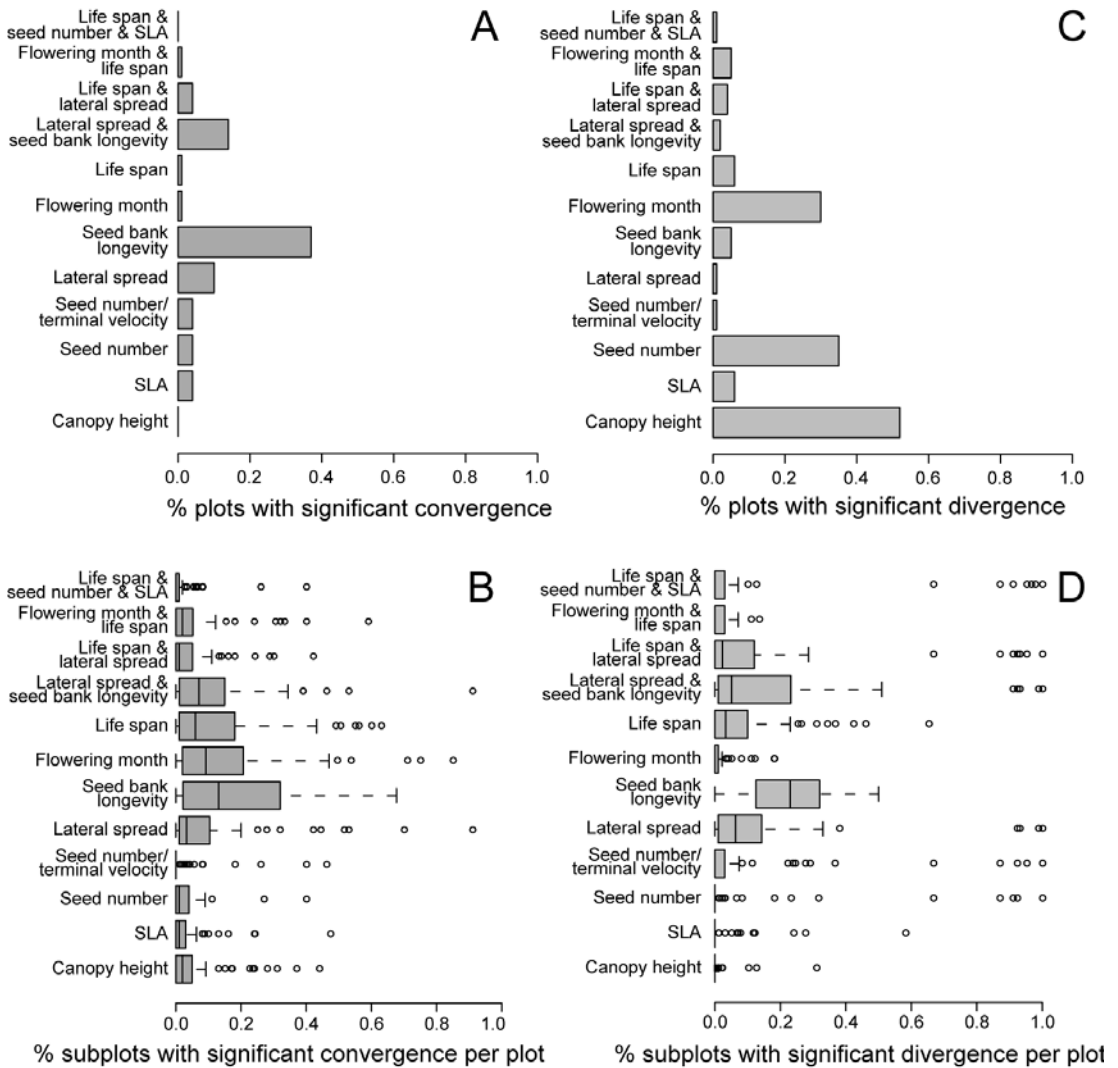
Fig. 4. – Frequencies of significant functional convergence (A, B) and divergence (C, D) at the community (plot) and the neighbourhood (subplot) scale. Bars in figures A and B represent fractions of plots with significant convergence and divergence observed at the community scale. Boxplots in figures C and D show percentages of subplots with significant convergence and divergence per plot observed at the neighbourhood scale. Indicated are medians, 25% and 75% quartiles, minimum and maximum, and outliers, respectively.

null models constrained by isolation yielded no qualitative and only minor quantitative differences to an unconstrained null model. Hence, we will only describe the results of the unconstrained null models.

However, the OMI demonstrated that among the soil variables, soil aeration contributed most to the explained variance. Therefore, soil aeration was included as a reliable estimate of the variation in physical stress among plots in subsequent analyses.

Functional community patterns

Comparison of observed and null model dispersions provided more support for trait-neutral than trait-driven assembly processes. Most observed FDis values were congruent with the values generated by the null model, both at the community and neighbourhood scales (Fig. 4). At the community scale, convergence in seed bank longevity and the combination of lateral spread and seed bank longevity occurred in 37% and 14% of the plots, respectively, whereas the remaining traits showed significant functional convergence in at most 4% of the plots (Fig. 4A). Divergence was more common than convergence. Divergence was observed in canopy height, seed number and month of flowering (in 52, 35 and 30% of the plots, respectively), while other traits diverged in at most 6% of the plots (Fig. 4C).

At the neighbourhood scale we observed a high variability within plots. In seed bank longevity, for example, there was significant divergence in almost 100% of the subplots in some plots, but the average percentage of the subplots with divergence was 22% (Fig. 4D). Similarly, the percentage convergence in seed number averaged only 3%, but in some plots all subplots showed significant convergence (Fig. 4B).

Occurrence of functional convergence and divergence along gradients of succession and stress

The results of the regression tree analyses suggested weak associations between functional patterns along gradients of succession and stress. Convergence and divergence in some traits corresponded to distinct stages in the succession and levels of soil aeration, however, the variation explained by the gradients was generally low (< 48% at the community scale, < 28% at the neighbourhood scale; Table 4). In the following, we only report results where regression trees explained at least 20% of the variation (Fig. 5).

At the community level, convergence towards transient seed banks was restricted to intermediate stages of succession (median community weighted mean: 1.05), i.e. convergence did not occur in plots older than 26 or younger than 18 years (median community weighted mean: 1.35, compared using a one-sided Wilcoxon rank test, P = 0.01, Fig. 5A). A strong relationship between divergence and gradients in succession and stress at the community level was not detected.

At the neighbourhood scale, however, four regression trees explained more than 20% of the variation. Convergence in the life span and lateral spread trait combination was more prevalent in plots with soil aeration < 18.3% (n = 3), compared to plots with reduced stress (n = 73, Fig. 5D). The community weighted means of life span and lateral spread converged to intermediate life span (range: 2.23–2.40) and intermediate lateral spread (range: 1.26–1.51) rather than those (ranges: 1.54–3.00 and 0.46–2.72, respectively) recorded in the remaining plots.

Divergence in seed number and the life span and lateral spread combination were largely restricted to early stages of succession. Plots younger than 2 years (n = 6) showed higher frequencies of divergence in seed number and the life span and lateral spread combination than older plots (n = 76, Fig. 5E, 5B). Increased frequencies of divergence in the lateral spread/seed bank longevity combination were detected in plots aged < 2 years or ≥ 27 years (n = 6, respectively, Fig. 5C). At intermediate plot ages, only an average of 12% of the subplots showed divergence (n = 70).

Table 4. – Summary of the results of the regression tree analysis of the occurrence of convergence and divergence, observed at the community and neighbourhood scales, in relationship to plot age (age) and soil aeration (SAer). Results in bold (explained variance > 20%) are referred to in the text. For each trait (combination) the location of the split (age in years, soil aeration in vol%) and the percentage of explained variance (in parentheses) are listed. If more than one significant split was obtained, the relationship with the variable that explained most of the variance is presented. NS designates non-significant splits. The function of interest for each trait or trait combination is given by letters, with D: dispersal capacity, C: competitive capacity, S: stress tolerance. Trait combinations are denoted by "&" between involved traits.

Functional trait	Function of interest	Community scale		Neighborhood scale	
		Convergence	Divergence	Convergence	Divergence
Seed number	D	Age < 2 SAer > 31.8 (13.9%)	NS	Age ≥ 2 (3.3%)	**Age < 2 (23.7%)**
Seed number/terminal velocity	D	NS	NS	NS	NS
Seed number & SLA & life span	D	NS	NS	NS	NS
Canopy height	C	Age > 0 (5.4%)	NS	SAer < 34.6 (4.6%)	NS
Earliest time of flowering (month)	C	NS	NS	NS	NS
Month of flowering & life span	C	NS	NS	SAer ≥ 32.8 (8.4%)	NS
SLA	C/S	NS	NS	NS	NS
Lateral spread	C/S	NS	SAer > 32.8 (17.1%)	NS	NS
Life span	C/S	NS	NS	SAer ≥ 32.9 (11.9%)	NS
Life span & lateral spread	C/S	NS	NS	**SAer < 18.3 (27.2%)**	**Age < 2 (20.1%)**
Seed bank longevity	S	**18 ≤ Age ≤ 26 (47.5 %)**	2 ≤ Age < 9 (12.5 %)	SAer < 18.3 (4.5%)	NS
Lateral spread & seed bank longevity	S	NS	NS	NS	**Age < 2 or Age ≥ 27 (27.4%)**

Discussion

In this study, convergence and divergence of a variety of traits were analyzed at two different scales. However, the results of the analyses provided little support for trait-driven assembly mechanisms. Not only were occurrences of convergence and divergence rare but their relationships with plot age and environmental stress were weak and accounted for very little of the variability explained by the regression trees. As the constrained null model provided no additional insights, the following text exclusively refers to the results of the unconstrained model.

Effects of filtering by dispersal

Most of the functional patterns revealed by the analyses were also not congruent with our hypotheses. During early succession, we expected convergence in dispersal traits but found divergence in seed number. This result may be a consequence of an over-dimensioned increase in the occupied trait volume due to the prevalence of species that produce an abundance of seed (e.g. *Salix* sp.). This markedly outweighed the reduction in volume due to the absence of species producing very few seeds.
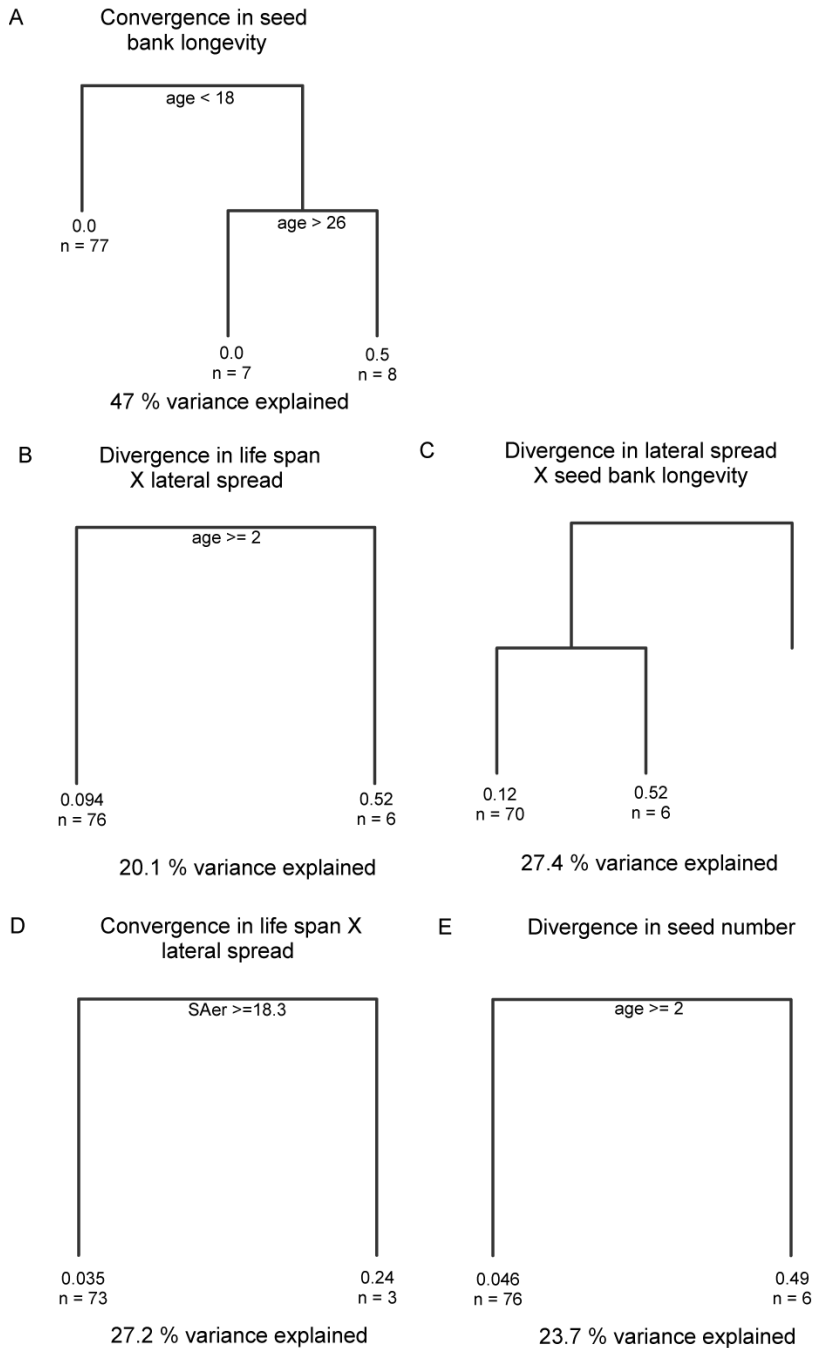
Fig. 5. – Regression trees indicating the relationship between functional convergence and divergence with plot age (age) and soil aeration (SAer). The response variables were the occurrence of functional convergence observed at the community scale (A), and the frequencies of functional convergence (D) or divergence (B, C, E) at the neighbourhood scale per plot. Respective traits or trait combinations are indicated in the headline. Each of the splits is labelled with the variable and its values (age in years, SAer in vol%) that determine the split. Each node is labelled with the percentage of observations (A) or the mean frequency (B–E) and number of observations in the group. % variation explained is indicated at the bottom of each tree.

Divergence in seed number was only loosely related to plot age. The other dispersal traits (seed number/terminal velocity and seed number & SLA & life span) did not show any strong functional patterns. We conclude that the assembly of the community was not mainly determined by a dispersal filter.

Effects of filtering by tolerance of stress

Our second hypothesis was that filtering by stress is common along a gradient of stages of succession, which was not supported due to the rarity of significant functional patterns. In addition, the patterns were associated only with plot age, which had no relationship with soil nutrient content or water availability in the study area (Schadek et al. 2009).

We considered the effects of seed bank longevity and lateral spread as strategies for surviving fluctuating environmental stress. A combination of these traits showed increased divergence in the youngest and the oldest plots at the neighbourhood scale, at which we had expected random patterns. Because the traits were not negatively correlated, higher FDis values may not necessarily suggest a trade-off between seed-bank longevity and clonal propagation (Eriksson 1996, Ehrlén & van Groenendael 1998). Species coexistence with and without persistent seed banks, or with low and high lateral spread may induce divergence. Indeed, divergence was observed in plots dominated by three species groups: plants exhibiting transient seed banks and high lateral spread (e.g. *Corynephorus canescens*, *Agrostis capillaris*), species with persistent seed banks and no lateral spread (e.g. *Vulpia myurus*) and plants with persistent seed banks and clonal propagation (e.g. *Rumex acetosella*, *Carex hirta*; Table 4). This observation, and in particular the presence of plants with the last trait syndrome, suggest that both investment in persistent seed banks and clonal propagation was favoured in this study area.

We found convergence in seed bank longevity at intermediate plot ages (Table 4). However, this observation may be interpreted as a consequence of competitive exclusion rather than filtering by stress, because shrub encroachment peaked at intermediate plot ages (results not shown). The absence of species forming short-term persistent seed banks under shrub canopies has previously been reported, and may be attributed to reduced regeneration success when competition is severe (Milberg 1995, Davies & Waite 1998). This convergence was observed at the community scale, i.e. the 1 m^2 scale, where some large shrubs were apparently able to affect the functional characteristics of the entire community.

The present study provided evidence that filtering by stress was restricted to divergence in the combination of seed bank longevity and lateral spread. However, only a small percentage of variability is accounted for by the regression tree (27.4%), which suggests that filtering by stress is not a viable predictor of functional community structure (Fig. 5). This is consistent with the small degree of niche differentiation demonstrated by the OMI.

Effects of filtering by competition

We assumed increasing convergence or divergence in traits associated with competitive ability at the neighbourhood scale in later stages of succession. However, convergence or divergence in canopy height and SLA, which are commonly associated with competitive ability, were not allied with plot age or environmental stress. Instead, life span and lateral spread yielded divergence in very young and convergence in the most fertile plots (Table 4). The correlation between the two traits suggest that divergence in life span and lateral

spread indicate coexistence of annuals and biennials, and perennials with high lateral spread in young plots. These results could be interpreted as evidence for limiting similarity. It is, however, not very plausible because limiting similarity implies strong competition, which is not likely at early stages of succession with ample bare ground. Divergence in life span and lateral spread could be better explained as co-occurrence of annuals and perennials. We observed that perennials with high lateral spread, particularly *Festuca rubra*, were as fast at colonizing young plots as annuals. Following initial colonization, the perennial species required many years to establish a dense clonal network (as also noted by Grime 2002) and were unable to completely exclude plants with other trait expressions in later stages of succession, particularly in stressful habitats.

Competitive exclusion occurred only in the most fertile plots, where we detected significant convergence consistent with our assumption of increased filtering by competition. Together with convergence in seed-bank persistence at intermediate plot ages, this points to competitive exclusion as a mechanism generating convergence, rather than to limiting similarity which is associated with divergence.

Empirical evidence for the limiting similarity theory is limited. Support is provided by Stubbs & Wilson (2004) who observed that divergence of leaf and root traits exceeded random expectations in a sand dune community. Kraft et al. (2008) show that co-occurring trees in an Amazonian forest are often less ecologically similar than a neutral model predicts. However, other studies report no significant functional convergence and divergence (Tokeshi 1986, Watkins & Wilson 2003, Schamp et al. 2008, Thompson et al. 2009). Based on studies using null model approaches in plant community ecology, there is more evidence opposing than supporting the limiting similarity theory.

Evidence for trait-neutral assembly

Do we have to adopt the hypothesis of trait-neutral community assembly? From a methodological point of view, there are several sensitive decisions that might have affected the general outcome of our study. We selected eight traits and analyzed various combinations of these traits associated with dispersal, establishment and persistence (Weiher et al. 1999). However, due to logistic reasons we were unable to include below-ground traits, which have been suggested to be important in ascertaining competition in nutrient-poor ecosystems (Aerts 1999). Yet, the soil profiles revealed that there was a very low density of roots associated with the plants in our plots (personal observation) and therefore below-ground competition is unlikely.

Another critical step is the choice of the functional statistic (Lepš et al. 2006, Poos et al. 2009). FDis has only recently been proposed and rarely applied. Yet, FDis is related to Rao's quadratic entropy (Rao 1982) and is the multivariate analogue of the weighted mean absolute deviation (Laliberté & Legendre 2010) and both have successfully been applied in studies on functional diversity (e.g. Lepš et al. 2006, Kraft et al. 2008, de Bello et al. 2009). Similarly, in our study, FDis was strongly correlated with functional richness as proposed by Villéger et al. (2008), which has proved suitable in plant and animal studies (e.g. Cornwell et al. 2006, Mason et al. 2008). Therefore, we have no reason to believe different results would have been generated if other statistics were applied.

The definition of the species pool is one of the most critical steps in null-model approaches. Our species pool is similar to that revealed by the annual botanical surveys of

the study area that have been carried out since 2003 (see Schadek 2006), which suggest we did not overlook a significant fraction of taxa. However, we clearly recognize our conclusions are scale-dependent, i.e. the species pool was limited to the study area, which was rather uniform in terms of soil resources. If we increased the scale of the study area to the wet meadows of the adjacent marshland, strong environmental filtering would certainly have been revealed, as these species could not thrive on the dry, sandy landfills of this industrial site.

Based on the species pool of the study area, our results strongly support our last hypothesis. Community assembly appeared to be the outcome of mechanisms that were neutral regarding the traits we used. Neutral processes are an important force in many but not all terrestrial systems (see Hubbell 2001 and references therein). Yet, the effect that neutral processes have on community assembly is dependent on several community characteristics (Foster et al. 2004, Chase 2007), including progress in the succession. Although our time gradient spanned more than 40 years, competitive equilibrium may not yet have been established. Succession in resource-limited systems can encompass long periods of time (Schadek et al. 2009) and so extend the phase during which neutral processes operate. Indeed, several studies have empirically demonstrated that species composition patterns can remain largely neutral for up to 20 years in a succession (Gitay & Wilson 1995, Cook et al. 2005, Holdaway & Sparrow 2006). Neutral mechanisms, such as the order in which the species of plants arrive, indicate a strong control on species composition during the first years of community assembly (Ejrnaes et al. 2006, Körner et al. 2008).

In addition, the dynamic character of this study area may have slowed down succession. Generally, disturbances and recruitment limitations, among other causes, may prevent competitive hierarchies from operating (Huston 1999, Solé et al. 2004). Industrial areas are typically very dynamic in terms of habitat turnover rates and underlie a range of small-scale disturbances (Rebele 1994, Kattwinkel et al. 2009). Habitat turnover in urban environments constantly changes the spatial configuration of source habitats for dispersal and therefore may increase stochasticity in colonization events. Our measure of plot age captured habitat turnover effects. However, we have no insights into the relevance of small-scale disturbances that occurred in this area before we initiated this study in 2003.

Several studies suggest neutral assembly processes at the taxonomic level (Cook et al. 2005, Ejrnaes et al. 2006, Körner et al. 2008) and the results of this study indicate that the initial phase of community assembly was largely neutral at a functional level. Our results support a trait-neutral view of community assembly in dynamic landscapes with rather homogeneous soil conditions, in which the spatiotemporal habitat configuration may be more important than filtering mechanisms.

Acknowledgements

Souhrn

Jen málo je dosud známo o tom, jak se význam funkčních vlastností a neutrálních procesů mění během sukcese rostlinných společenstev. Obecně předpokládáme posun od velkého významu šiřitelnosti semen v iniciálních stádiích sukcese k velké důležitosti kompetičních vlastností v pozdních stádiích. V naší studii jsme vycházeli z předpokladu, že pokud formování společenstva závisí na funkčních vlastnostech druhů, bude se měnit jeho funkční složení, a je-li formování společenstva založeno na náhodných procesech, bude funkční složení společenstva také náhodné. Proto jsme testovali přítomnost konvergence či divergence funkčních vlastností podél sukcesního gradientu. Na dvou prostorových škálách (100 × 100 cm a 10 × 10 cm) jsme hodnotili funkční vlastnosti rostlin (kapacitu šíření semeny, schopnost tolerovat stres, kompetiční schopnost) a srovnávali jsme výsledky s nulovým modelem. Následně jsme použili metodu regresních stromů, abychom porovnali konvergenci či divergenci funkčních vlastností se stářím plochy, dostupností vody a živin. Většina vlastností nevykazovala ani konvergenci ani divergenci a variance vysvětlená metodou regresních stromů byla vždy nižší než 20 %. Zjistili jsme divergenci u počtu semen (místo očekávané konvergence směrem k vysokým počtům semen), dobrou šiřitelnost větrem (nízké hodnoty rychlosti dopadu) a jednoletý životní cyklus v raných stádiích sukcese. Stres hrál ve filtrování funkčních vlastností malou roli. Konvergence v persistenci semenné banky byla nalezena u středně starých ploch a konvergence v kombinaci délky života a laterálního šíření u ploch s nejvyšší dostupností živin, a tedy nejsilnější kompeticí. Naopak předpoklad o konvergenci výšky rostlin díky kompetici nebyl v naší analýze potvrzen. Na základě rostlinných vlastností analyzovaných v naší studii jsme podpořili představu, že se během 40 let sukcese společenstvo formovalo nezávisle na funkčních vlastnostech druhů.

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