

# Soil conditions and phylogenetic relatedness influence total community trait space during early plant succession

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## Abstract

### Aims

The total space of traits covered by the members of plant communities is an important parameter of ecosystem functioning and complexity. We trace the variability of trait space during early plant succession and ask how trait space co-varies with phylogenetic community structure and soil conditions. Particularly, we are interested in the small-scale variability in trait space and the influence of biotic and abiotic filters.

### Methods

We use data on species richness and soil conditions from the first 7 years of initial succession of an artificial catchment in north-eastern Germany. Total functional attribute diversity serves as a proxy to total trait space.

### Important Findings

Total trait space steadily increased during succession. We observed high small-scale variability in total trait space that was positively correlated with species richness and phylogenetic segregation and negatively correlated with total plant cover. Trait space increased with soil carbonate content, while pH and the fraction of sandy material behaved indifferently. Our results indicate that during early succession, habitat filtering processes gain importance leading to a lesser increase in trait space than expected from the increase in species richness alone.

**Keywords:** primary succession, trait space, phylogenetic signal, habitat filtering, species co-occurrence, null model

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## INTRODUCTION

In the early years of plant ecology, succession was viewed either as a directional development of the vegetation of a given homogeneous area over a period of time towards a single climax structure (Clements 1916) or as a historically influenced random process leading to different stable states despite identical environmental conditions (Diamond 1975;

Gleason 1926). Elements of both views are currently considered realistic (Götzenberger *et al.* 2011). Thus, species might be more prone to a historically contingent mode of assembly, while functional traits are rather deterministically assembled within similar environmental conditions (Fukami *et al.* 2005; Helsen *et al.* 2012). During early states of succession, randomly arriving species from a larger regional pool pass abiotic filters to assemble local plant communities

(Götzenberger *et al.* 2011). Species that possess appropriate physiological, morphological or life history adaptations have a high probability to colonize a particular habitat successfully (Wiens and Graham 2005). These early arriving species may influence the establishment of later arriving species by means of competition or soil legacies (the 'priority effect'; Helsen *et al.* 2012; Körner *et al.* 2008).

A somewhat less-covered issue in early plant succession concerns the total trait space covered by a community in the course of succession. In this respect, plant functional traits are morphological, physiological or life history characteristics that directly or indirectly influence plant fitness *via* their effects on survival, growth and reproduction (Violle *et al.* 2012). Depending on the ecological processes selecting for or against species occurrences from the regional pool (abiotic, biotic and dispersal filters; Götzenberger *et al.* 2011), the total trait space might also underlie successional development. Particularly, strong environmental filtering limits total trait space and there might be less successful strategies among coexisting species (Cornwell *et al.* 2006 and citations therein). If species with very similar habitat requirements tend to co-occur, total niche space should be smaller than expected from a random assembly from the regional species pool (Weiher and Keddy 1995). Then, an increase in species richness during succession should not change, or only inconsiderably, the total trait space covered by the community, because only species with similar traits successfully pass the filters.

Conversely, when competition plays the major role in community assembly, the total trait space should be greater than expected from a random assembly from the regional pool. This is caused by a tendency of species with similar niche space not to co-occur within the same community. In other words, the coexistence of species requires a limit to their ecological similarity (MacArthur and Levins 1967). When new species arrive from the regional pool, only those whose niche is not already occupied will be able to establish in the community (Grime 2006). As a consequence, total trait space and species richness will increase correspondingly.

Neutral community assembly (Hubbell 2001) assumes ecological equivalence of species (identical trait space) within a given ecological guild and ecological drift as the major process of colonization. Neutrality predicts therefore random patterns of species co-occurrence (Gotelli and McGill 2006, but see Ulrich 2004) and neither phylogenetic nor trait convergence or divergence during succession (Götzenberger *et al.* 2011). Because species are assumed to have identical properties, the total realized trait space of a community is predicted to be independent of species richness and to be roughly constant during succession. If at least some random variability in species trait space is assumed, differences in species traits should result in a positive correlation between species richness and total trait space (Weiher *et al.* 2011). Thus, neutrality and competition might cause a temporal increase in total trait space, albeit space should be less closely linked to species richness under neutral assembly. Of course, filtering and neutral

processes can act simultaneously. Thus, the outcome might depend on their relative strength (Weiher *et al.* 2011).

Theory on habitat filtering in combination with niche conservatism (Ackerly 2004; Lord *et al.* 1995) predicts that phylogenetically closely related species co-occur more often than expected by chance in similar environments (Losos 2008). The effect is called phylogenetic aggregation (Pausas and Verdú 2010). To some extent, this corresponds with Tilman's (1990) central concept of succession that includes organismal trade-offs according to specific combinations of environmental constraints. Since there is no species equally adapted to all environmental constraints, succession proceeds. In turn, the classical assembly rule concept (Diamond 1975; Weiher and Keddy 1999) focuses on competitive exclusion and predicts species of similar ecological traits to occur in a segregated manner (Svenning *et al.* 2008). However, phylogenetic analyses alone cannot provide a full understanding of community assembly (Mayfield and Levine 2010). For example, phylogenetically segregated communities can have either segregated traits that are conserved within lineages or clustered traits that converge across lineages (Weiher *et al.* 2011). When the total trait space does not change due to strong abiotic filters, phylogenetic relatedness could increase as traits converge between lineages and decrease as new colonizers are from the same lineages as the species already present, while disappearing species are distantly related (Mayfield and Levine 2010). Phylogenetic relatedness can also remain constant when new species are from the same lineages as those already present in the community. Finally, neutrality predicts a rather stable phylogenetic structure throughout time, because members of all lineages in the regional pool have the same probability of colonizing the local community (Kraft *et al.* 2007).

Within the habitat filtering framework, species composition is generally mediated by environmental factors in plants, particularly by soil properties and light regimes (Götzenberger *et al.* 2011). Soil characteristics often show a considerable variability, even at very small scales, leading to vegetation patches of differing species composition (Robertson *et al.* 1988, Van der Maarel and Sykes 1993) and phylogenetic diversity (W. Ulrich *et al.* 2013, submitted for publication). The question how total trait space and functional diversity varies in response to soil characteristics at small spatial scales has gained much less attention (He *et al.* 2011). Depending on which process dominates (competition or filtering) there might be either an increased or a decreased variability with respect to a neutral colonization pattern.

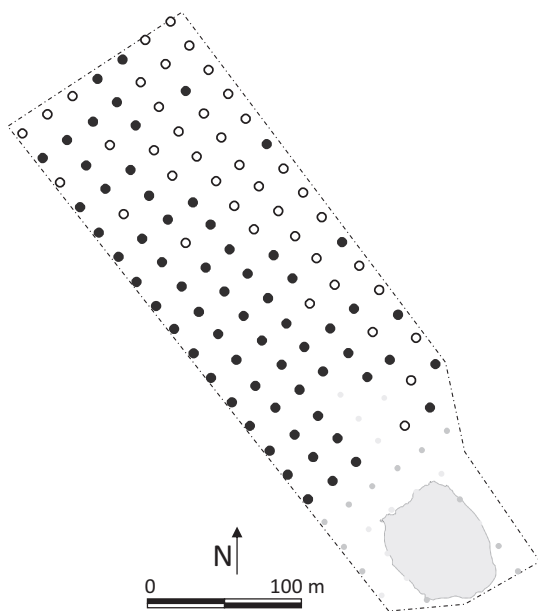
We use a unique data set on early plant succession (W. Ulrich *et al.* 2013, submitted for publication; Zaplata *et al.* 2013) to assess the degree of total trait space in dependence of the spatial distribution of species. We ask how trait space changes during early succession and how trait space co-varies with phylogenetic community structure. Previously, we reported that competition (Zaplata *et al.* 2013) and filtering processes (W. Ulrich *et al.* 2013, submitted for publication) increased during succession rejecting a neutral community

assembly. Therefore, we first expect a higher increase in total trait space in comparison to a neutral pattern of species equivalence. Second, habitat filtering should lead to a lower increase in comparison to a pure random colonization process. Third, we are interested in the small-scale variability in trait spaces and its dependence on soil conditions and expect trait space to co-vary with those soil conditions that might act as filters. We try to disentangle the influences of species richness and plant cover on the variability of small-scale trait space and to assess how biotic and abiotic filters and neutral processes shape patterns of total resource use.

## METHODS

### Study area and plant sampling

From 2005 to 2011, we studied the early vegetation succession in a 6-ha artificial water catchment (the ‘Chicken Creek’) formed after partial reclamation of an open-cast lignite mine in north-east Germany (Schaaf *et al.* 2013). Sand or loamy sand material originating from Pleistocene sediments was used for the construction of the up to 3.5 m top layer of the catchment (details in Gerwin *et al.* 2009). Immediately after completion of construction, soil samples were taken from the upper 30 cm at the points of a regular grid (20 m × 20 m) (Gerwin *et al.* 2010). Here, we relate carbonate C content, fraction of sand and pH to the fine scale variability in total trait and phylogenetic space. Floristic sampling was based on a total of 426 plots of 1 m<sup>2</sup>, four of each being arranged within 5 m × 5 m around the points of the regular grid (Zaplata *et al.* 2013; Fig. 1). Vegetation



**Figure 1:** the Chicken Creek catchment with its permanent plot grid. Hierarchical cluster analysis separated the catchment soil into an eastern part (○; 41 plots) characterized by a higher fraction of sand and a western part (● 66 plots) having higher fractions of silt, clay, nitrogen and organic and inorganic carbon (Zaplata *et al.* 2013).

records started in 2005 with 360 subplots, thereafter in all plots. For each year, we constructed cover-based species × plot matrices **M**. A complete list of plant species is contained in the [online supplementary material](#). Succession started with an almost monodominant stand of the Canadian Horseweed *Conyza canadensis* (L.) Cronquist (Zaplata *et al.* 2011). In 2011, the predominant vegetation type was species-rich sandy xeric grassland typical also for the vegetation outside the catchment (Felinks 2000).

We used the Leda (Kleyer *et al.* 2008) and BioFlor (Klotz *et al.* 2002) databases and compiled a total of 14 plant functional (lifespan, light, soil fertility, pH and nitrogen requirements, seeds per shoot and duration of seedling, seed bank longevity, duration of flowering, type of reproduction and life strategy type), genetic (degree of polyploidy) and morphological (specific leaf area, canopy height) traits ([online supplementary material](#)) that might be important for colonization during early succession. Categorical variables were appropriately recoded prior to analysis. Missing values were in all cases replaced by the respective values of the nearest relatives (always congeners). Due to the heterogeneity of these traits, we compressed the information into eigenvectors by principal component analysis and used the first five principal components with eigenvalues >1.0 that contained a total of 58.7% of total variance ([online supplementary material](#)). The first axis explained 17.0% of variances and was particularly linked to lifespan, duration of flowering and life strategy. The second axis explained 12.2% of variance and was related to soil fertility and soil nitrogen requirements. We constructed phylogenetic trees and the respective matrices of phylogenetic distances for all species using the *PhyloMatic* phylogenetic database and toolkit for the assembly of phylogenetic trees (Webb and Donoghue 2005) and the R package *ape* (Paradis *et al.*, 2004). Trees generated by this software were based on the most recent phylogeny contained in Angiosperm Phylogeny Group (APG 2009) III enriched by recent data to resolve the majority of polytomies contained in APG III. Because DNA sequence data were not available for all taxonomic levels of resolution, we assigned branch lengths to the tree with the Branch Length Adjustment option in *Phylocom* (Webb *et al.* 2008), using minimum ages for genera and families and higher taxa from the molecular dating of Wikström *et al.* (2001). Undated nodes were evenly spaced between dated ones.

### Statistical analysis

Functional attribute diversity (FAD, Walker *et al.*, 1999) is a measure of total trait space covered by the species of a given community and is calculated as the normalized sum of the Euclidean distances (below termed raw FAD values) between species in trait space. It performed well in previous tests with simulated and empirical data (Petchev and Gaston 2002; Petchev *et al.* 2004) although Schmera *et al.* (2009) criticized the application of raw FAD scores for its non-linear behaviour and sample size dependence. Another intuitive way to assess trait space is the use of convex hulls (CH; Cornwell *et al.* 2006;

Jackson *et al.* 2011). We calculated the CH area of the first two eigenvectors. Because raw metrics of FAD and CH face the same undesired statistical properties, we calculated respective normalized FAD and CH values (see below) for each study year as a whole and for each plot within each year. We compared these normalized scores with the average phylogenetic distance of the species involved using the net relatedness index (NRI), which is the negative standardized effect size (SES) of the average phylogenetic distance of all species pairs (Webb *et al.* 2002). NRI increases with increasing phylogenetic clustering.

We used general linear modelling and simultaneous autoregression (Rangel *et al.* 2010) (to account for the mediate degree of spatial autocorrelation of soil variables and traits space; Moran's I coefficient always <0.3) to relate the SES scores of FAD and CH to species richness, total abundance, NRI and soil properties. Autoregression analysis was done with SAM 4.0 (Rangel *et al.* 2010) using default settings.

The calculation of FAD, CH and NRI needs a baseline for comparison. Here, we base statistical inference of these scores on a null model approach (Gotelli and Ulrich 2012). The question which null model to use is crucial in any phylogenetic analysis, and results might depend on proper null model choice (Gotelli and Ulrich 2012; Ulrich and Gotelli 2013). In the present case, the equal size of our sample plots together with the small catchment size (400 m × 150 m) means that a suited null assumption implies a random appearance of individuals on single plots constrained only by differences in regional species abundance and plot quality. Therefore, we take advantage of our quantitative data structure and apply an abundance based null model. Recently, Ulrich and Gotelli (2010) showed that such null models that are based on the resampling according to observed abundance distributions instead of species occurrences are indeed sensitive tools for inferring matrix patterns. In accordance with our null assumptions, we apply the AA null model of Ulrich and Gotelli (2010) that resamples the matrix proportional to both row (species abundances) and column (plot abundances) marginal distributions. Note that such a null model is close to a neutral modelling approach (Hubbell 2001; Rosindell *et al.* 2012) without speciation and dispersal limitation where the probabilities of occurrence in single

cells depend only on the relative abundance distribution of species (Ulrich and Zalewski 2007). These assumptions seem appropriate in the present case. Note also that a neutral colonization process cannot be tested positively for with this null model. Null expectations and standard deviations of the AA null distributions were in all cases based on 200 randomizations. Because the null model distributions were in most cases approximately normally distributed, we calculated Z-transformed standardized effect sizes (SES) ( $SES = (x - \mu) / \sigma$ , where  $x$  denotes the observed score,  $\mu$  the average score of the simulated matrices, and  $\sigma$  the respective standard deviation). Assuming normality, SES scores should have approximate values of  $\pm 2$  at the two-sided 95% confidence limits.

## RESULTS

Numbers  $N$  of plots occupied, total species richness,  $S_{total}$ , and average species richness per plot  $S_{plot}$  steadily increased during the 7 study years (Table 1).  $S_{plot}$  increased exponentially with  $S_{total}$  ( $S_{plot} = 0.7e^{0.02S_{total}}$ ,  $r^2 = 0.98$ ,  $P < 0.01$ ) and did not reach a clear plateau after 7 years of succession (Table 1). Annual total raw FAD scores increased to the square of species richness ( $FAD = S^{2.01}$ ,  $r^2 = 0.99$ ,  $P < 0.01$ ).

General linear (Table 2) and simultaneous autoregression (Fig. 2) modelling applied to the normalized FAD and CH values (SES scores) indicated a significant increase in the SES scores with species richness (Table 2, Fig. 2). In all analyses (Table 2, Fig. 2), FAD and CH behaved qualitatively similarly. Total plant cover had an even stronger but negative effect on the normalized trait spaces (Fig. 2). Among the soil variables particularly carbonate content increased trait space (Table 2, Fig. 2), while pH did not have any significant effect. In 2006, higher fractions of sand decreased trait space.

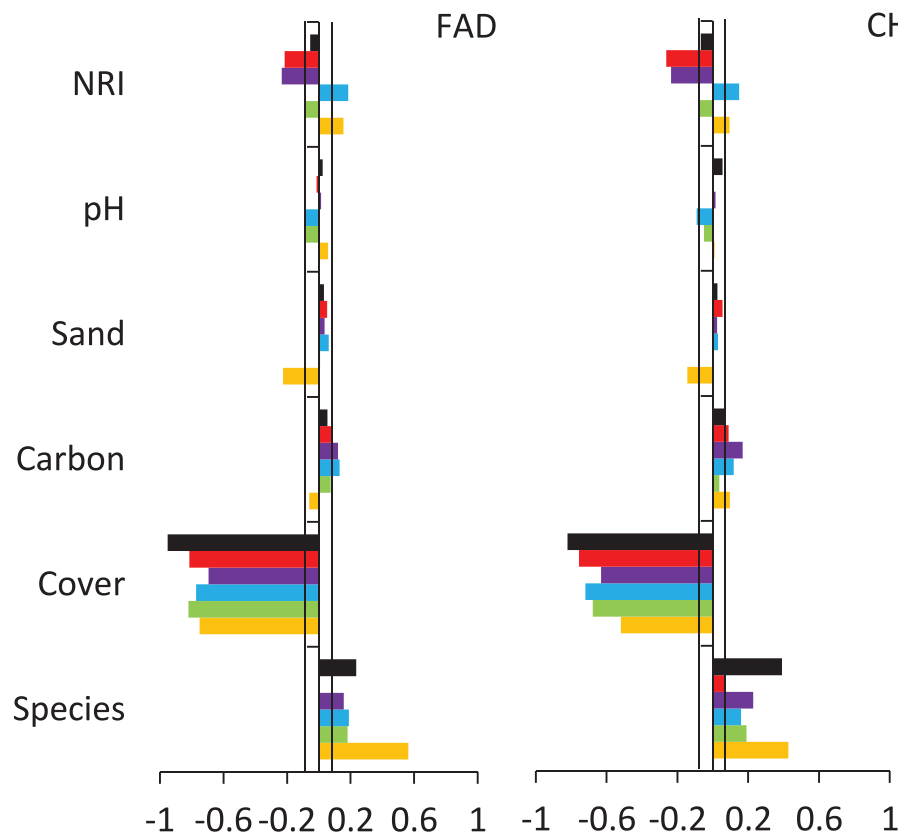
There was no clear trend in the influence of NRI on total trait space (Table 2, Fig. 2). In 2006 and 2008, we observed an increase in trait space with increasing net relatedness, while in the other study years a significant ( $P < 0.01$ ) negative influence occurred (Fig. 2). A closer look at the relationship between the SES of FAD and NRI pointed to significantly negative correlations between both variables except for 2008 (Fig. 3, using CH instead of FAD gave a qualitatively

**Table 1:** summary data on species richness and colonization and extinction and FAD of the vascular plant species at the Chicken Creek catchment during seven study years (2005–2011)

Study year	Total annual species richness	Number of colonizations	Number of disappearances	Average species richness per plot	Number of plots occupied
2005	17	17	0	1.23	47
2006	43	28	2	1.85	382
2007	70	29	2	3.12	425
2008	94	30	6	7.09	425
2009	118	29	5	11.16	426
2010	120	14	12	14.67	426
2011	123	12	9	14.74	426

**Table 2:** general linear modeling (sums of squares *SS* and degrees of freedom *df*) of the SES scores of FAD and CH (*AA* null model) in dependence on study year (categorical variable), species richness, NRI and important soil properties (metric variables)

Variable	SES trait FAD			SES trait CH			
	SS	df	<i>P</i>	SS	df	<i>P</i>	<i>P</i>
Constant	16.46	1	<0.001	9.29	1	<0.001	<0.001
Species richness	84.79	1	<0.001	68.81	1	<0.001	<0.001
Cover	2196.03	1	<0.001	688.87	1	<0.001	<0.001
CaCO <sub>3</sub>	33.49	1	<0.001	21.06	1	<0.001	<0.001
Sand	6.01	1	0.001	0.97	1	0.110	0.110
pH	0.87	1	0.220	0.04	1	0.736	0.736
NRI	46.18	1	<0.001	34.37	1	<0.001	<0.001
Study year	690.39	6	<0.001	353.48	6	<0.001	<0.001
Error	1176.00	2001	—	756.26	2001	—	—
Model <i>r</i> <sup>2</sup>	0.83	—	<0.0001	0.70	—	<0.0001	<0.0001

**Figure 2:** standardized values of simultaneous spatial autoregression of the SES scores of FAD and CH (*AA* null model) for 2006 (yellow bars), 2007 (green), 2008 (blue), 2009 (violet), 2010 (red) and 2011 (black) in dependence on species richness, total plot cover, NRI and three soil variables. The vertical lines denote approximately the upper and lower significance levels of beta at the 1% two-sided error level. The year 2005 was excluded due to the low number of species per plot.

identical pattern, data not shown). Additionally, trait space steadily decreased during succession with respect to our random expectation, while the degree of phylogenetic clustering increased (Fig. 4). We observed a change in phylogenetic relatedness from an initial random pattern to an aggregated pattern in the last 3 study years (Fig. 4).

## DISCUSSION

Each year within the first 4 years of succession, we observed an increase in species richness and average richness per m<sup>2</sup>, followed by a lower increase in the subsequent 3 years. This is accompanied by a decline in the rate of floristic change (i.e.



increase in inertia of the community) as it is well known for secondary succession (cf. Grime 2001, pp. 254–256) and many mechanisms were listed as being responsible for such a pattern. Particular interest focussed on the replacement of short lived (*r* strategists) by long lived (*K* strategist) species and increasing competitive exclusion (Grime 2001; Prach *et al.* 1997). The recent study focussing on niche assembly theory puts emphasis on changes in trait space and phylogenetic diversity during early succession. We found a close correlation of species richness and total trait space. Trait space, in turn, was in all but one (2008) study years negatively correlated with the degree of phylogenetic clustering (Fig. 3). Such a pattern is expected within the framework of niche conservatism where closely related species tend to have similar ecological requirements and thus share important traits (Prinzing *et al.* 2008). Then, a higher degree of phylogenetic clustering implies the co-occurrence of closely related species. Therefore, the total trait space occupied by these species should be smaller than expected from a random assembly of species (Cornwell *et al.* 2006) as expected by our second starting hypothesis.

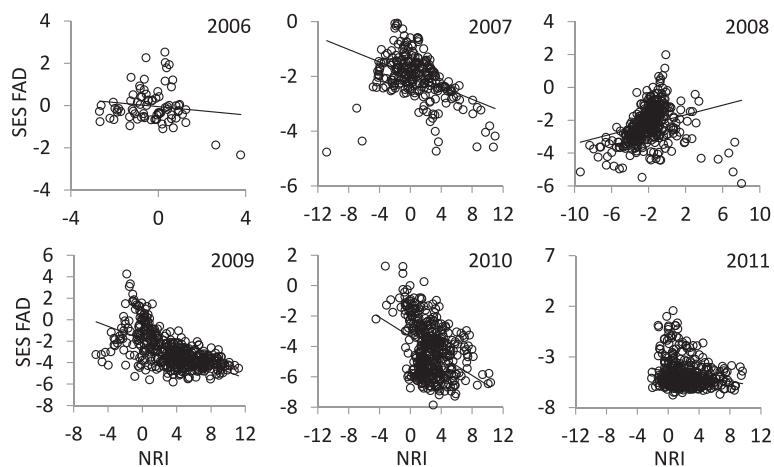
We observed two temporal trends in phylogenetic clustering and trait space (Fig. 4). First, there was a steady decline in trait space with respect to our random expectation, while the degree of phylogenetic clustering increased (W. Ulrich *et al.* 2013, submitted for publication). The relative decline in trait space is in accordance with a small-scale dominance of filtering processes over species competition. According to theoretical and empirical studies on tropical forest succession (Letcher 2010; Norden *et al.* 2012), early successional states should be characterized by homogeneous conditions that support the presence of similar species and imply a comparably lower trait space in comparison to a random expectation. In a similar way, Tilman's (1990) succession theory predicts that environmental constraints allow a specific set of species to colonize a given site. As succession proceeds, other processes such as

competitive exclusion and mutualistic interactions become more important and favour larger absolute trait spaces and phylogenetic segregation (Letcher *et al.* 2012; Whitfeld *et al.* 2011).

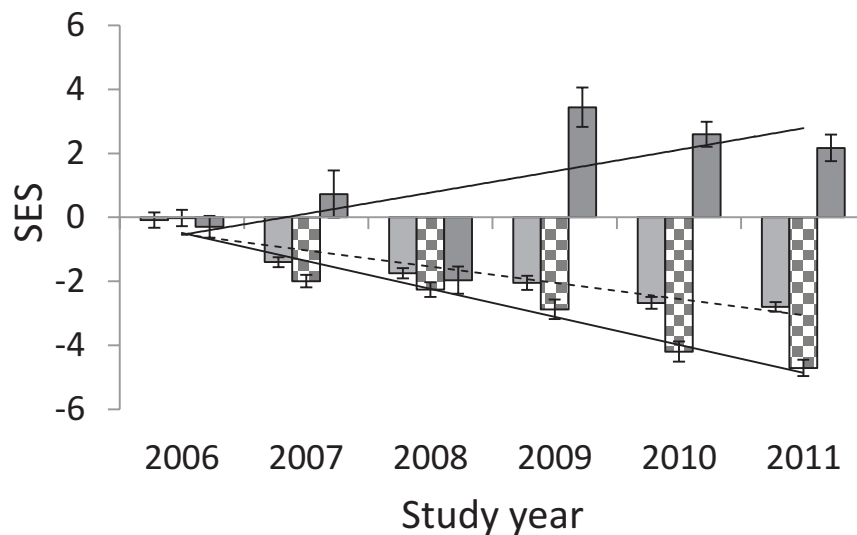
However, this increase in trait space is countered by filtering processes that reduce the total trait space occupied by a given set of species. This should cause a decline in relative trait space. Our results (Fig. 4) are in agreement with such an expectation. In previous studies on the same data, we have already shown a strong temporal trend towards increasing spatial segregation of species (Zaplata *et al.* 2013). However, our findings on the increase in phylogenetic clustering (W. Ulrich *et al.* 2013, submitted for publication) contradict the findings of Letcher *et al.* (2012) and; Whitfeld *et al.* (2011) regarding the increase in phylogenetic segregation in tropical forest succession.

Our data indicate that during the initial period of succession, functional traits and the respective available trait spaces are filled by colonizing species and by species already present in the seed bank (Zaplata *et al.* 2010). After this initial state, newly entering species encounter an increasing number of functionally similar potential competitors. Here, we argue that a limiting functional space might be one of the major triggers to slow down the increase in species richness during later states of succession. This hypothesis is in line with classical competition theory, which predicts the number of species to be restricted by the number of available niches (Wilson *et al.* 1987). Consequently, within a given habitat there should also be a limited total niche space and hence the traits and the total trait space fitting this niche space are also limited.

The parallel increase in trait space with species richness and the according slow down in the increase from 2009 to 2011 are expected if an upper limit to the number of niches exists in a given environment. However, our study was not designed to directly test the limiting niche hypothesis. Possible tests invoke



**Figure 3:** the relationship between the SES scores of FAD and the NRI for the years 2006 to 2011. Simultaneous autoregressions: 2006:  $r = -0.13$ , 2007:  $r = -0.42$ , 2008:  $r = 0.27$ , 2009:  $r = -0.60$ , 2010:  $r = -0.39$ , 2011:  $r = -0.20$ . Except 2006 all  $P$  ( $r = 0$ )  $< 0.01$ . The year 2005 was excluded due to the low number of species per plot.



**Figure 4:** average standardized effects sizes SES of FAD (chequered bars) and CH (light grey bars) decreased significantly (both  $P < 0.01$ ) during the study time while the respective SES scores of NRI (dark grey bars) increased ( $r = 0.62$ ,  $P = 0.19$ ). Error bars denote two standard errors.

comparisons of observed and expected variation in diversity (reviewed in Götzenberger *et al.* 2012) among similar sites. Then a low observed variability indicates constraints on the number of niches. However, in cases of small-scale environmental variability, such tests might be heavily biased towards the rejection of niche limitation. Further studies should investigate the distribution of niche spaces during succession across spatial scales.

If soil conditions are correlated with trait space (Table 2, Fig. 2), they should also be correlated with niche space. Under this premise, we hypothesized (hypothesis 3) that one of the potential limiting factors of the number of niches is the range in soil properties (Huston 1980). Of the measured soil variables, carbonate content was positively correlated with trait space, while the fraction of sand and pH gave indifferent signals. In a previous study (W. Ulrich *et al.* 2013, submitted for publication), we demonstrated a significant positive correlation of carbonate content with phylogenetic segregation. Assuming high niche conservatism for the selected traits (Wiens *et al.* 2010), phylogenetic segregation should be linked to increasing trait diversity and therefore trait space (Dinnage *et al.* 2012). Therefore, we argue that soil conditions might ultimately mediate the number of realized traits already in early plant succession.

The observed small-scale heterogeneity in trait space could be traced down to respective differences in species richness, plant cover and soil variables (Table 2, Fig. 2). Besides species richness, a high cover of single species reduced the standardized trait space (Table 2) and caused subsequent successional phases. There were phases of *Conyza canadensis* in 2006 and *Trifolium arvense* L. in 2008–09 (Zaplata *et al.* 2011, 2013). A high dominance caused a sharp decline in total trait space and was responsible for the strong negative signal of cover on total trait space (Fig. 2). The *T. arvense* phase in 2008 was apparently also responsible for the reversed (positive) correlation of FAD and NRI (Fig. 3). This effect points to a

possible pitfall in trait space analysis. Trait space and phylogenetic relatedness might be positively or negatively correlated depending on the dominance structure of the community.

Lastly and in accordance with our first starting hypothesis, our study does not support a neutral view of trait assembly during succession. Species equivalence implies no, or at least a very low, variability in trait space among species. Unlike what is observed here, this implies a much smaller increase in total trait space with species richness. Recently, Purves and Turnbull (2010) reviewed this point and argued that trait equivalence is a highly improbable state leading to a substantial decrease in species diversity in the course of community assembly. However, even if we relax the equivalence assumption and assign traits by a Poisson random distribution, we expect a linear increase in total trait space with species richness. Instead, we found a quadratic increase. Neutrality also implies a comparably low and random variability of total trait space among study sites. Again this is not what we found. The significant variability among our study plots combined with the correlation with important environmental variables (Table 2) points to directional successional transitions imposed by small-scale filtering processes that were particularly assigned to soil characteristics.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Plant Ecology online.

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*Conflict of interest statement.* None declared.

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