

Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes

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Summary

1. Theory predicts that the processes generating biodiversity after disturbance will change during succession. Comparisons of phylogenetic and functional (alpha and beta) diversity with taxonomic diversity can provide insights into the extent to which community assembly is driven by deterministic or stochastic processes, but comparative approaches have yet to be applied to successional systems.

2. We characterized taxonomic, phylogenetic and functional plant (alpha and beta) diversity within and between four successional stages in a > 270-year-long arable-to-grassland chronosequence. Null models were used to test whether functional and phylogenetic turnover differed from random expectations, given the levels of species diversity.

3. The three facets of diversity showed different patterns of change during succession. Between early and early-mid succession, species richness increased but there was no increase in functional or phylogenetic diversity. Higher than predicted levels of functional similarity between species within the early and early-mid successional stages, indicate that abiotic filters have selected for sets of functionally similar species within sites. Between late-mid and late succession, there was no further increase in species richness, but a significant increase in functional alpha diversity, suggesting that functionally redundant species were replaced by functionally more dissimilar species. Functional turnover between stages was higher than predicted, and higher than within-stage turnover, indicating that different assembly processes act at different successional stages.

4. Synthesis. Analysis of spatial and temporal turnover in different facets of diversity suggests that deterministic processes generate biodiversity during post-disturbance ecosystem development and that the relative importance of assembly processes has changed over time. Trait-mediated abiotic filtering appears to play an important role in community assembly during the early and early-mid stages of arable-to-grassland succession, whereas the relative importance of competitive exclusion appears to have increased towards the later successional stages. Phylogenetic diversity provided a poor reflection of functional diversity and did not contribute to inferences about underlying assembly processes. Functionally deterministic assembly suggests that it may be possible to predict future post-disturbance changes in biodiversity, and associated ecosystem attributes, on the basis of species' functional traits but not phylogeny.

Key-words: alpha diversity, arable-to-grassland succession, beta diversity, chronosequence, community assembly, determinants of plant community diversity and structure, environmental filtering, null model, semi-natural grasslands, trait

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Introduction

The world's ecosystems are becoming increasingly affected by anthropogenic disturbance (Hoekstra *et al.* 2005) which may have a profound impact on plant biodiversity and ecosystem functioning (Loreau *et al.* 2001; Magurran & Dornelas 2010; Isbell *et al.* 2011). To be able to predict ecosystem responses to future disturbance events, we need a better understanding of the processes that govern community assembly, and thus generate biodiversity, during succession (Connell & Slatyer 1977; Noble & Gitay 1996; Prach & Walker 2011). If community assembly is driven by deterministic processes, patterns of species co-occurrence are expected to be non-random with respect to species' traits (Keddy 1992; Zobel 1997; Götzenberger *et al.* 2012). Abiotic filtering will select for species that are more similar than expected by chance, because of shared adaptations to a particular environment (Diaz, Cabido & Casanoves 1998; Cornwell, Schwilk & Ackerly 2006), whereas biotic filtering (e.g. processes of competitive exclusion and resource partitioning) is often assumed to select for functionally dissimilar species (MacArthur & Levins 1967; Weiher *et al.* 2011; but see Mayfield & Levine 2010; de Bello *et al.* 2012). In contrast, stochastic ('trait-neutral') processes (Hubbell 2001) are expected to result in species co-occurrence patterns that are random with respect to species traits.

Theory predicts that, as succession proceeds, the relative importance of abiotic and biotic filtering processes is likely to change. Environmental and trait-based dispersal filtering are expected to dominate during early succession, with biotic filtering becoming increasingly important in the later stages of succession (Connell & Slatyer 1977; Leibold *et al.* 2004). Earlier studies of plant community assembly during succession have mainly focussed on temporal changes in taxonomic (species) composition, on changes in single traits or on changes in functional groups (Noble & Slatyer 1980; Prach, Pyšek & Šmilauer 1997; Garnier *et al.* 2004; Kahmen & Poschlod 2004). However, a purely taxon-based approach cannot take into account ecological differences between species. Approaches based on single traits do not allow for multivariate correlations between traits, and approaches based on functional groups do not consider the fact that species within functional groups may be functionally different (Reich *et al.* 2004; Marquard *et al.* 2009). These limitations may have biased conclusions about the processes underlying community assembly (Cornwell, Schwilk & Ackerly 2006; Villéger, Mason & Mouillot 2008).

A recently proposed approach (Hardy & Senterre 2007; Eastman, Paine & Hardy 2011; Baraloto *et al.* 2012) uses comparisons between taxonomic, phylogenetic and functional trait diversity to test the extent to which stochastic and filtering processes drive community assembly. Based on the assumption that a particular assembly process will generate a specific spatial pattern of biodiversity (Diamond 1975; Pausas & Verdu 2010), this comparative approach uses between-species differences (phylogenetic or functional) to partition diversity into within- (alpha) and between- (beta) community components. If the species co-occurring in local communities

are functionally more similar than expected, given the levels of species diversity, this would suggest environmental filtering and/or trait-based dispersal limitation (Keddy 1992; Webb *et al.* 2002; de Bello *et al.* 2009). A lower than expected functional similarity between co-occurring species would be a predicted consequence of the competitive exclusion of functionally similar species (Pacala & Tilman 1994).

Because measures of functional diversity are based on a finite set of traits, phylogenetic diversity is often used as a proxy for functional trait diversity (see Webb 2000; Silvertown, Dodd & Gowing 2001; Webb *et al.* 2002), as it potentially integrates a greater amount of trait information than is provided by a limited set of measurable traits. However, inferences about community assembly processes based on phylogenetic diversity rely on the assumption of trait conservatism – the expectation that closely related species will be ecologically similar (Wiens & Graham 2005). A mismatch between functional and phylogenetic diversity would indicate that the phylogenetic diversity does not reflect the diversity of phylogenetically conserved traits and/or suggest that important traits were missing from the analysis (Pavoine & Bonsall 2011).

A few recent studies have quantified temporal changes in particular facets of plant functional or phylogenetic diversity during succession. Studies of changes in phylogenetic alpha diversity during tropical forest succession found that late-successional communities contained more-distantly related species than early successional communities (Letcher 2010; Norden *et al.* 2011; Ding *et al.* 2012; Letcher *et al.* 2012). A study of phylogenetic and functional beta diversity of tropical tree communities showed that, whereas phylogenetic turnover between successional stages was random (given the species turnover), functional turnover was either higher or lower than expected (Swenson *et al.* 2011b). In contrast, Schleicher, Pepler-Lisbach & Kleyer (2011) found that levels of functional alpha diversity in urban plant communities did not differ from random expectations within the different successional stages. However, these studies were based on single facets of diversity or focussed on diversity components either within or between successional stages. To gain an insight into the extent to which the processes governing community assembly during post-disturbance ecosystem development (i) are deterministic and (ii) change over time, there is a need for studies of succession that include different facets of diversity within as well as between stages.

In the present study, we assessed taxonomic, phylogenetic and functional (alpha and beta) diversity at different successional stages, as well as turnover between stages, within a chronosequence representing a more than 270-year-long arable-to-semi-natural grassland succession. Old semi-natural grasslands are among the most diverse plant communities within the European landscape and have developed as a result of centuries of low-intensity grazing management which has prevented development into forest communities (Eriksson, Cousins & Bruun 2002; Poschlod & Wallis De Vries 2002). Landscapes containing semi-natural grasslands are often characterized by a mosaic of grassland patches that represent different stages in the

succession from arable cultivation to permanent pasture. A chronosequence approach, in which different-aged patches of vegetation are assumed to represent a temporal sequence of change in community composition, provides the only means of studying the long-term (over several centuries) dynamics of such successional systems (Knops & Tilman 2000; Peltzer *et al.* 2010; Walker *et al.* 2010). Chronosequences are most suited for the analysis of community characteristics, such as biological diversity, that change in a linear fashion over time, and, despite critiques (Johnson & Miyanishi 2008), can contribute to an understanding of landscape processes, even in systems where plant community trajectories do not match changes in soil development (Walker *et al.* 2010).

First, we quantified taxonomic, phylogenetic and functional diversity within grassland communities (alpha diversity), together with the taxonomic, phylogenetic and functional turnover between communities (beta diversity), at four successional time steps.

Secondly, to obtain insights into stochastic and deterministic processes, we examined, for each successional time step, whether species co-occurring within sites were phylogenetically or functionally more (or less) similar than expected, given the taxonomic diversity. If community assembly during succession is deterministic, levels of functional similarity are expected to be either higher or lower than predicted by an appropriate null model. If abiotic filtering is the dominant assembly process in the initial phases of succession, functional similarity between species co-occurring within communities should be higher than expected within the early successional stages.

Third, we assessed phylogenetic and functional turnover between successional stages. If the phylogenetic or functional turnover between sites belonging to different stages is higher than the turnover between sites from the same successional stage, this would indicate that there is phylogenetic and functional turnover, possibly caused by differential environmental filtering, during the course of succession.

Materials and methods

STUDY AREA AND SAMPLING

We studied grassland plant communities in a chronosequence representing an arable-to-semi-natural grassland succession within a 4.5 × 4.5 km landscape (centred on 56°40'49" N, 16°33'58" E) on the Baltic Island of Öland, Sweden. The overall topography in the study area is flat and the landscape consists of a mosaic of grasslands, arable fields and forests. Öland has a history of grazing management dating back to the early Neolithic (3900–3300 BC), but the proportion of grassland in the study area has declined progressively over the last three centuries – from 86% in 1723 to 9% at the present day (Johansson *et al.* 2008). The remaining grassland fragments are still extensively grazed by free-ranging cattle. Younger grasslands have developed on previously arable fields (Johansson *et al.* 2008).

All grassland fragments in the present-day landscape were classified according to their grazing continuity (grassland age), with the help of GIS overlay analysis of land-use maps from 1730, 1959, 1994 and 2005 (see Johansson *et al.* 2008), and assigned to one of

four successional stages (early, early-mid, late-mid and late succession), representing 5–15, 16–50, 51–270 and > 270 years of grassland continuity. Grassland fragments < 50 m² were excluded from the study, and fragments > 2500 m² were subdivided into smaller units (ranging from 1250 to 2500 m²), giving a total of 1335 grassland units with areas ranging between 56 and 2500 m². Within each successional stage, 55 grassland units were randomly selected, without replacement. Presence/absence data for all non-woody, vascular plant species (234 in total) were collected from a single 2 × 2-m plot (between mid-May and mid-July 2009) within each of the 55 selected grassland units representing each of the four successional stages (giving a total of 220 plots). The amount of disturbance was characterized by the percentage of bare ground within each plot.

TRAIT DATA

The plant species recorded in the plots were scored for 11 functional traits associated with their response to and/or tolerance of disturbance (Fig. S1 in Supporting Information). All traits were compiled/derived from large data bases for the North-West European flora (Poschlod *et al.* 2003; Kleyer *et al.* 2008). The total set of traits consisted of: (i) five vegetative traits, mainly related to the species' competitive ability, growth rate and ability to respond to disturbance [canopy height, plant life-form, specific leaf area (SLA), leaf size, leaf dry matter content (LDMC)] and (b) six regenerative traits, related to species' ability to disperse in space and time (epizoochory, wind dispersal potential, adult plant longevity, seed bank persistence, seed mass, seed production per ramet; Poschlod, Tackenberg & Bonn 2005). Qualitative data on plant life-form (Raunkiaer 1934) were coded as a quantitative variable: cryptophytes and therophytes = 1, hemicryptophytes = 2, chamaephytes = 3 and phanerophytes = 4 (*cf.* Pakeman, Lennon & Brooker 2011). Wind dispersal potential, on an ordinal scale, was derived from data on seed terminal velocity and seed release height (Tackenberg, Poschlod & Bonn 2003). Cattle are the main grazing livestock in the study area, and cattle-coat seed retention potential, predicted from seed mass and seed morphology using the regression model in Römermann, Tackenberg & Poschlod (2005), was used as an indicator for epizoochorous dispersal potential. Adult plant longevity was inferred from data on plant life span and on clonal propagation, using three ordinal classes 'annual and biennial', 'perennial/without the ability to spread clonally' and 'perennial showing clonality'. Seed bank persistence was characterized by the longevity index (Bekker *et al.* 1998), calculated as the proportion of non-transient seed bank records in the data base of Thompson, Bakker & Bekker (1997).

Because data for all 11 traits were not available for the full set of species ($n = 234$), estimates for missing values (9.1% of the cases) were obtained by predictive mean matching based on the observed trait values, using multivariate imputation by chained equations (MICE) as implemented in the package 'mice' (van Buuren & Groothuis-Oudshoorn 2011) in the R statistical package (R Development Core Team 2012).

PHYLOGENETIC DATA

We extracted a phylogenetic tree for the 234 species in the study from a dated, ultrametric supertree for 4685 Central European vascular plant species (DAPHNE 1.0, Durka & Michalski 2012). The final tree included 221 internal nodes of which 9 (4%) were polytomies. All but one of the polytomies (families within the Malpighiales) were below the family level, with three polytomies involving genera in the Poaceae, and five polytomies involving species within different dicot genera (Fig. S1).

DIVERSITY MEASURES

Measures of taxonomic, phylogenetic and functional alpha and beta diversity were calculated for each plot within the four successional stages. Taxonomic alpha and beta diversity were characterized by species richness and the 1 – Jaccard index [Koleff, Gaston & Lennon 2003; R-package ‘vegan’ (Oksanen *et al.* 2012)], respectively. Following Hardy & Senterre (2007) (see also Baraloto *et al.* 2012), phylogenetic and functional diversity were estimated within a consistent framework, based on the spatial decomposition of between-species evolutionary relatedness or trait similarity into within- (alpha) and between- (beta) community components that are independent of taxonomic diversity.

Within the Hardy & Senterre (2007) framework, phylogenetic and functional alpha diversity are, respectively, equivalent to the mean phylogenetic or functional trait distance between species (MPD_w^p , MPD_w^f) within a community and, in the case of presence/absence data, measure phylogenetic and functional distinctness.

Phylogenetic and functional turnover (beta diversity) were calculated, respectively, using the Π_{ST} and τ_{ST} statistics (Hardy & Senterre 2007): $\Pi_{ST} = 1 - mMPD_w^p / MPD_a^p$ and $\tau_{ST} = 1 - mMPD_w^f / MPD_a^f$, where $mMPD_w^p$ and $mMPD_w^f$ are the mean within-community phylogenetic and functional distance (MPD_w^p , MPD_w^f), respectively, averaged over all communities. MPD_a^p and MPD_a^f are the mean phylogenetic and functional distance between distinct species sampled from different communities. Values of Π_{ST} or $\tau_{ST} > 0$ indicate that species within communities are phylogenetically more related, or functionally more similar, than species from different communities (phylogenetic or functional clustering). Π_{ST} or $\tau_{ST} < 0$ indicate that species within communities are phylogenetically less related, or functionally less similar, than species from different communities (phylogenetic or functional overdispersion). In our study Π_{ST} and τ_{ST} were calculated for each pair of plots.

Phylogenetic diversity was calculated from a phylogenetic cophenetic distance matrix. The functional diversity indices were obtained from a species distance matrix based on the 11 functional traits. We carried out principal component analysis (PCA) on the log-transformed and standardized (mean = 0, SD = 1) trait data to correct for dominance of the distance matrix by highly correlated traits (see Devictor *et al.* 2010; Swenson, Anglada-Cordero & Barone 2011a). The resulting PCA axes were used to construct the interspecies functional distance matrix from which the mean pairwise distances, within and between communities, were calculated.

Differences in mean diversity between the four successional time steps were assessed with ANOVA and *post hoc* pairwise comparisons using a permutation approach [5000 permutations; R-package ‘ImPerm’ (Wheeler 2010)]. The Benjamini & Yekutieli (2001) correction for *P*-values was used to control for false discovery rates.

Phylogenetic and functional beta diversity (Π_{ST} and τ_{ST}) were calculated between pairs of plots belonging to the same or to different successional time steps, to assess temporal turnover in phylogenetic and functional diversity. The phylogenetic and functional diversity measures were calculated using the R-packages ‘picante’ (Kembel *et al.* 2010) and ‘spacodiR’ (Eastman, Paine & Hardy 2011).

NULL MODEL ANALYSIS

To assess whether species within communities were phylogenetically or functionally more (or less) similar than expected from a random draw from the pool of species found in each successional time step,

we compared the observed Π_{ST} and τ_{ST} values with the Π_{ST} and τ_{ST} values from 999 random communities. ‘Relative’ diversity measures, such as Π_{ST} or τ_{ST} , have been shown to provide more robust tests of phylogenetic or functional community structure than absolute measures such as MPD (Hardy 2008). Random communities were generated using the null model ‘1a’ in Hardy (2008), shuffling the names of the species across the phylogenetic or functional distance matrix. Permutations were restricted to species that have similar occurrence frequencies within the study landscape, grouping species into distinct frequency classes characterized by a fixed ratio: maximal/minimal occurrence frequency = 4, resulting in limits between frequency classes of 1, 4, 16, 64 and 256. This type of null model is appropriate when overall species’ frequencies are distributed non-randomly across the phylogeny or the functional trait space, as was the case in our study (see Appendix S1 and Fig. S2), and maintains (i) the species richness of each community, (ii) the species turnover between communities, (iii) the occurrence frequency of the species across the landscape, (iv) patterns of spatial clustering (e.g. caused by dispersal limitation), (v) the species identity within each time step and (vi) the phylogenetic and functional signal in overall species frequencies. All null model tests were carried out on the average Π_{ST} and τ_{ST} values (global estimates) for the 2×2 -m plots within the respective successional stages. Tests on global diversity estimates have been shown to have greater power than those based on estimates from pairs of sites (Hardy 2008).

Significant positive (or negative) values of Π_{ST} or τ_{ST} (beta diversity) indicate that species within plots belonging to a particular successional stage are more (or less) similar than expected by chance. Higher phylogenetic or functional turnover (Π_{ST} , τ_{ST}) between plots belonging to different successional stages than between plots from the same successional stage would suggest that different filtering processes act at different successional stages.

PHYLOGENETIC SIGNAL IN TRAITS

To assess the extent to which the phylogenetic relatedness between species reflects ecological similarity (i.e. phylogenetic conservatism), we used Blomberg’s *K*-statistic (Blomberg *et al.* 2003) to quantify the tree-wide phylogenetic signal in each of the 11 traits [R-package ‘phytools’ (Revell 2012)]. *K* values close to zero indicate less phylogenetic signal than expected from a Brownian motion model of trait evolution (Blomberg *et al.* 2003), implying that closely related species are functionally distinct. The significance of the phylogenetic signal was assessed by comparing the observed *K* values with a null distribution of *K* values generated by shuffling (999 times) the species’ names across the tips of the phylogenetic tree. There is a significant signal if the observed *K* values are within the top 2.5% of the randomized *K* values. We assessed node-level phylogenetic signal at different depths in the phylogeny following the approach proposed by Moles *et al.* (2005) (see Appendix S2).

SHIFTS IN COMMUNITY-LEVEL MEAN TRAIT VALUES

Successional shifts in single traits were used as an aid to the interpretation of results from the null model analysis. Community-level mean trait values, for each of the 11 functional traits, were calculated for each plot. Mean trait values for each successional stage were used to summarize changes in trait values over time. Differences in mean trait values between successional stages were assessed on the basis of ANOVA and *post hoc* pairwise comparisons using a nonparametric permutational approach. *P*-values were obtained from randomization testing

(999 runs) and controlled for false discovery rates (Benjamini & Yekutieli 2001).

Results

CHANGES IN DIVERSITY DURING SUCCESSION

The three facets (taxonomic, phylogenetic and functional) of alpha diversity all increased over succession but differed in their temporal patterns (Fig. 1). Taxonomic alpha diversity (species richness; Fig. 1a) increased significantly between early and late-mid succession (5–270 years), but showed no further increase in the last successional time step (> 270 years). In contrast, there was no significant increase in phylogenetic or functional diversity (MPD_w^P , MPD_w^T) between the early and early-mid successional stages (5–50 years; Fig. 1b,c). Instead, both functional and phylogenetic diversity increased between the early-mid and late-successional stages (16 to > 270 years).

All three facets of between-plot diversity decreased throughout succession (Fig. 2). Π_{ST} and τ_{ST} values (phylogenetic and functional turnover) were positive within all the successional stages as well as between successional stages.

The measures of phylogenetic and functional beta diversity were both significantly, positively correlated with taxonomic beta diversity (Table S3; $rM = 0.136$, $P < 0.05$ and $rM = 0.446$, $P < 0.05$). Π_{ST} and τ_{ST} had similar mean values for pairs of plots within each of the successional stages (Fig. 2). However, only functional turnover (τ_{ST} , Fig. 2c) showed significant deviations from random expectations, given the levels of taxonomic turnover: throughout succession, species within sites tended to be functionally more similar to each other than to species from other sites (functional clustering). τ_{ST} values were largest within the first and second successional time steps, indicating that functional clustering is strongest during early and early-mid succession.

Phylogenetic turnover (Π_{ST}) did not significantly differ from random expectations in any of the successional time steps (Fig. 2b).

PHYLOGENETIC AND FUNCTIONAL TURNOVER BETWEEN SUCCESSIONAL STAGES

Levels of functional turnover between different successional stages were on average higher than random predictions ($\tau_{ST} = 0.0093$, $P < 0.001$) and higher than those for the between-stage phylogenetic turnover, which did not differ significantly from null expectations ($\Pi_{ST} = 0.005$, $P = 0.068$). There were no significant deviations from random expectations when estimates of phylogenetic turnover were made between pairs of plots belonging to different successional stages (Fig. 3a). In contrast, levels of functional turnover (τ_{ST}) between the first and third successional time steps (T1–T3) as well as between the first and the last time steps (T1–T4) were higher than expected (Fig. 3b) and higher than τ_{ST} values estimated within each of the stages T1, T3 and T4, respectively (Fig. 2c), indicating that there is significant functional turnover between the early and late-successional stages as well as between the early-mid and late-successional stages.

PHYLOGENETIC SIGNAL IN TRAITS

The 11 traits that were used to calculate functional diversity had Blomberg's K values of less than one (Table S4), ranging from 0.099 (canopy height) to 0.315 (LDMC). However, all traits, apart from canopy height, had K values that were higher than expected by chance, indicating a low but significant phylogenetic signal. When the phylogenetic signal was examined at different depths in the phylogenetic tree, all traits, apart from LDMC, showed a low, non-significant signal throughout the phylogeny (Fig. S3).

SHIFTS IN COMMUNITY-LEVEL MEAN TRAIT VALUES

Mean trait values for canopy height, SLA, leaf size, seed mass and seed production were highest in early succession and decreased towards late succession, whereas LDMC increased over time (Fig. 4), suggesting that the grassland communities at the beginning of succession contain a higher

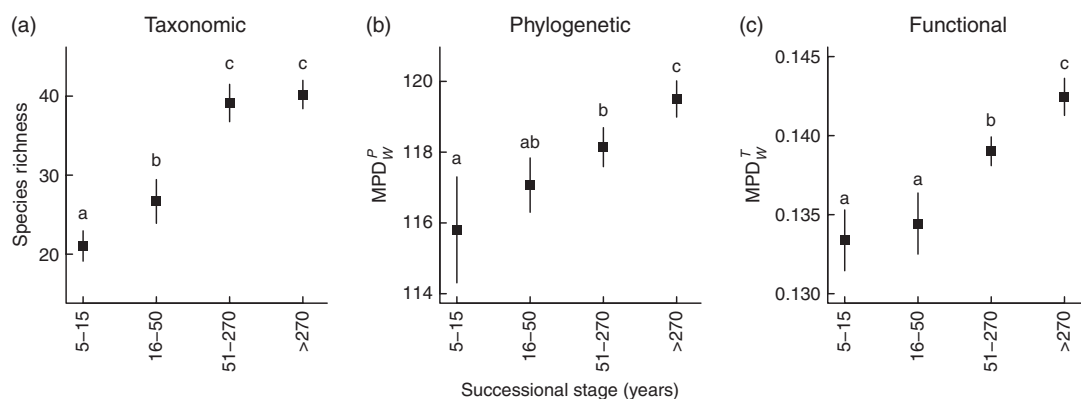


Fig. 1. (a) Taxonomic, (b) phylogenetic and (c) functional alpha diversity (mean \pm 1 SE) within the four successional stages. Phylogenetic and functional diversity are expressed, respectively, as the mean pairwise phylogenetic and functional trait distance between species within a community (MPD_w^P , MPD_w^T) and are equivalent to phylogenetic and functional distinctness. Letters indicate significant differences ($\alpha = 0.05$) between the stages.

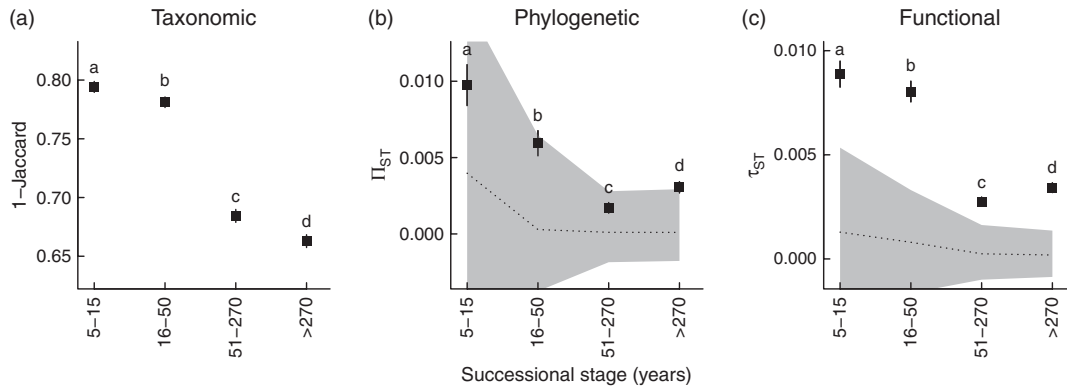


Fig. 2. (a) Taxonomic, (b) phylogenetic and (c) functional turnover (beta diversity), for all pairs of plots (black squares, mean \pm 1 SE) within each of the four successional stages. Phylogenetic and functional turnover (Π_{ST} or τ_{ST}) are based on the partitioning of the mean pairwise phylogenetic or functional trait distance into within- and between-community components. Letters indicate significant differences ($\alpha = 0.05$), based on permutation testing, between the stages. Π_{ST} or τ_{ST} values > 0 indicate that species co-occurring within communities are phylogenetically more related, or functionally more similar, to each other than to species from other sites (phylogenetic or functional clustering). The black dotted line and the grey-shaded area represent the mean and the 95%-confidence interval for the Π_{ST} or τ_{ST} values, respectively, from the 999 random communities. τ_{ST} values outside the interval indicate significant functional clustering.

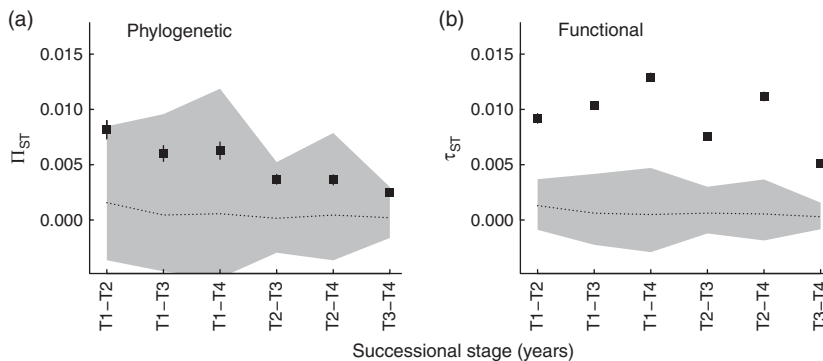


Fig. 3. Temporal (a) phylogenetic and (b) functional turnover between successional stages (black squares, mean \pm 1 SE). T1–T4 correspond to the four successional stages (5–15, 16–50, 51–270 and >270 years of grassland continuity). Between-stage functional, but not phylogenetic, turnover is significantly higher than random expectations (τ_{ST} values are above the grey-shaded area, i.e. above the 95% confidence interval for the τ_{ST} values from the 999 random communities).

proportion of ruderal (fast growing and disturbance-tolerant) species than late-successional communities. Early successional communities had greater wind dispersal potential, higher levels of epizoochory and higher seed bank persistence than late-successional communities, indicating that species that have a high long-distance dispersal potential and long-term persistent seed banks are more often found in the early than later successional stages.

Discussion

The present study shows that taxonomic, phylogenetic and functional diversity show different patterns of change during a more than 270-year-long arable-to-grassland succession. Between early and early-mid succession, there was an increase in species richness that was not accompanied by significant increases in phylogenetic or functional alpha diversity. Throughout succession, species co-occurring within sites were functionally more similar than expected by chance (functional clustering), indicating that community assembly is deterministic with respect to species traits. High levels of functional clustering within the early and early-mid successional stages suggest that abiotic filters have selected for sets

of functionally similar species. Although there was no change in species richness between the late-mid and late-successional stages, there was a significant increase in phylogenetic and functional alpha diversity, with functionally similar and closely related species being replaced by functionally and phylogenetically more distinct species. Functional turnover between successional time steps was higher than expected, and higher than within-stage turnover, suggesting that differential environmental filtering has selected for different species traits in the different successional stages. Phylogenetic turnover did not differ significantly from random expectations, either within or between successional stages, and provided no insights into the temporal dynamics of the processes underlying community assembly.

CONTRASTING PATTERNS OF TEMPORAL CHANGE IN THE DIFFERENT FACETS OF DIVERSITY

Taxonomic, phylogenetic and functional alpha diversity all increased during succession but showed different temporal patterns of increase, indicating that the different facets of within-community diversity provide complementary information on successional changes in community composition

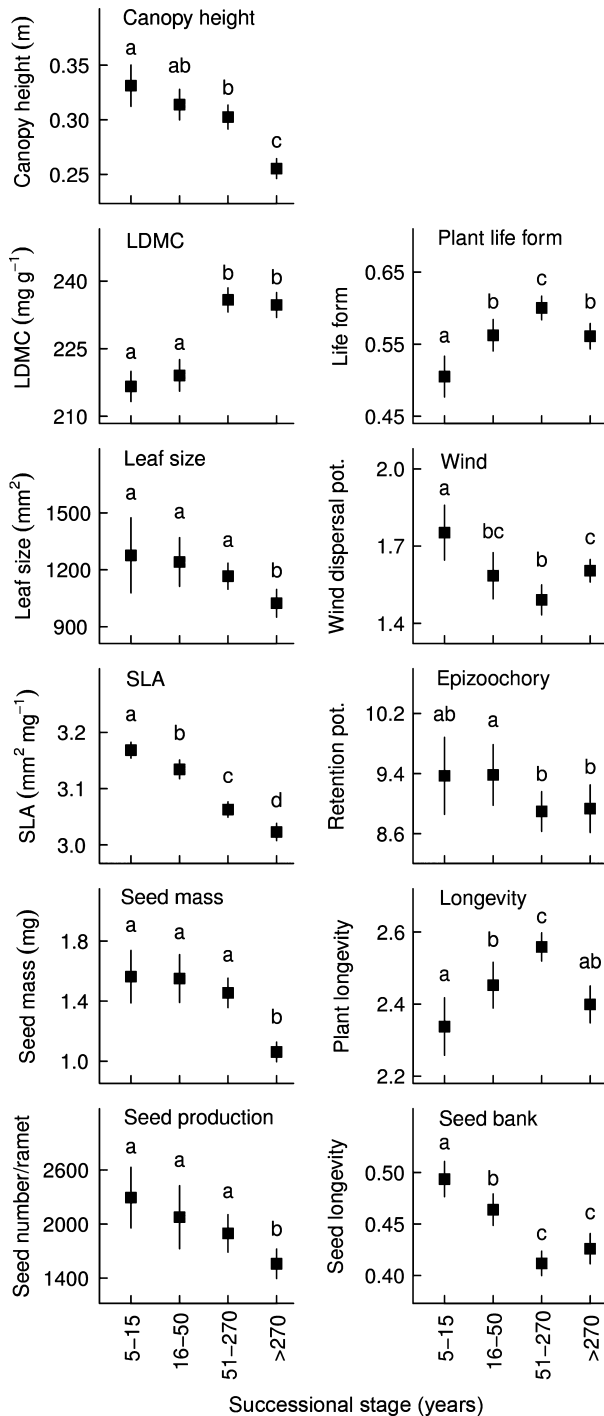


Fig. 4. Community-level mean values (mean \pm 1 SE) for the 11 plant functional traits that were used to calculate functional diversity within each of the four successional stages. Letters indicate significant differences ($\alpha = 0.05$) between the stages.

(Fig. 1). The number of species increased between the early and early-mid successional time steps (Fig. 1a). However, the absence of significant, concurrent increases in phylogenetic or functional alpha diversity (Fig. 1b,c) indicates that the increase in species richness between the early and early-mid successional stage mainly reflects the entry of closely related, and functionally similar, species. In contrast, there were no

significant changes in species richness between the late-mid time step and the last successional time step. Despite the lack of change in the number of species, significant increases in functional and phylogenetic diversity reveal that closely related and/or functionally similar species are replaced by functionally and phylogenetically more distinct species between the late-mid and late-successional stages (Römermann *et al.* 2009).

TEMPORAL CHANGES IN ASSEMBLY PROCESSES: THE RELATIVE IMPORTANCE OF ABIOTIC FILTERING DECREASES OVER TIME

Functional turnover between plots was higher than expected (functional clustering) within all successional stages, indicating that species co-occurring within communities were functionally more similar than predicted, given the levels of taxonomic diversity. The functional turnover between plots within each successional stage suggests that deterministic processes independent of the process of succession contribute to the species turnover between plots. However, levels of functional clustering were highest within the early and early-mid successional stages (Fig. 2a,b). The fact that the species within sites were functionally more similar to each other than to species from other sites during early and early-mid succession, may be explained by the effects of strong environmental filtering (Dinnage 2009; Helmus *et al.* 2010). Effects of large-scale disturbance and fertilization during arable cultivation have been shown to persist during the early stages of subsequent arable-to-grassland succession (Fraterrigo *et al.* 2005; Carbajo *et al.* 2011; Ceulemans *et al.* 2011), and the habitats of the early and early-mid successional communities in the present study were still characterized by a high proportion of bare soil (used as an indicator for disturbance in our study; Fig. S4). Previous agricultural disturbance regimes, such as ploughing, are likely to have acted as environmental filters which selected for ruderal (fast growing and disturbance-tolerant) species that produce large numbers of seeds (high SLA, canopy height and high seed production; Fig. 4; Marrs 1993; Dinnage 2009). At the same time, lower levels of interspecific competition in the less dense vegetation of the early and early-mid successional habitats may allow the coexistence of functionally similar species (*cf.* Dinnage 2009; Pakeman 2011). Our finding that the species occurring within the late-mid and late-successional grasslands are functionally more distinct than those in the early and early-mid successional communities suggests that, as succession proceeds, the relative importance of environmental filtering decreases. This finding agrees with the theoretical prediction (Connell & Slatyer 1977; Leibold *et al.* 2004) that the relative importance of the processes generating biodiversity after disturbance will change over time. Competitive exclusion of functionally similar species (MacArthur & Levins 1967; Grime 2006) may be expected to play a stronger role in community assembly as the grass sward becomes more dense and resources, such as phosphorus, become limiting in the old grasslands (Wardle *et al.* 2004; Lambers *et al.* 2008). The high levels of

functional diversity in the older grasslands are consistent with previous studies which conclude that, under conditions of resource limitation, plant communities tend to be comprised of species with complementary nutrient-acquisition strategies – allowing the exploitation of a wider range of the available resources (e.g. Tilman, Wedin & Knops 1996; Oelmann *et al.* 2011; MacDonald, Bennett & Taranu 2012).

The fact that the functional turnover between the earlier and late-successional stages was higher than the within-stage turnover (Fig. 3b) suggests that different environmental filtering processes govern community assembly at different successional stages, but may also be a reflection of species filtering based on dispersal traits (Purschke *et al.* 2012), with species that have high long-distance dispersal potential being favoured during early and early-mid succession (Fig. 4).

FUNCTIONAL AND PHYLOGENETIC DIVERSITY SHOW DIFFERENT PATTERNS OF DEVIATION FROM NULL EXPECTATIONS

There are at least three possible explanations for the fact that functional and phylogenetic diversity show different patterns of deviation from null expectations (Fig. 2). First, phylogenetic relationships may be a poor reflection of the species' ecological similarity if the traits under consideration are not phylogenetically conserved. Although nearly all traits in our study had higher than expected Blomberg's K values, K values were considerably lower than one (Table S4). The study by Hardy & Pavoine (2012) demonstrated that values of K can be biased downwards if information on intraspecific trait variation is not provided, and such data were not available in the present study. Nevertheless, the fact that most traits showed weak and non-significant phylogenetic signal throughout the phylogenetic tree (Fig. S3) suggests that closely related species are not functionally similar (see Fig. S1). Second, phylogenetic diversity may represent a more inclusive overall measure of ecological similarity than measures of functional diversity, which are based on a limited set of traits (Cadotte *et al.* 2009; Meynard *et al.* 2011). However, the fact that (i) most traits in our study showed a low phylogenetic signal and (ii) functional, but not phylogenetic, diversity showed significant deviations from random expectations, suggests that the traits that were used in our study are involved in the process of community assembly. Third, the finding that Π_{ST} and τ_{ST} values (phylogenetic and functional turnover) were similar within each successional stage, but Π_{ST} values for random communities had a larger confidence interval compared to τ_{ST} (Fig. 2a,b), suggests that the power to detect significant community structure is higher when using data on multiple traits than when using phylogenetic data.

Conclusions

Comparative analysis of taxonomic, phylogenetic and functional diversity within and between different stages during succession provides insights into the temporal dynamics of the processes that drive post-disturbance biodiversity changes.

Our results show that changes in functional and phylogenetic diversity over time differ from those shown by taxonomic diversity. Non-random patterns in functional turnover (both in space and time) indicate that, at the scale of our study, (i) ecosystem development after disturbance is driven by deterministic processes, and (ii) that there is a shift in the relative importance of filtering processes as succession proceeds, as has been predicted theoretically. Trait-mediated filtering plays an important role in community assembly during the early and early-mid stages of arable-to-grassland succession whereas the relative importance of competitive exclusion increases towards late succession. Phylogenetic diversity, often used as a proxy of functional diversity (Winter, Devictor & Schweiger 2012), did not contribute to inferences about underlying assembly processes. The finding that community assembly was deterministic with respect to traits, but not phylogeny, suggests that it may be possible to predict future changes in biodiversity and associated alterations in ecosystem functioning, based on species traits, but not phylogeny. Differences in the temporal patterns of change between different facets of biodiversity also suggest that assessments of biodiversity change after disturbance may be misleading if based on a single facet of diversity.

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Supporting Information

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

Appendix S1. Non-random structure in species frequencies.

Appendix S2. Node-level phylogenetic signal.

Table S1. Pearson's product-moment correlations (r) between the plant traits.

Table S2. Pearson's product-moment correlations (r) between taxonomic, phylogenetic and functional alpha diversity.

Table S3. Mantel correlations (r_M) between taxonomic, phylogenetic and functional beta diversity.

Table S4. Tree-wide phylogenetic signal (Blomberg's K) in each of the traits.

Figure S1. Distribution of the plant traits across the phylogeny of the 234 plant species.

Figure S2. Non-random structure in species frequencies.

Figure S3. Node-level phylogenetic signal.

Figure S4. Amount of bare soil (in %) within the four successional stages.