Research article

Spatial distribution of functional traits indicates small scale habitat filtering during early plant succession

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ABSTRACT

Two major theories on community assembly (habitat filtering and limiting similarity) predict contrasting patterns in the spatial distribution of plant species. The respective distribution of species functional traits has received much less attention but is essential to understand facilitative and competitive species interactions. Here we apply a recently developed technique for phylogenetic analysis to study the spatial distribution of major functional traits during seven years of primary plant succession at a re-established catchment in a German lignite mine. Habitat filtering induced a significant temporal trend towards underdispersed functional trait diversity leading to patches of functionally similar vegetation. This functional convergence was not mirrored by a respective trend towards species aggregation. Differences in soil pH and nitrogen content were positively correlated with respective differences in trait expression. Separate analyses of trait distribution for aggregated and segregated species revealed trait convergence in co-occurring and random patterns in spatially segregated species pairs except for leaf size showing a strong temporal tendency for trait convergence in spatially segregated species. Contrasting patterns of species co-occurrence did not translate into respective contrasts in trait distribution. We interpret the prevalence of random trait associations in spatially segregated species as an indication that species occurrence patterns alone are weak predictors of assembly mechanisms. Mechanistic inference of species co-occurrence needs to be accompanied by a detailed assessment of the patterns of functional trait assembly.

1. Introduction

Since the pioneering work of Clements (1916) and Gleason (1926) the change in species composition during plant succession has been in the centre of ecological interest (Weiher and Keddy, 1999; Götzenberger et al., 2012). Two largely contrasting theories try to describe this change in community structure: 1) habitat filtering (Maire et al., 2012) supposedly causes species of similar functional traits to jointly colonize sites due to similar environmental characteristics, 2) interspecific competition should counteract the co-occurrence of species with similar functional traits causing respective limiting trait similarity (Hutchinson, 1959; MacArthur and Levins, 1967).

Both theories of community assembly are essentially species centred. They focus on the spatial distribution and co-occurrence of species representing the basic units in ecology. In contrast, the spatial arrangement (the geometry) of species functional traits, and therefore

also the pattern of co-occurrence of these traits, has received much less attention. However, decisive geometry-shaping processes such as filtering and competition are mediated by functional traits and the spatial patterning of traits might even be stronger than the respective patterning of species. Further, trait composition systematically changes, particularly after disturbance or during succession (Prach et al., 1997). Consequently Ulrich et al. (2017) have advocated the analyses of the spatial arrangement of functional, life history, and morphological traits as being a promising approach to the understanding of community assembly.

Despite the common view that interspecific competition is an important driver of community assembly (Götzenberger et al., 2012) and a strong indication of species spatial segregation among local communities (Lyons et al., 2016), evidence supporting limiting similarity in functional traits and therefore the spatial segregation of traits is scarce (e.g. Abrams and Rueffler, 2009; Van Leeuwen and Etienne, 2013). In

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contrast, filter effects are well documented in animal (e.g. Barnagaud et al., 2014) and plant (Maire et al., 2012) communities and should lead to communities with more similar traits than expected from the respective effective species pool (Mayfield and Levine, 2010). Therefore the "limiting similarity" and "habitat filtering" theories predict contrasting patterns in the spatial distribution of functional traits.

Functional traits are supposed to react differentially to the processes that assemble plant communities in dependence on the intensity of environmental premises to which these traits respond. In this respect, the concept of plant interaction horizons is essential for the interpretation of the patterns of trait co-occurrence (Lasky et al., 2014). Interaction horizons demarcate the spatial extent within which plant species interact and possibly compete. Consequently we expect to see competitively induced trait segregation only within this horizon. Detecting spatially segregated traits would corroborate the idea of limiting similarity (Ulrich et al., 2017). In contrast, filter effects that cause trait aggregation might act within and above the interaction horizon. A comparison of trait geometry within and across the horizons might therefore allow a distinction to be made between the fundamental drivers of community assembly.

The variability of functional traits among local plant communities has been studied mainly within a phylogenetic framework centred on niche conservatism and filter processes (Grime, 2006; Wiens et al., 2010), particularly along ecological gradients (Cadotte et al., 2015; Símová et al., 2015). For instance, Kraft and Ackerly (2010) and Lasky et al. (2014) reported trait-associated niche partitioning (trait divergence) of tree species promoting co-existence in tropical forest communities. In contrast, Velázquez et al. (2015) found a positive association of tropical tree species functional traits and spatial distribution (trait convergence) indicating filter effects at small spatial scales. Respective studies on the distribution of functional traits (reviewed in Swenson, 2013) focused particularly on forest communities (Kraft et al., 2015; Kunstler et al., 2016) and compared trait spaces among communities. Thus, these approaches quantify the distribution of traits within a focal community but do not reveal the precise spatial geometry of traits as co-occurrence analysis does in the case of taxonomic units (Ulrich et al., 2017). Here we follow the approaches of Ulrich et al. (2012, 2017) and study the geometry of functional traits to assess how patterns of trait co-occurrence change during early plant succession. This analysis extends common comparisons of total functional trait spaces among habitats (Swenson, 2013) and pairwise comparisons of co-occurring species (Velázquez et al., 2015). It allows the identification of species characteristics that drive the formation and differentiation of ecological communities.

Applying the methodological framework of Ulrich et al. (2017) we study the geometry of functional traits during the early succession of vascular plants in a re-established catchment site at a partly decarburised open-pit mine (Zaplata et al., 2010, 2013). Previously we used these data to detect a temporal progression towards small and large-scale negative spatial species associations (Zaplata et al., 2013; Ulrich et al., 2016) and towards increased utilization of plant trait space (Ulrich et al., 2014a). We further detected variability in phylogenetic community composition at small spatial scales that could be traced back to important soil attributes (Ulrich et al., 2014b). As these studies demonstrated clear temporal trends in species co-occurrences, we here ask whether these trends are mirrored by respective non-random spatial distributions of important functional traits. With respect to our methodological approach our study is therefore based on three assumptions (Fig. 1).

First, spatial aggregation of functional traits indicates filter effects where species of similar life history and morphology jointly colonize appropriate patches. Second, the respective spatial segregation either indicates small scale soil heterogeneity or competitive effects. Third, comparisons of trait and soil variability allow the separation of soil and competitive effects as competition should segregate traits even at low soil variability while habitat induced trait segregation should correlate

with a respective variability in soil parameters (Fig. 1).

Given the prevalence of negative species associations at our study site (Ulrich et al., 2016) we hypothesize:

(1) A temporal trend towards spatial segregation of the traits under selective pressure (trait divergence) should be initiated by interspecific competition while respective neutral trends (not under selective pressure) should either be randomly distributed in space or be aggregated due to filter effects.
(2) Functional trait distribution of randomly colonizing pioneer species at the very beginning of succession should also be random in space.
(3) Small scale variability in soil properties should be mirrored in trait convergence within patches of similar environmental conditions and trait divergence among these patches.

2. Material and methods

2.1. Study area and sampling

From 2005–2011, we studied the early vegetation development in a relatively plane six ha (150 × 400 m) constructed catchment (*Chicken Creek*, German: Hühnerwasser), located (125–140 m a.s.l.) within the partly decarburised lignite mine Welzow Süd (51°36′N, 14°16′E) in NE Germany (Fig. 2). Sand and loamy sand material originating from Pleistocene sediments was used for the construction of the 1–3.5 m top layer of the catchment to cover a 1–1.5 m clay layer (details in Gerwin et al., 2011). This construction theme guaranteed that initial soil and microclimate conditions were comparable across the whole catchment (Gerwin et al., 2011; Zaplata et al., 2010, 2013).

A 20 m × 20 m grid net was established in October 2005, immediately after catchment construction ended on completion of the top layer. Within this grid, 119 25-m^2 cells (Fig. 2), and, in their corners, 474 single plots of 1-m^2 (Zaplata et al., 2010) were censused in terms of quality (species) and quantity (species cover). Vegetation first appeared in 2005 and was censured on 360 1-m^2 plots, and since 2006 annually on all plots and cells. The complete data of species abundances of all study years used in this study are already contained in Ulrich et al. (2016).

We used the Leda (Kleyer et al., 2008) and BioFlor (Klotz et al., 2002) databases and compiled a total of three plant life history (life span, speed of plant growth, seed weight), two genetic (DNA content, degree of polyploidy), two physiological (pH and nitrogen requirements), and two morphological (specific leaf area, canopy height) functional traits that might be important for colonisation during early succession (Schleicher et al., 2011; Sanaphre-Villanueva et al., 2017). 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). To assess the small scale variability in basic soil parameters during succession we used Ellenberg indicator values (Ellenberg et al., 1992) and calculated for each plot the annual average indices for pH and soil nitrogen from the respective indices of the plants present. We note that the twofold use of Ellenberg values (as species trait and, averaged over all species, as soil characteristics) might introduce a small degree of non-independence of data in analyses of species occurrences. Further, Ellenberg values might indicate changes in factors that actually did not change, but co-varied with factors that did change (Chytrý et al., 2009). Here we try to minimise these statistical pitfalls by using only two Ellenberg indicators of soil property, pH and nitrogen demand, that performed well in comparative tests (Schaffers and Sýkora, 2000). All species trait data used in the present study are contained in Ulrich et al. (2014b).

2.2. Analysis of community structure

We organized the trait, floristic, and environmental data in four types of matrices, a species × traits matrix **T**, an environmental