Beta diversity of plant species in human-transformed landscapes: Control of community assembly by regional productivity and historical connectivity

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ABSTRACT

Spatial variation in species composition ('beta diversity') is comprised of two components, spatial turnover and nestedness. Disentangling the drivers of each component allows a refined evaluation of the community assembly mechanisms that generate regional diversity patterns. This study examines how environmental sorting as well as past and present dispersal processes regulate spatial turnover and nestedness of plant species in human-transformed grassland landscapes, and whether the relative importance of these drivers varies among two landscapes with contrasting regional soil productivity. We found that nestedness always resulted from differences in historical connectivity to the characteristic species pool of pre-transformed calcareous grassland landscapes, irrespective of regional productivity. This was probably due to dispersal limitation of numerous species from this rich species pool under current landscape configuration and management, the absence of which cannot be compensated for by contemporary immigration rates in modern landscapes. By contrast, spatial turnover was driven by opposing mechanisms in nutrient-rich vs. nutrient-poor landscapes. In the landscape with low soil fertility due to phosphorous (P) limitation, spatial turnover was generated by variation in past and present dispersal processes. In the fertile landscape, species turnover was driven by environmental factors and increased mainly with differences in P and nitrate supply. The findings are consistent with theoretical considerations and empirical evidence from small-scale experiments that often find a reduced importance of dispersal at higher soil resource supply, showing that this pattern also manifests at the landscape scale. In summary, our study indicates that contrasting assembly mechanisms generate spatial compositional turnover in landscapes with contrasting soil conditions, which has significant implications for conservation and habitat restoration. It also demonstrates that detailed reconstructions of the land-use history of individual sites and their surroundings are critical for understanding beta diversity in human-transformed landscapes.

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1. Introduction

Understanding what causes site-to-site variation in species composition ('beta diversity') is a classic challenge in plant community ecology (Anderson et al., 2011; Jaccard, 1912; Socolar et al., 2016; Whittaker, 1960). Patterns of beta diversity are sensitive to a range of external drivers, including environmental variation (Chase, 2010; Tuomisto et al., 2003), dispersal limitation (Cadotte, 2006; Hubbell, 2001), and historical factors at different temporal scales (Dexter et al., 2012; Purschke et al., 2012). Disentangling their relative importance can therefore generate significant insights into the local and regional controls over community assembly (Cottenie, 2005; Myers et al., 2013).

Inference of ecological processes from patterns of beta diversity has been limited by the fact that identical values of beta diversity can derive from two different components: (i) spatial turnover of species, i.e. the replacement of species from site to site, and (ii) nestedness, i.e. the species composition of one site is a subset of that of another site (Harrison et al., 1992; Legendre, 2014). This limits inference from beta diversity in two important ways: First, it remains unknown which of the two components contributes more

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to compositional dissimilarity among communities. Second, external drivers might influence either spatial turnover or nestedness, or both but with different effect sizes. A better understanding of how ecological or anthropogenic drivers control the two components of beta diversity would thus substantially advance community assembly models. Recently, methods have been developed that additively partition popular indices of compositional dissimilarity into their turnover and nestedness components (Baselga, 2010, 2012). These can then separately be modelled as a function of environmental, spatial or historical variables to shed more light on the mechanisms that generate spatial variation in community composition (e.g. Svenning et al., 2011).

Here, we use this approach to investigate mechanisms of plant community assembly in two human-transformed calcareous grassland landscapes with contrasting soil productivity. Specifically, we explore the role of local environmental conditions, as well as present and historical dispersal processes as drivers of community assembly, and whether their relative importance varies among two landscapes with contrasting soil productivity. In Europe, semi-natural calcareous grasslands expanded markedly in the bronze age and during the medieval period as a consequence of pastoral land use (Poschlod and WallisDeVries, 2002). Land-use change during the early 20th century led to strong habitat loss and fragmentation of the grassland landscapes. Today, only few historically old grassland patches remain (most of them within nature reserves or military sites), which often contain the most unique and species-rich communities (Dengler et al., 2014; Wilson et al., 2012). Together with younger grasslands recovering from interim agricultural land use, they form environmentally heterogeneous metacommunities with variable present and historical connectivity. Such a combination of old and young patches with different habitat quality is a feature of most human-transformed landscapes, and regional dynamics involve both old and young patches that together can potentially contribute to species' persistence at the landscape scale (Hobbs et al., 2014; Mendenhall et al., 2014). Understanding the mechanisms generating site-to-site variation in species composition in such landscapes is thus fundamental for guiding conservation and restoration.

Based on metacommunity theory (Leibold et al., 2004), which provides a conceptual framework for the interpretation of beta diversity patterns (Chase and Myers, 2011; Cottenie, 2005; Myers et al., 2013), and the specific empirical evidence for historical drivers of community structure in fragmented landscapes, we evaluated the following hypotheses about how beta diversity and its components are generated:

1) Environmental sorting

Differences in local community structure are determined by interspecific differences in resource requirements and physiological tolerance limits that confine species to certain sections of environmental gradients. Hence, beta diversity is explained by environmental variation in this scenario (Chase and Myers, 2011). In human-transformed landscapes, environmental sorting might be an important driver of community structure because habitat patches often differ in soil properties due to contrasting land-use histories (Conradi and Kollmann, 2016; Freschet et al., 2013; Verheyen et al., 1999). In the environmental sorting scenario, environmental variation can produce nestedness when soil gradients reach into marginal habitats where only a subset of species can survive. Alternatively, high resource availability may lead to competitive displacement of many species by a subset of few competitive species, thus resulting in nestedness (Harpole and Tilman, 2007). Finally, when environmental sorting is important, nestedness might also result from variation in soil spatial heterogeneity because of the contrasting numbers of niches provided (Adler et al.,

2013; Tilman, 1982). However, environmental sorting can also produce spatial turnover when different species replace each other along environmental gradients.

2) Dispersal-driven assembly

Differences in local community structure result from dispersal limitation (Hubbell, 2001). Hence, beta diversity is related to variation in landscape spatial configuration and factors that influence colonization probabilities such as patch size (MacArthur and Wilson, 1967), habitat connectivity (Hanski, 1998), or edge effects (Tscharntke et al., 2012). Dispersal assembly can result in nestedness when some species are dispersal-limited and others do not compensate for their absence. In human-transformed landscapes, this might result from the limited capability of the species-poor, intensively used agricultural matrix to provide colonists. If dispersal-limited species are replaced by others, dispersal assembly will result in spatial turnover.

3) Historical contingency

A special case of dispersal assembly in which variation in local community structure is explained by past dispersal processes. Previous investigations of alpha and beta diversity in fragmented landscapes showed diversity patterns often reflect past rather than present habitat connectivity (Conradi and Kollmann, 2016; Helm et al., 2006; Lindborg and Eriksson, 2004; Purschke et al., 2012). Hence, in this scenario, beta diversity is related to historical variation in landscape configuration. Mechanisms leading to nestedness and turnover are similar to the dispersal-driven assembly scenario, with the exception that the dispersal processes happened in the past and are no longer occurring in the contemporary landscape.

4) Contrasting assembly mechanisms in regions with productive vs. marginal soils

Seed addition experiments in grasslands showed that effects of dispersal on community structure decline with increasing plant productivity (Foster, 2001; Myers and Harms, 2009). Because plant productivity itself is most strongly driven by soil fertility in grasslands (Grace et al., 2016), we hypothesized that this pattern observed in experiments would also manifest at the landscape level, so that (historical) dispersal assembly should be more important for beta diversity in landscapes with low soil fertility as compared to landscapes with higher soil resource supply, where environmental sorting should be the main driver of community assembly.

2. Methods

2.1. Study system and areas

To disentangle the drivers of beta diversity in human-transformed landscapes, we studied plant species composition, abiotic site conditions, as well as current and historical landscape context of in total 33 old (>514 years as per 2014) and young (16–174 years; see reconstruction of age below) calcareous grasslands in two geographically separated study areas, the Lech River Valley (LRV; 48°15′ N, 10°54′ E) and the Munich Gravel Plain (MGP; 48°15′ N, 11°37′ E) in southern Germany. Data on the young grasslands are also used within a related study (Conradi and Kollmann, 2016) focusing on functional trait composition and species richness patterns.

The climate in both study areas is temperate and humid with an annual rainfall of ca. 835 mm and ca. 8.5 °C mean annual tem-