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Plant community assembly at small scales: Spatial vs. environmental factors in a European grassland

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ABSTRACT

Dispersal limitation and environmental conditions are crucial drivers of plant species distribution and establishment. As these factors operate at different spatial scales, we asked: Do the environmental factors known to determine community assembly at broad scales operate at fine scales (few meters)? How much do these factors account for community variation at fine scales? In which way do biotic and abiotic interactions drive changes in species composition?

We surveyed the plant community within a dry grassland along a very steep gradient of soil characteristics like pH and nutrients. We used a spatially explicit sampling design, based on three replicated macroplots of 15×15, 12×12 and 12×12 m in extent. Soil samples were taken to quantify several soil properties (carbon, nitrogen, plant available phosphorus, pH, water content and dehydrogenase activity as a proxy for overall microbial activity). We performed variance partitioning to assess the effect of these variables on plant composition and statistically controlled for spatial autocorrelation via eigenvector mapping. We also applied null model analysis to test for non-random patterns in species co-occurrence using randomization schemes that account for patterns expected under species interactions.

At a fine spatial scale, environmental factors explained 18% of variation when controlling for spatial autocorrelation in the distribution of plant species, whereas purely spatial processes accounted for 14% variation. Null model analysis showed that species spatially segregated in a non-random way and these spatial patterns could be due to a combination of environmental filtering and biotic interactions. Our grassland study suggests that environmental factors found to be directly relevant in broad scale studies are present also at small scales, but are supplemented by spatial processes and more direct interactions like competition.

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1. Introduction

Plant community assembly is significantly driven by processes on several scales, like competition (Aarssen, 1989), dispersal limitation (Ai et al., 2012) and environmental conditions (Latimer and Jacobs, 2012). Understanding the processes involved in the assembly of communities is considered one of the most important challenges in ecology today (HilleRisLambers et al., 2012; O'Neill, 1989; Turner and O'Neill, 1995). While the understanding of community assembly has advanced significantly within the last 50 years, ecologists still lack precise insight on how the interplay of organisms and their environment determines the structure of natural communities (Götzenberger et al., 2012; Naaf and Wulf, 2012).

One common idea in ecology about the assembly of a diverse community involves filtering by the environment and interactions of organisms that establish local populations. This led to the niche-partitioning concept (Leibold, 1995; Silva and Batalha, 2011), where assemblages of species are viewed as having different tolerances to the abiotic environment and differing abilities to exploit resources.

With the rise of neutral theory (Hubbell, 2001; Rosindell et al., 2012), the debate on the processes influencing biodiversity was reinvigorated and the search for a unified theory has dominated the field (Adler et al., 2007). It has been suggested that the combination of investigating both local and short-term mechanisms as well as regional processes occurring over longer timescales may be crucial for a complete understanding of ecosystem assembly and function (HilleRisLambers et al., 2012).

Grasslands cover one fourth of the Earth's land surface and harbour the majority of annual plant diversity (Shantz, 1954). A significant amount of studies on grassland ecosystems are focused on the influence of soil characteristics on plant community composition (Wellstein et al., 2007), which, together with water, wind and sunlight, represents the bulk of abiotic influences on a plant community (Callaway, 1997; Parfitt et al., 2010). Soil characteristics can be strong predictors of plant community composition (Gough et al., 2000; Tilman and Olff, 1991), although the scale of the studies influences the predictive power of soil parameters like pH, carbon, nitrogen or phosphorus content (Sebastiá, 2004). But not only abiotic factors are influenced by the scale of a study; positive and negative interspecies associations can occur at small scales and disappear with increasing scale (Wiegand et al., 2012).

In this study we aimed at increasing the understanding of scale-dependence in community patterns by analysing the plant community composition of a semi-natural grassland (Leibold et al., 2004). While a lot of studies on grasslands are trying to approach community composition mechanisms by inferring local interactions via the observation of larger-scale composition (Eckhardt et al., 1996; Thomas and Palmer, 2007; Toogood et al., 2008), we were aiming at understanding these processes by looking for patterns of species composition that could be either deterministically or stochastically structured while choosing the smallest local community possible: a single focal plant and its direct rhizosphere interaction partners, making the community unit as small and replicable as possible. Other small-scale studies have dealt with similar grain sizes like ours (Chu et al., 2007; Reitalu et al., 2009; Turtureanu et al., 2014), however, they do not approach single plants with their rhizosphere environment or combine small grain and extent. We consider the single plant rhizosphere environment a community, implicitly embodying the idea of interactions of plants with the environment and each other.

Our study area offers unique possibilities of studying steep environmental gradients within only a few meters in very species-rich grassland which also harbours one highly abundant plant species, enabling us to observe potential environmental filtering as well as spatial processes and biotic interactions in a spatially well-defined small-scale area. We selected this plant species, namely *Festuca brevipila* R. TRACEY (Aiken and Darbyshire, 1990; Klotz et al., 2002), as our focal plant to be able to target the whole gradient of environmental conditions which our study area offers, and still be able to standardize the community perspective on one species. We used patterns of co-variation among plant species, environmental and spatial variables derived from a neighbour matrix to answer the following questions: i) Do the environmental factors, specifically soil properties, that are known to determine community assembly at broad scales also operate at fine scales (1–15 m) and how much do these factors account for community variation at fine scales? ii) In which way do biotic and abiotic factors drive changes in species composition? Our questions involve the disentanglement of patterns at various small scales, which calls for tools able to quantify the contributions of environmental and spatial patterns plus their shared effect. We therefore applied state-of-the-art multivariate analysis (Borcard et al., 1992; Dray et al., 2006) to test our hypotheses and contrast patterns due to environmental variables with spatial patterns potentially due to biotic

interactions (e.g. segregation caused by competition) and/or dispersal dynamics. Large-scale environmental effects that determine plant community structure in a range from a few to several hundred kilometres, include climatic gradients (Ludewig et al., 2014), altitudinal changes (Krömer et al., 2013) or differences in soil biogeochemistry (Khan et al., 2013). At the small scale of our study we focused on soil since this is the only variable forming gradients at such scales. Although our sampling design captured strong gradients in soil variables, we expected a relatively smaller influence of environmental variables on our plant communities in comparison to larger scaled studies, because biotic interactions or neutral-like effects could outweigh environmental drivers at the small scale of our study.

2. Materials and methods

2.1. Data collection

The grassland studied is situated in a natural reserve (Mallnow Lebus, Brandenburg, Germany, 52°27.778′ N, 14°29.349′ E). The region is influenced by sub-continental climate with a mean annual precipitation of below 500 mm (Ristow et al., 2011) and the area is managed by sheep grazing twice a year. The sampling strategy was based on a hierarchical nesting of macroplots and plots, and was done at the end of June 2011 to minimize influences by spring ephemerals. Three macroplots of 15×15, 12×12 and 12×12 m, respectively (Fig. 1), were located on the slopes of hills in an area of about 5 ha. We found only minor traces of sheep trails which indicate a low grazing pressure on our macroplots, likely due to the strong slope. We ensured that all macroplots were part of two closely related grassland communities found in Mallnow, namely *Sileno otitae-Festucetum-brevipilae* Libbert 1933 corr. Kratzert and Dengler, 1999 and *Festuco psammophilae-Koelerietum glaucae* Klika 1931. Our macroplots were comparable concerning vegetation and soil related factors like distance from trees, stone content or depth of A-horizon, as well as slope and sun exposure, and therefore can be considered a replicated design. The uphill–downhill axes of the macroplots are characterized by a steep textural gradient from highly sandy (downhill macroplot) to sandy-loamy (uphill macroplot) soils. Preliminary analyses revealed that this gradient causes gradients in many other soil parameters, namely pH, carbon, nitrogen and plant available phosphorus. Each macroplot was divided into 3×3 m plots (Fig. 1). From each macroplot the vegetation of the four corner plots (top left, top right, bottom left, bottom right) was sampled: For the measurement of soil properties one soil core per plant was taken atop of five randomly chosen *F. brevipila* plants per plot, creating 60 samples in total. In a radius of 15 cm around the chosen *F. brevipila* plant, the local plant community was assessed visually as presence or absence of plant species. This sampling unit represents our main community unit and below we refer to it as "sample". With regard to the smallest sampling unit ("sample"), the 15 cm radius ensures that interactions within the rhizosphere of *F. brevipila* plants were captured. We preferred this method to a totally random location of the sampling units (i.e. not having a focal species) for the following mutually reinforcing reasons: a random location would have been strongly biased towards *F. brevipila* in a non-controlled way because *F. brevipila* is by far the most abundant species in the area (in some case the species can cover up to 70% of one plot); by controlling for this critical source of certain bias, we could minimise possible very small scale environmental heterogeneity that could confound the interpretation of co-occurrence analysis based on null models (see methods below) and the comparison between null models and multivariate analyses based on RDA; the plant assemblage can be objectively defined at a biologically meaningful small scale (i.e. rhizosphere) as the neighbourhood