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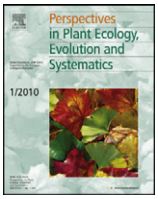

Research article

A functional trait-based approach to understand community assembly and diversity–productivity relationships over 7 years in experimental grasslands

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ABSTRACT

Several multi-year biodiversity experiments have shown positive species richness–productivity relationships which strengthen over time, but the mechanisms which control productivity are not well understood. We used experimental grasslands (Jena Experiment) with mixtures containing different numbers of species (4, 8, 16 and 60) and plant functional groups (1–4; grasses, legumes, small herbs, tall herbs) to explore patterns of variation in functional trait composition as well as climatic variables as predictors for community biomass production across several years (from 2003 to 2009). Over this time span, high community mean trait values shifted from the dominance of trait values associated with fast growth to trait values suggesting a conservation of growth-related resources and successful reproduction. Increasing between-community convergence in means of several productivity-related traits indicated that environmental filtering and exclusion of competitively weaker species played a role during community assembly. A general trend for increasing functional trait diversity within and convergence among communities suggested niche differentiation through limiting similarity in the longer term and that similar mechanisms operated in communities sown with different diversity. Community biomass production was primarily explained by a few key mean traits (tall growth, large seed mass and leaf nitrogen concentration) and to a smaller extent by functional diversity in nitrogen acquisition strategies, functional richness in multiple traits and functional evenness in light-acquisition traits. Increasing species richness, presence of an exceptionally productive legume species (*Onobrychis viciifolia*) and climatic variables explained an additional proportion of variation in community biomass. In general, community biomass production decreased through time, but communities with higher functional richness in multiple traits had high productivities over several years. Our results suggest that assembly processes within communities with an artificially maintained species composition maximize functional diversity through niche differentiation and exclusion of weaker competitors, thereby maintaining their potential for high productivity.

Introduction

A number of biodiversity experiments have shown that positive species richness–productivity relationships strengthen through time (Cardinale et al., 2007; Fargione et al., 2007; Marquard et al., 2009; van Ruijven and Berendse, 2009), but the mechanisms which control community productivity in the longer term are not well understood. Meta-analyses of time series and across different biodiversity experiments have suggested that increasing interspecific complementarity in niche use or facilitation among species, diversity-related effects on element cycling and biotic interactions in addition to the contribution of particularly productive species may explain long-term positive plant diversity effects on productivity (Cardinale et al., 2007, 2011; Reich et al., 2012)

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So far, most studies of biodiversity–ecosystem functioning relationships have focused on species richness as predictor variable, although there is increasing evidence that functionally important aspects of biodiversity are better represented through the presence, abundance, diversity and distribution of relevant plant functional attributes within species assemblages (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Reiss et al., 2009). A crucial issue in functional community ecology is which components of functional trait composition determine ecosystem properties (Díaz et al., 2007). A larger functional dissimilarity among plant species is likely to increase the diversity in strategies of resource acquisition and use and to decrease species overlap along niche axes. In contrast, the prominent influence of particular species on ecosystem properties might be attributable to particular functional characteristics that allow them to capture a greater proportion of available resources than other species. Recent studies in experimental plant communities have shown that functional trait diversity promotes primary productivity (Petchey et al., 2004; Cadotte et al., 2009; Flynn et al., 2011; Mouillot et al., 2011). When functional trait composition as functional trait diversity and dominant trait values (i.e. community mean traits) were considered, the combination of both components were identified as valuable predictors for primary productivity (Mouillot et al., 2011; Roscher et al., 2012). In semi-natural grassland systems, environmental conditions such as fertilization have large effects on community mean traits, which in turn correlate with levels of productivity, but functional trait diversity has additional positive effects on primary productivity (Díaz et al., 2007; Mokany et al., 2008; Schumacher and Roscher, 2009).

Functional trait composition is the result of community assembly processes (Weiher and Keddy, 1995; Grime, 2006). Environmental filtering, i.e., abiotic control, favors high abundances of species with ecological characteristics which are optimal for a particular local environment. Therefore, environmental filtering is expected to decrease within-community functional trait differentiation and lead to trait convergence among communities (Mouillot et al., 2007; Chase, 2010). In contrast, biotic forces may differently affect the functional relatedness among species in plant communities. Niche differentiation through resource competition (limiting similarity; MacArthur and Levins, 1967) is likely to increase within-community functional trait differentiation. But competition may also limit the coexistence between functionally dissimilar species by excluding species with trait combinations associated with low competitive abilities (Grime, 2006; Mayfield and Levine, 2010). Functional trait spectra may provide an integrated view of ecological differentiation among plant species. Plant traits differ in their association with different ecological processes, reflecting trade-offs in functional requirements which affect species performance in terms of survival, growth and reproduction (Suding et al., 2003). Communities may be simultaneously constrained by abiotic and biotic forces, thus requiring the evaluation of patterns in functional traits associated with multiple assembly processes (Weiher et al., 2011; Spasojevic and Suding, 2012). For instance, it has been shown that productivity-related plant traits converge due to environmental filtering and equalizing fitness processes, while traits associated with regeneration diverge due to greater diversity in opportunities for establishment, growth and reproduction in natural grasslands (Grime, 2006).

The present study was carried out in a regularly mown multi-year grassland biodiversity experiment (Jena Experiment; Roscher et al., 2004), containing 50 mixtures sown with different species richness (4, 8, 16, and 60) and functional group number and composition (1–4; legumes, grasses, small herbs, tall herbs), where a previous study has shown that positive plant diversity effects on community biomass production increase through time (Marquard et al., 2009). Functional traits associated with the acquisition of light and nitrogen, probably the most critical resources limiting productivity in temperate grasslands, and attributes characterizing establishment, growth and regeneration were used to assess community mean traits (=CMTs, Garnier et al., 2004) and indices of functional trait diversity (Mason et al., 2005), their within- and between-community variations and relationships to community biomass production over several years. We tested the following hypotheses: (1) Community mean traits indicating fast growth and exploitation of growth-related resources are replaced by trait values suggesting a conservation of growth-related resources over several years. (2) Community mean traits indicating species' abilities to complete their life cycle and re-establish from seeds increase over several years. (3) Environmental filtering and competitive ability differences increase between-community convergence in means of productivity-related traits throughout the experiment. (4) Evolving species interactions which are in favor of complementary resource use and diverse strategies of establishment, growth and regeneration lead to an increase and between-community convergence in functional trait diversity over several years. (5) Community means of productivity-related traits, i.e., the dominance of a species or species group with particular trait values, have a large impact in explaining community biomass production, while effects of functional trait diversity mainly explain mixture productivity increase over time.

Materials and methods

Experimental design

The study is part of a long-term biodiversity experiment (Jena Experiment; Roscher et al., 2004) established in May 2002 in the floodplain of the river Saale near to Jena (Thuringia, Germany, 50°55′ N, 11°35′ E, 130 m a.s.l.). Mean annual air temperature in the region is 9.3 °C and annual precipitation is 587 mm (Kluge and Müller-Westermeier, 2000). The field site was used as highly fertilized agricultural land for at least four decades prior to the establishment of the biodiversity experiment. The soil is an Eutric Fluvisol developed from up to 2 m-thick loamy fluvial sediments. A gradient in soil characteristics, mainly represented by variation in soil texture from sandy loam near the river to silty clay with increasing distance from the river, is due to the fluvial dynamics of the Saale river.

The study system is based on the species composition of Central European mesophilic grasslands (Arrhenatherion community; Ellenberg, 1988), traditionally used as hay meadows. A pool of 60 plant species was chosen and a literature-derived plant-trait matrix comprising morphological and phenological species characteristics as well as N_2 fixation ability served to classify plant species into four functional groups: 16 grasses, 12 legumes, 12 small herbs and 20 tall herbs (Roscher et al., 2004). The experimental design is near-orthogonal whereby the factors species richness (1, 2, 4, 8, and 16) and functional group number (1, 2, 3, and 4) vary as independently as possible with the restriction that plant functional group number cannot exceed species richness in a given mixture. Each species-richness level had 16 replicates with exception of the 16-species communities because there were not enough species to create pure legume and small-herb species mixtures at this species-richness level. Species composition for each species richness × functional group number combination was chosen by random draws with replacement from the respective plant functional groups. In addition, mixtures of all 60 species were established with four replicates, resulting in a total of 82 plots of 20 m × 20 m size. We included a subset of 50 large plots sown with 4, 8, 16 or 60 species in the present analyses.