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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 vicifolia*) 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.

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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 N₂ 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.

All experimental species were also grown in replicated monocultures of 3.5 m × 3.5 m size. Plots were arranged in four experimental blocks parallel to the river to account for the gradient in soil texture. Each block contained an even number of large plots per species-richness level and small monoculture plots per functional group. Seeds were sown with an initial density of 1000 viable seeds per m² as indicated by the individual germination rates of the species determined in prior germination trials (Roscher et al., 2004). Seeds were equally distributed among species to achieve a constant total sowing density in mixtures.

The sown species combinations were maintained by weeding twice per year (April, July). All plots were mown twice a year (early June and September) and the mown plant material was removed according to the traditional management of hay meadows in the study region. No fertilizer was applied during the experiment.

Data collection

Aboveground biomass and species abundances

Aboveground biomass production was estimated by cutting plants 3 cm above soil surface in four (or three) randomly placed rectangles of 0.5 m × 0.2 m in all large plots at estimated peak biomass shortly before first mowing (late May). Plant material was sorted to sown species, weeds and detached dead plant material. Samples were dried for 48 h (70 °C) and weighed. Community biomass per harvest (2003–2009) was calculated as the mean of all samples per plot. The abundance of individual species was estimated visually as cover on an area of 3 m × 3 m size, using a decimal scale (Londo, 1976) just before biomass harvesting. Numerical values for species cover were coded as 0.5 (<1%), 3 (1–5%), 10 (6–15%), 20 (16–25%), 30 (26–35%), 40 (36–45%), 50 (46–55%), 60 (56–65%), 70 (66–75%), 80 (76–85%), and 90 (>85%). In 2003 and 2004, cover values were based on two subplots of 2.00 m × 2.25 m size that were pooled. For details and data see Weigelt et al. (2010).

Trait data

Plant trait data were derived from measurements in monocultures in May 2006 (corresponding to the time of biomass harvest), except for six species which were studied in May 2008 or 2009: *Anthriscus sylvestris* (L.) Hoffm., *Bromus hordeaceus* L., *Cynosurus cristatus* L., *Holcus lanatus* L., *Pastinaca sativa* L., and *Sanguisorba officinalis* L. Trait data for three species either extinct in their monocultures (*Cardamine pratensis* L.) or not abundant enough for sampling (*Campanula patula* L., *Luzula campestris* (L.) DC.) were collected in a low-diversity mixture containing these species. Single shoots served as basic unit for all measurements because the ability of many grassland species to grow with below- or aboveground runners impedes the identification of plant individuals (genets) in dense vegetation. Transects excluding the outer 70 cm of the plots were installed for sampling. After intervals of 25 cm, shoots rooting closest to these points were chosen along the transects and cut off at the ground level, until five to seven shoots per species were sampled. Shoots were put into sealed plastic bags to prevent dehydration and stored in a cool box. In the laboratory, stretched shoot length was measured before shoots were separated into compartments: stems (including leaf sheaths in case of grasses and secondary axes in case of herbs), leaves (being leaf blades in case of grasses and including petioles and rachis in case of forbs with compound leaves) and reproductive parts (flowers and fruits). Three to five fully expanded leaves (leaf blades in case of grasses) from the upper shoot part were selected for leaf area determination using a leaf area meter (LI-3100 Area Meter, Li-COR, Lincoln, USA). Plant material was dried for 48 h at 70 °C and weighed. Samples of measured leaves and residual plant compartments for each species, were pooled per plot and ground with a ball mill. Nitrogen ($\delta^{15}\text{N}$)

and carbon ($\delta^{13}\text{C}$) isotope ratios were measured from leaf material with an isotope-ratio mass spectrometer (IRMS, Delta^{plus} XP and Delta C prototype Finnigan MAT respectively, Bremen, Germany); sample ratios of $^{15}\text{N}/^{14}\text{N}$ are given relative to the international standard for atmospheric N₂, and sample ratios of $^{13}\text{C}/^{12}\text{C}$ refer to the VPDB standard for C. The residual plant compartments were analyzed for carbon and nitrogen concentrations with an elemental analyzer (Vario EL Element Analyzer, Elementar, Hanau, Germany).

Seedling density (plant individuals with cotyledons) was estimated in all small monocultures three times (April, July, October) in 2007 to account for species-specific differences of seedling emergence. Each time, three quadrats of 30 cm × 30 cm size were randomly placed to count all available seedlings of the respective species. Total numbers of emerged seedlings per m² were calculated for each monoculture based on pooled data from all census dates, although it is not possible to completely rule out the possibility that further seedlings appeared in between (underestimation of seedling densities) or that seedlings persevered for a longer period in this stage (overestimation of seedling densities). Average seed mass was taken from Roscher et al. (2004) where seed material purchased from commercial suppliers (Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany) and used for the establishment of the biodiversity experiment was weighed in 5 batches of 50 seeds per species.

Additional data, which were not available from own measurements such as root morphology and life-history characteristics, were compiled from literature (Kutschera and Lichtenegger, 1982, 1992; Rothmaler, 2002) as categorical variables. For an overview of all plant trait data see Table 1.

Climatic variables

Air temperature (HMP35D Humidity/Temperature Sensor, Vantaa, Vaisala, Finland) at 2 m height and precipitation (Precipitation Transmitter, Thies GmbH, Göttingen, Germany) were measured at a central weather station at the field site and stored with a datalogger (CR23X, Campbell Scientific, Logan, USA). The following climatic variables relevant for plant growth during the growing season (Woodward, 1987) until estimated peak biomass before first mowing (March–May) were derived for each study year: (1) mean air temperature (°C), (2) sum of precipitation (mm), (3) growing degree days (=sum of degrees by which each days' mean air temperature ≥ 5 °C, (°C)), and (4) first growing degree day (mean air temperature ≥ 5 °C, (°C)), derived by using fitted values from a local polynomial fit, to define the starting point of the growing season (Cleveland, 1979, 1981). Local polynomial regressions (parameter $\alpha = 0.75$ controlling the degree of smoothing) were performed using R software (version R2.11.1, R Development Core Team, <http://www.R-project.org>; function "loess", <http://127.0.0.1:11391/library/stats/html/loess.html>).

Data analyses

Calculation of trait-based measures of functional diversity and community mean traits

Community mean traits (CMTs) were calculated separately for each of the 18 candidate traits (Table 1) by weighting the trait values of a species i (t_i) by its proportional abundance (p_i) in the community derived from species cover estimates for each study year, as

$$\text{CMT} = \sum_{i=1}^S p_i t_i, \quad (1)$$

where S is the number of species (Garnier et al., 2004).

Table 1
Overview of plant traits used in analyses.

Variable	Type of variable	Source
Light acquisition (light)		
Shoot length	Continuous (cm)	Measurement
Stem mass fraction	Continuous ($\text{mg}_{\text{stem}} \text{mg}_{\text{shoot}}^{-1}$)	Measurement
Specific leaf area	Continuous ($\text{mm}^2_{\text{leaf}} \text{mg}_{\text{leaf}}^{-1}$)	Measurement
Leaf distribution	Ordinal: (0) whole phytomass near the ground (rosette), (1) main part of phytomass near ground, but minor part along the stem, and (2) equal parts of phytomass near the ground and along the stem	Literature
Foliar $\delta^{13}\text{C}$	Continuous (‰)	Measurement
Nitrogen acquisition and use (nitrogen)		
Leaf nitrogen concentration	Continuous ($\text{mg N g}_{\text{leaf}}^{-1}$)	Measurement
Biomass:N ratio	Continuous ($\text{g}_{\text{dw}} (\text{g N})^{-1}$)	Measurement
Foliar $\delta^{15}\text{N}$	Continuous (‰)	Measurement
Type of the root system	Ordinal: (1) long-living primary root system (beet- or stake-like taproots), (2) secondary fibrous roots in addition to the primary root system, and (3) short-living primary root system, extensive secondary root system	Literature
Depth of the root system	Ordinal: (1) up to 20 cm, (2) up to 40 cm, (3) up to 60 cm, (4) up to 100 cm, and (5) >100 cm	Literature
Establishment, growth and regeneration (life history)		
Life cycle	Ordinal: (1) annual, (2) biennial or monocarpic perennial, and (3) perennial	Literature
Clonal growth	Ordinal: (0) no clonal growth and (1) clonal growth	Literature
Seasonality of foliage	Ordinal: (1) deciduous, (2) partly deciduous (most foliage dies off in winter), and (3) evergreen (all-season with foliage)	Literature
Start of flowering period	Ordinal: (1) before May, (2) May, (3) June, and (4) July	Literature
Duration of flowering period	Ordinal: (1) two months or less, (2) three months, (3) four months, and (4) more than 4 months	Literature
Inflorescence mass fraction	Continuous ($\text{mg}_{\text{inflorescence}} \text{mg}_{\text{shoot}}^{-1}$)	Measurement
Seed mass	Continuous (mg)	Measurement
Seedling number	Continuous (m^{-2})	Measurement

Functional trait diversity (FD_Q) using Rao's quadratic entropy (Rao, 1982) was computed as

$$\text{FD}_Q = \sum_{i=1}^S \sum_{j=1}^S p_i p_j d_{ij}, \quad (2)$$

where p_i is the proportion of i th species in the community, d_{ij} is the pair-wise trait dissimilarity of species i and j , and S is the number of species. Thus, FD_Q is the sum of the dissimilarities among all possible pairs of species in the trait space weighted by the product of species relative abundances. Recently, Mason et al. (2005) identified three complementary components of functional diversity, which have been shown to be rather independent from each other (Mouchet et al., 2010). (1) Functional richness (FRic) represents the amount of functional trait space filled by a community (Villéger et al., 2008). It is expressed as the smallest convex set (=minimum convex hull) enclosing the volume of the n -dimensional trait space occupied by the species in a community (Cornwell et al., 2006). (2) Functional evenness (FEve) describes the regularity by which the n -dimensional functional trait space is filled by species weighted by their abundances and was based on the minimum spanning tree. It is an estimate of the minimum sum of branch length of all points contained in the n -dimensional trait space (Villéger et al., 2008). (3) Functional divergence (FDiv) assesses how abundance-weighted species diverge from the center of gravity in the volume of the n -dimensional trait space (Villéger et al., 2008). Calculations of functional diversity indices were based on the principal coordinate analysis (PCoA) axes from a Gower dissimilarity matrix (Gower, 1971) to account for different trait data types (continuous, ordinal) (Laliberté and Legendre, 2010). All traits were equally weighted and either summarized to a matrix comprising all candidate traits or grouped into separate matrices according to their association with light acquisition, nitrogen acquisition and use or establishment, growth and regeneration (see Table 1). To avoid the loss of information due to the reduction of trait axes, all analyses were restricted to mixtures containing 4, 8, 16 and 60 species (in total 50 plots). If necessary, trait data were log-transformed for calculations of functional diversity to achieve normal distribution for

residuals, while no transformation was applied in calculations of CMT.

All calculations of functional trait composition were based on fixed trait values measured in monocultures of the biodiversity experiment or derived from the literature. Our approach neglects intra-specific trait variation among mixtures (Gubsch et al., 2011; Roscher et al., 2011b) or interannual variation. Therefore, observed changes in functional trait composition are exclusively due to species turnover or shifts in species abundance distributions, while ignoring possible effects of intra-specific trait variation (Lepš et al., 2011).

Statistical analyses

Linear mixed-effects models were applied to evaluate the temporal dynamics in indices of functional trait diversity and CMT. Block and plot identity were treated as random factors in a nested sequence. Starting from a constant null model fixed effects were entered in the following sequence: sown species number (SR, as log-linear term), functional group number (FG, as linear term), year of the experiment (as linear term to test for directional changes since the establishment of the experiment), and the interaction terms between plant diversity (SR, FG) and year. The maximum likelihood method and likelihood ratio tests were applied to assess the statistical significance of model improvement. In series of separate models, the presence of each particular plant functional group was entered after the previously mentioned terms. In alternative models, year was entered as a categorical variable to test for fluctuations among years other than directional changes and compared with models, where linear trends were tested. Furthermore, the Gower dissimilarity (Gower, 1971) was calculated for trait-based indices between all pair-wise plot combinations per year of the experiment and averaged for each plot. Linear mixed-effects models fitting year of the experiment (as linear term) as fixed effect were used to evaluate whether communities converged (decreasing Gower dissimilarities) or diverged (increasing Gower dissimilarities) in functional trait composition through time. In alternative models, differences among years were tested with year as categorical variable.

Finally, the explanatory power of different groups of predictor variables and year of the experiment for variation in community biomass production was explored in a mixed model analysis: (1) community mean traits (CMTs) for each of 18 candidate traits (Table 1), (2) functional diversity (FD_Q, FRic, FEve and FDiv based on multiple traits and trait groups, Table 1), (3) sown plant diversity (species richness, functional group number, presence–absence of particular functional groups), (4) species identity (i.e., the presence–absence of particular highly productive species), and (5) climatic variables. Species identity was tested as the presence–absence of species supposed to have extraordinary large effects on community productivity. The species were selected based on the criterion that they obtained a biomass proportion $\geq 20\%$ in all communities, where they belonged to the sown species combinations (averaged across plots and years of the experiment). These species were *Arrhenatherum elatius* (L.) Presl (grass), *Knautia arvensis* (L.) J.M. Coult. and *Leucanthemum vulgare* Lam. (tall herbs) and *Onobrychis viciifolia* Scop. (legume). Correlations between different groups of predictor variables were mostly not significant. Correlations within groups were mostly low, except for variables related to FRic. This is due to the fact that FRic does not account for species abundances. Numerical variables were standardized before analysis to obtain standardized partial regression coefficients. First, we fitted linear mixed-effects models with each single predictor variable to evaluate their significance in explaining variation in community biomass. Second, models fitting initially all significant variables per predictor group as fixed effects were simplified through backward selection and step-wise exclusion of non-significant variables. Third, the remaining candidate variables per predictor group were entered in a combined model including year of the experiment (as linear term) and its interactions with the predictor variables. This combined model was successively reduced by eliminating non-significant interaction terms first and non-significant main effects afterwards. R^2 statistics for the mixed models were calculated based on likelihood ratio test statistics comparing the log-likelihood of the model of interest with the log-likelihood of the intercept-only model (Magee, 1990). Data analyses were done with R software (version 2.11.1, R Development Core Team, <http://www.R-project.org>) and the packages *FD* (Laliberté and Shipley, 2010), *nlme* (Pinheiro et al., 2009) and *lme4* (Bates et al., 2011).

Results

Community mean traits as related to plant diversity and year of the experiment

Community mean traits did not depend on sown species richness or functional group number, but community means of most traits were related to the presence of particular functional groups (Fig. 1; Supplementary Material, Table S1). Community means of all studied traits except for start of the flowering period and clonal growth varied among years of the experiment (Table S1). In addition to undirected year-to-year fluctuations, directional temporal changes were observed in 11 out of 18 traits. The early phase of the biodiversity experiment was characterized by mean trait values indicating high abundances of species with fast growth (high CMTs in leaf nitrogen, specific leaf area; Fig. 1). Changes in community mean traits with year of the experiment were in favor of trait values indicating a more conservative resource use (increasing CMTs in biomass:N ratios, foliar $\delta^{15}\text{N}$ values and foliar $\delta^{13}\text{C}$ values, decreasing CMTs in specific leaf area and leaf nitrogen concentrations) and a higher investment in sexual reproduction (increasing

CMTs in seedling number, allocation into reproductive structures, decreasing CMTs in seed mass and life cycle in favor of shorter-lived species; Fig. 1).

Between-community differences in community means of all investigated traits fluctuated among years. Community mean traits in five out of ten studied traits associated with light and nutrient acquisition, i.e., shoot length, stem mass fraction, biomass:N ratios, leaf nitrogen concentrations and root type, converged among communities with year of the experiment (Supplementary Material, Fig. S1). In contrast, CMTs in other growth-related traits diverged (root depth, foliar $\delta^{13}\text{C}$ values) among communities. Community mean traits in life-history and phenological characteristics became either more similar (four traits) or more dissimilar (four traits) among communities with year of the experiment (Fig. S1).

Functional diversity as related to plant diversity and year of the experiment

Functional trait diversity (FD_Q) and functional richness (FRic) of all trait groups increased with increasing number of sown species and functional groups (Fig. 2a–h). Functional evenness (FEve) and functional divergence (FDiv) did not depend on sown plant diversity (Fig. 2k–q and Table S1). Functional trait diversity (FD_Q) increased with year of the experiment, but this increase depended on sown species richness and was more pronounced in communities with a lower number of sown species (Fig. 2a–d). Consequently, FD_Q among communities became more similar with year of the experiment (Appendix, Fig. S2). In general, functional richness (FRic) did not change with year of the experiment (Fig. 2e–h), although directional temporal pattern in FRic based on the whole set of traits depended on sown species richness (Fig. 2e) and FRic in traits associated with regeneration fluctuated among years (Table S1). Nevertheless, decreasing pair-wise Gower dissimilarities among communities suggested a convergence in FRic through time (Supplementary Material, Fig. S2). Functional evenness (FEve) and functional divergence (FDiv) in life-history traits increased through time (Fig. 2m and q) and became more similar among communities with year of the experiment (Fig. S2). The temporal increase in FEve of traits associated with light acquisition (Fig. 2l) was dependent on sown species richness and led to a convergence among communities (Fig. S2). FDiv of traits associated with nitrogen acquisition (Fig. 2o) also increased through time dependent on sown species richness.

Biomass production as related to functional trait composition and environmental variation

Each individual group of predictor variables explained a significant proportion of total variation in community biomass: community mean traits (23%), functional diversity (8%), sown plant diversity (2%), species identity (i.e., presence of *O. viciifolia*, 17%), climatic variables (4%) and year of the experiment (14%). The final model combining different groups of predictor variables explained over 49% of total variation in community biomass production (Fig. 3). Higher community mean traits in seed mass, leaf nitrogen concentrations, shoot length as well as lower foliar $\delta^{15}\text{N}$ values had positive effects on community biomass. Functional trait diversity in nitrogen-acquisition traits was the most important component of functional diversity with positive effects on community biomass production. Functional richness in multiple traits and FEve in light-acquisition traits were also positively related to community biomass production. Increasing sown species richness and species identity, i.e., the presence

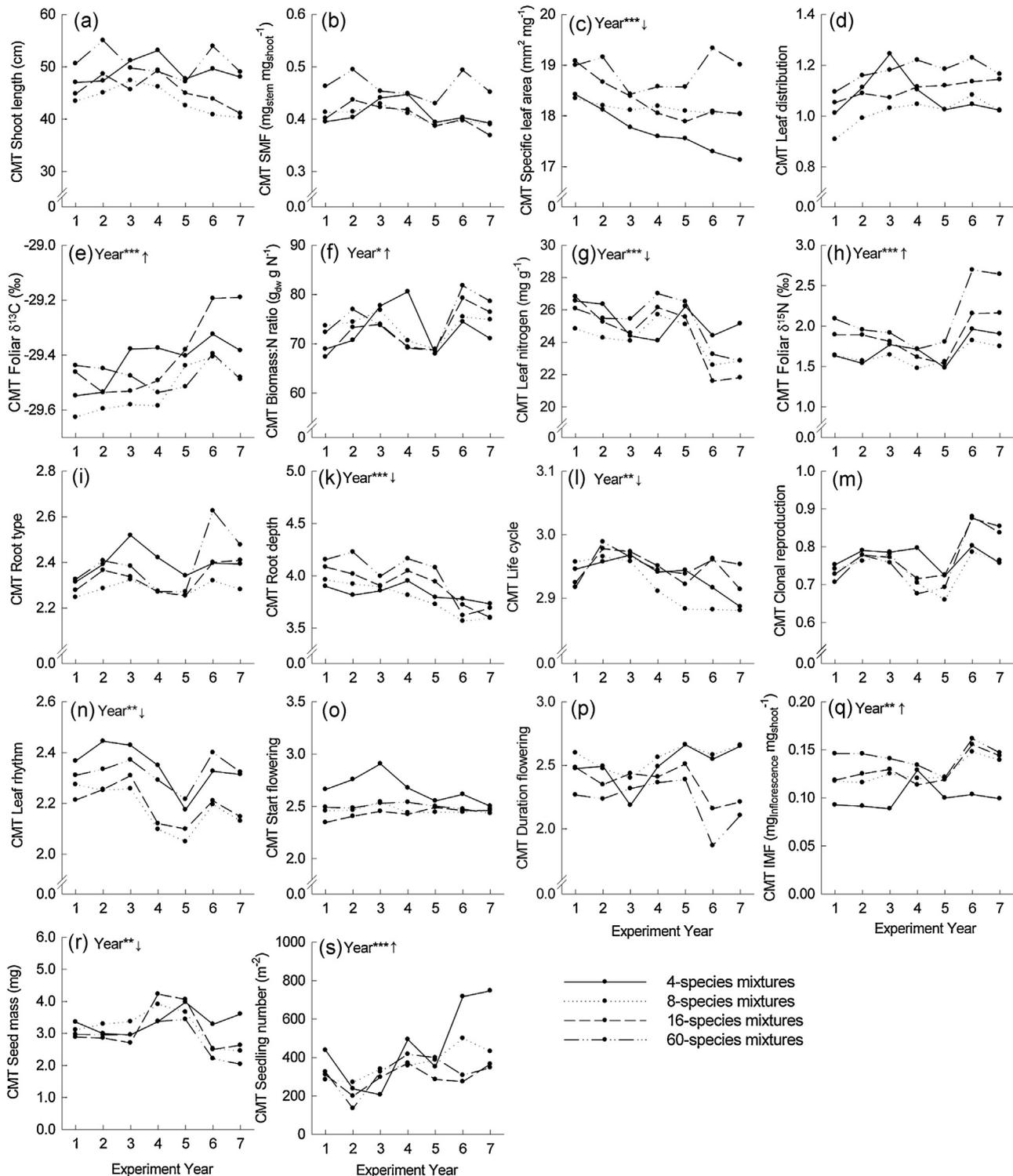


Fig. 1. Abundance-weighted community means of shoot length (a), stem mass fraction (b), specific leaf area (c), vertical leaf distribution (d), foliar $\delta^{13}\text{C}$ values (e), biomass:N ratio (f), leaf nitrogen concentration (g), foliar $\delta^{15}\text{N}$ values (h), root type (i), root depth (k), life cycle (l), clonal reproduction (m), seasonality of foliage (=leaf rhythm) (n), start of flowering (o), duration of flowering (p), inflorescence mass fraction (q), seed mass (r), and seedling number (s) as a function of experiment year. Values are means across mixtures sown with 4, 8, 16 and 60 species (2003–2009). The statistical significance of effects of sown species richness (=SR), experiment year as a linear variable (=year) are shown with $*p \leq 0.050$, $**p < 0.010$, and $***p < 0.001$. Arrows indicate significant increase (\uparrow) or decrease (\downarrow) of the variables with species richness and over time, respectively.

of the highly productive legume *O. viciifolia*, had additional positive effects on community biomass production. In general, higher precipitation and a higher sum of growing degree day values (mean air temperature $\geq 5^\circ\text{C}$) increased community biomass

production. Overall, community biomass production decreased through time (Fig. 4), but this directional decline was less pronounced when communities had a higher FRic in multiple traits (Fig. 3).

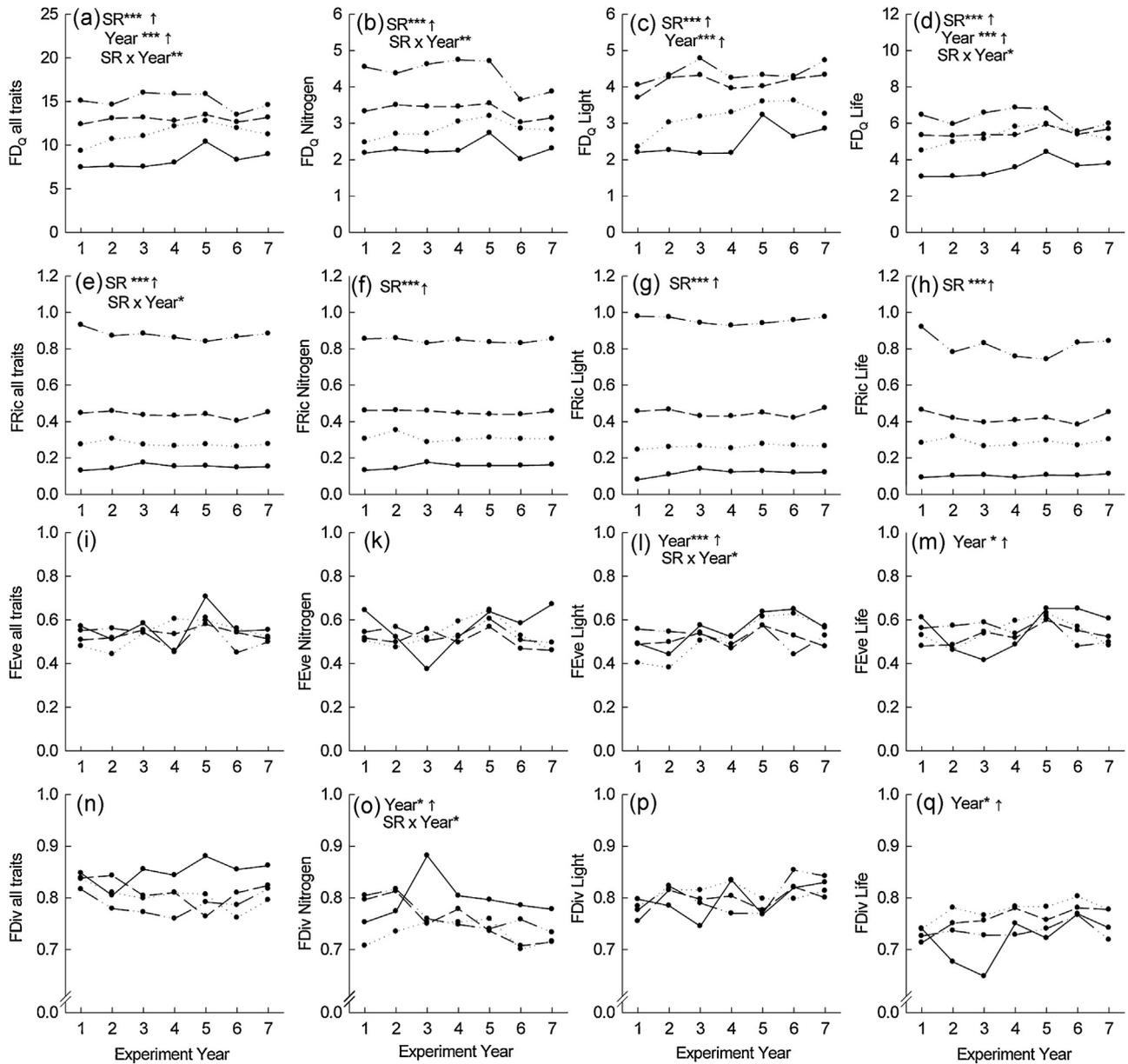


Fig. 2. Functional diversity (FD_Q) (a–d), functional richness (FRic) (e–h), functional evenness (FEve) (i–m), and functional divergence (FDiv) (n–q) based on multiple traits (a, e, i, n), based on traits related to nitrogen acquisition and use (b, f, k, o), based on traits related to light acquisition (c, g, l, p), and traits related to establishment, growth and regeneration (d, h, m, q) as a function of experiment year. Values are means across mixtures sown with 4, 8, 16 and 60 species (2003–2009). The statistical significance of sown species richness (= SR), experiment year as a linear variable (=year) are shown with * $p \leq 0.050$, ** $p < 0.010$, and *** $p < 0.001$. Arrows indicate significant increase (\uparrow) of the variables with species richness and over time, respectively. For symbols representing different levels of sown species richness see Fig. 1.

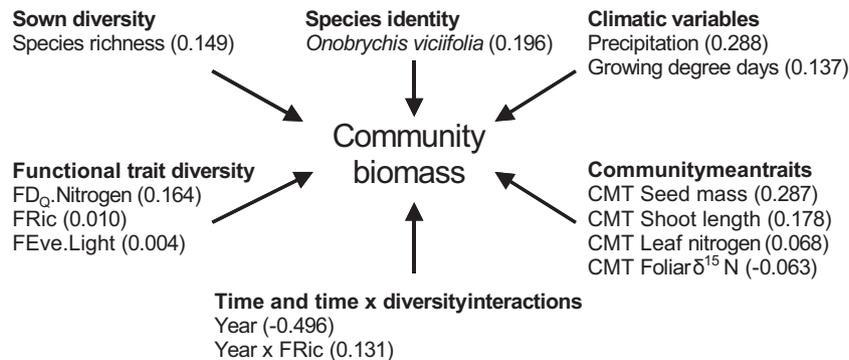


Fig. 3. Mixed model analysis of different groups of predictor variables on community biomass production of mixtures sown with 4, 8, 16 and 60 species from 2003 to 2009. Reported estimates are standardized partial regression coefficients.

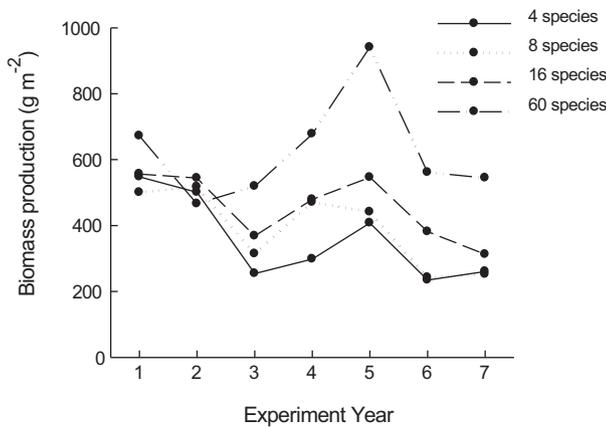


Fig. 4. Community biomass production at estimated peak biomass before first mowing (late May) as a function of experiment year. Values are means across mixtures sown with 4, 8, 16 and 60 species (2003–2009).

Discussion

Meta-analyses of different experiments have shown that positive diversity effects on community biomass production mostly result from interspecific complementarity in combination with species-specific selection effects (large contribution of particular species). Increasing interspecific complementarity has also been suggested as one possible mechanism explaining the increasing strength of positive plant diversity effects on community biomass production over several years (Cardinale et al., 2007; Marquard et al., 2009; Reich et al., 2012). These results led to our initial hypothesis that both community mean traits (i.e., the most abundant values of traits) and functional trait diversity are important predictors for community biomass with an increasing importance of the latter in the longer term, which has not been tested in a biodiversity experiment so far.

Changes in functional trait composition through time

Several methods using simulated random communities have been suggested to test for trait convergence and divergence during community assembly processes and to separate effects of biotic and abiotic processes (Götzenberger et al., 2011; de Bello et al., 2012). Biodiversity experiments, where the desired species composition per plot is maintained through weeding unwanted species, have the peculiarity that communities are artificial species combinations selected from the experimental species pool and assembly processes may only act via the extinction of sown species or shifts in their abundance distributions. Therefore, we directly analyzed temporal trends in functional trait composition of each experimental community and tested for patterns of convergence and divergence among communities based on average Gower dissimilarities.

The overall decline in community means of specific leaf area and leaf nitrogen concentrations and the increase in community means of shoot biomass:N ratios and foliar $\delta^{15}\text{N}$ values through time (Fig. 1) confirmed our hypothesis 1. The dominance of trait values associated with extensive exploitation of productivity-related resources and fast growth was increasingly replaced in favor of trait values indicating a more conservative acquisition and use of resources (Aerts and Chapin, 2000; Craine et al., 2002). The directional change in these resource-related traits was most pronounced in the last two years of our study (from 2008 onwards). A closer inspection of temporal trends in functional group proportions showed that the abundances of legumes

decreased and the abundances of grasses increased noticeably between 2007 and 2008 (years 5 and 6, see Fig. S3). In a previous study we have shown that the decline in legume abundances after several years could be attributable to phosphorus limitation (Roscher et al., 2011c). Temporal changes in community mean traits related to regeneration confirmed that a species' ability to complete its life cycle and to re-establish from seeds is important for long-term persistence (confirming hypothesis 2). In spite of the fixed species compositions of the experimental communities, from which newly colonizing species were regularly removed, we observed an increasing between-community convergence in means of several growth-related traits due to a shift in the relative abundances of species with particular trait combinations (see Fig. S1); this confirms hypothesis 3. The between-community convergence in mean traits associated with light acquisition (i.e., shoot length, stem mass fraction) was not paralleled by any temporal trend in community means of these traits suggesting that communities with extreme (high or low) values became closer to average community values through time. In contrast, the between-community convergence in mean traits associated with nitrogen acquisition (i.e., biomass:N ratios, leaf nitrogen concentrations) went in parallel with their directional changes. Nevertheless, it is not possible to disentangle the role of environmental filtering and biotic forces excluding competitively weaker species for functional trait convergence because both processes may constrain communities to certain trait values (Grime, 2006; Spasojevic and Suding, 2012). In contrast, community means in traits characterizing establishment, growth and regeneration either diverged (became more dissimilar) or converged (became more similar) among communities, suggesting that filtering processes probably act strongest on traits associated with the acquisition and use of productivity-related resources (Grime, 2006). However, functional trait diversity quantified as the average of abundance-weighted functional distances among species (FD_Q) increased over several years and this increase was most pronounced at lower levels of sown diversity (Fig. 2a–d). The increasing similarity in FD_Q and functional richness (FRic) among all communities indicated that assembly processes even in communities with artificially maintained species pools converge to limit similarity among co-occurring species (confirming hypothesis 4).

Biomass production as related to functional trait composition

Our findings that community mean traits explained a larger proportion of variation in community biomass production than functional trait diversity support the importance of dominance effects, i.e., high abundances of species or species groups with particular traits (hypothesis 5). Especially, a high CMT in seed mass was positively correlated with community biomass. Species with heavy seeds tend to establish more successfully when competing with neighbors (Grime and Jeffrey, 1965; Leishman, 2001). In our experiment, *O. vicifolia*, a highly productive legume species, has particularly large seeds. We also tested whether the presence of highly productive species may explain high levels of community productivity. We found only in the case of *O. vicifolia* that the presence of a highly productive species had consistent positive effects on community biomass production, which is in line with previous analysis of the Jena Experiment showing for a single year that this legume species was the only species which occurred more often than expected by chance in highly productive mixtures (Roscher et al., 2011a). However, even after controlling for effects of species identity, CMT in seed mass remained an important predictor for high community productivity. A closer inspection of the principal coordinate analyses (PCoA) of the functional trait matrix of the 60 experimental species showed that seed mass was among the most

important variables on the second axis. Small herbs were separated from species assigned to other functional groups. Tall herbs, grasses and legumes showed a larger spread along this trait axis (Fig. S4 and Table S2), suggesting that species classified into different functional groups contributed to the observed positive effects of CMT in seed mass.

Nevertheless, the combination of community mean traits and functional trait diversity led to a significantly better prediction of variation in community biomass than a separate consideration of different components of functional trait composition. Positive effects of functional diversity in traits associated with plant nitrogen as well as large CMTs in leaf nitrogen concentration and low CMT in foliar $\delta^{15}\text{N}$ values (characterizing legumes, see Table S1) clearly indicated that diversity in nitrogen-acquisition strategies and high legume abundances within plant communities are important for high mixture productivity. These results are in line with those reported from a strongly N-limited system (Cedar Creek), where combinations of nitrogen-fixing legumes and C4 grasses, which are superior competitors for soil nitrogen, caused the positive diversity–productivity relationships and positive complementarity effects through increased input and retention of nitrogen (Hille Ris Lambers et al., 2004; Fargione et al., 2007). Positive effects of CMTs in shoot length suggested that the dominance of species vertically foraging for light was related to high mixture productivity. In addition, we found a significant positive effect of functional evenness in light-acquisition traits. However, small values of standardized regression coefficients in the final model (Fig. 3) suggested that complementarity among species to optimize light acquisition (Anten and Hirose, 1999; Wacker et al., 2009) was of minor importance for community biomass production.

In spite of the major role of functional trait-based metrics in explaining mixture productivity, sown species richness had additional positive effects on community biomass production. Therefore, other diversity-related processes are likely to contribute to positive effects on community biomass production such as interactions with organisms at other trophic levels like soil microbes, pathogens or herbivores (e.g. Knops et al., 1999; Schnitzer et al., 2011) or element cycling (Fornara and Tilman, 2009). For example, soil mutualists, such as arbuscular mycorrhizal fungi, which may enhance plant resource uptake and protect host plants from soil pathogens, are probably more abundant at increasing species richness (Klironomos et al., 2000). In contrast, if species-specific antagonists, such as soil or foliar fungal pathogens or herbivores, limit plant growth through density-dependent regulation, their negative impact should decrease at increasing species richness because of decreasing probability that conspecifics grow in the near neighborhood (Mitchell et al., 2002; Scherber et al., 2006; Schnitzer et al., 2011; Maron et al., 2011).

Analyses of biomass production over several years showed that community productivity decreased over time (Fig. 4). The initial higher productivity of the Jena experimental communities is probably due to the establishment of the experiment on a formerly fertilized agricultural field, while constant removal of mown biomass reduced nutrient and therefore productivity levels over time. Inter-annual variation in productivity was partly explained by variation in climatic variables, i.e., higher precipitation and higher sum of growing degree days resulted in a higher community biomass, but climatic variables did not show any systematic trend over the study period (Fig. S5). Sown species richness and soil N storage over several years correlate positively in the Jena Experiment (Oelmann et al., 2011), thus improving soil fertility through increasingly closed N-cycling. A higher sown species richness and diversity in strategies of nitrogen acquisition and use diminished decreasing community biomass production over time (Fig. 3). Thus, in accordance with our initial hypothesis (hypothesis 5), a higher

functional diversity ensured higher stability in community properties such as productivity.

Results from short-term biodiversity experiments have been criticized for the supposed transience of their results (Thompson et al., 2005). Our analyses of different measures of functional trait composition and the temporal evolution of diversity–productivity relationships suggest that different mechanisms such as environmental filtering, niche differentiation and differences in the competitive ability among species affect community assembly processes. It is well possible that indices of functional trait composition do not completely capture the relevant functional characteristics to explain community assembly or ecosystem processes. Selection and weighting of traits or functional trade-offs, which are not adequately incorporated in trait-based indices, might affect functional composition. However, the major mechanisms driving ecosystem properties such as biomass production were consistent over several years and confirmed earlier results of a single year (Roscher et al., 2012). Apart from species identity effects attributable to the presence of a single species, *O. vicifolia*, community mean traits explained a larger proportion of variation in community biomass than functional trait diversity in our experiment, suggesting that functional identity, i.e., dominant trait values, largely determine ecosystem processes. Small positive effects of functional evenness in light-acquisition traits in addition to the larger positive contribution of diversity in nitrogen acquisition strategies on community biomass production over multiple years, however, indicated that processes at different resource-related niche axes are important for high mixture productivity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2013.02.004>.

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