

Differential effects of functional traits on aboveground biomass in semi-natural grasslands

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Despite increasing evidence on the importance of species functional characteristics for ecosystem processes, two major hypotheses suggest different mechanisms: the ‘mass ratio hypothesis’ assumes that functional traits of the dominant species determine ecosystem processes, while the ‘complementarity hypothesis’ predicts that resource niches may be used more completely when a community is functionally more diverse. Here, we present a method which uses two different groups of biotic predictor variables being (1) abundance-weighted mean (=aggregated) trait values and (2) functional trait diversity based on Rao’s quadratic diversity (FD_Q) to test the competing hypotheses on biodiversity–ecosystem functioning relationships after accounting for co-varying abiotic factors. We applied this method to data recorded on biodiversity–biomass relationships and environmental variables in 35 semi-natural temperate grasslands and used a literature-based matrix of fourteen plant functional traits to assess the explanatory power of models including different sets of predictor variables. Aboveground community biomass did not correlate with species richness. Abiotic factors, in particular soil nitrogen concentration, explained about 50% of variability in aboveground biomass. The best model incorporating functional trait diversity explained only about 30%, while the best model based on aggregated trait values explained about 54% of variability in aboveground biomass. The inclusion of all predictor variable groups in a combined model increased the predictive power to about 75%. This model comprised soil nitrogen concentration as abiotic factor, aggregated traits being indicative for species competitive dominance (rooting depth, leaf distribution, specific leaf area, perennial life cycle) and functional trait diversity in vegetative plant height, leaf area and life cycle. Our study strongly suggests that abiotic factors, trait values of the dominant species and functional trait diversity in combination may best explain differences in aboveground community biomass in natural ecosystems and that their isolated consideration may be misleading.

It has been widely accepted that both biotic factors, i.e. species-specific characteristics and species interactions, as well as environmental conditions, i.e. climate, nutrient availability and disturbance, affect ecosystem processes (Schulze and Mooney 1993, Hooper et al. 2005). The ongoing debate on the biodiversity–productivity relationship mainly focuses on the apparent controversy between conclusions drawn from experimental studies with artificially created plant assemblages and studies from natural plant communities (Grime 1997, Huston and McBride 2002, Thompson et al. 2005). In natural systems, biodiversity as well as ecosystem processes are affected by environmental conditions and the causality of an interrelation is difficult to extract (Lepš 2004). In contrast, manipulative field experiments established to study effects of biodiversity on ecosystem processes under controlled environmental conditions have been criticized because of their immature plant communities, their random species selection that ignores the impact of biotic and environmental filters constraining species diversity of natural ecosystems and the constant manipulation needed to

maintain the anticipated species composition (Lepš 2004, Thompson et al. 2005).

Apart from this, recent discussions have centered on a useful quantification of biodiversity because the simplest surrogate for biodiversity, species richness, contributes little to a mechanistic understanding of biodiversity–ecosystem functioning relationships. It is becoming increasingly accepted that functional traits of the constituent species, i.e. the identity, abundance and range of species traits, strongly affect ecosystem processes (Naeem and Wright 2003, Mouillot et al. 2005). Two opposing hypotheses have emerged to explain effects of functional traits on ecosystem processes. Firstly, the ‘mass ratio hypothesis’ (Grime 1998) postulates that the effects of functional traits of individual species are related to their relative abundance and that trait values of the dominant species have proportionally more influence on ecosystem processes. The mass ratio hypothesis motivated the calculation of ‘aggregated trait values’ to quantify the dominance of certain traits (Garnier et al. 2004, Vile et al. 2006). Aggregated trait values are mean values for each particular trait weighted according to the

abundance of species with given trait values. Secondly, the concept of functional diversity proposes that trait dissimilarity among species maximizes the diversity of resource use strategies and that less niche overlap along resource axes increases ecosystem functioning ('complementarity hypothesis', Tilman 1997). The number of methods proposed to assess functional diversity of a community ranges from initially discontinuous (number of functional groups, Lavorel et al. 1997) to continuous measures (reviewed by Petchey and Gaston 2006). Several criteria have been established for a useful definition of functional diversity (Mason et al. 2003). Rao's quadratic diversity (FD_Q ; Rao 1982) which is a generalization of Simpson's index of diversity is gaining increasing appraisal because it comprises valuable properties for describing functional diversity and can be based on various measures of dissimilarity among species (Botta-Dukát 2005, Ricotta 2005, Lepš et al. 2006).

In natural ecosystems, highest species richness often has been found to occur at intermediate productivity levels and to decrease at high or low levels of productivity (Grace 1999, Waide et al. 1999, Mittelbach et al. 2001). It has been suggested that at very low levels of productivity, species richness is limited as only few species are adapted to nutrient-poor conditions. At high levels of productivity, competition for light and space leads to a competitive exclusion of species and only few species will become dominant. Based on the assumptions of the mass ratio hypothesis (Grime 1998) functional traits of the dominant species have overwhelming influence on ecosystem processes. In addition, the increasing likelihood at high productivity levels that one or a few highly competitive species out-compete other species could also counteract resource use complementarity and finally diminish functional diversity. Thus, it is necessary to consider both the mass ratio hypothesis and the complementarity hypotheses when biodiversity-productivity relationships are investigated. Although the mechanisms behind both hypotheses are not mutually exclusive, so far only few case studies have compared the explanatory power of indices based on these competing hypotheses. Thompson et al. (2005) and Mokany et al. (2008) found that functional traits of the dominant species had the largest impact on ecosystem processes and supported the mass ratio hypothesis, but they tested both hypotheses separately. Díaz et al. (2007) proposed a stepwise procedure including abiotic factors, aggregated trait values and functional diversity of single traits. Despite overwhelming importance of abiotic effects and aggregated trait values, they found differential effects of these components on ecosystem functioning.

Here, we present a method that allows for the inclusion of three groups of predictor variables being (1) abiotic variables, (2) aggregated trait values, and (3) functional diversity FD_Q to test directly the competing hypotheses on biodiversity-ecosystem functioning relationships after accounting for co-varying abiotic factors. We apply this method in a case study on aboveground community biomass of mesophilic grasslands with similar management selected for different species richness to cover a non-random gradient of species extinction in this ecosystem. Species number and aboveground community biomass were only weakly related. We confirm that functional characteristics of dominant species have a large predictive power for

variability in aboveground biomass, but we demonstrate that functional trait diversity explains an additional proportion of variability in aboveground biomass and show that both mechanisms have an impact on ecosystem processes in natural ecosystems.

Methods

Study site and data collection

The study was conducted in semi-natural grasslands of the Arrhenatheretalia type according to the vegetation classification of Ellenberg (1988). Grasslands of this type are one of the most species-rich ecosystems in central Europe. They were governed by strong changes during the last decades due to the intensification of agriculture. The originally extensive utilization was replaced in many cases by fertilization and altered management regimes resulting in high-yielding, species-poor agricultural grasslands, while only few remnants kept the original species-rich composition. Our study sites were located in an area of 20×10 km on the floodplains or adjacent slopes of the river Saale around Jena and its tributary Ilm south of Weimar (Thuringia, Germany, $50^{\circ}55'N$, $11^{\circ}35'E$, $140\text{--}255$ m a.s.l.). Annual average air temperatures are $9^{\circ}C$, average annual precipitation amounts to approximately 600 mm in the region (Kluge and Müller-Westermeier 2000). In spite of differences in their management history, the selected sites are usually cut twice a year, although sometimes only one cut occurs, sites are left unmanaged over a season or the second cut is replaced by extensive grazing with cattle. We harvested aboveground biomass in 35 grasslands at estimated peak of stand biomass before first mowing in June (23 sites in 2001, and additional 12 sites in 2002). An area of 1 m^2 size was surveyed for species occurrences and cover using a decimal scale (Londo 1976). Vegetation was clipped to the ground level. Dry weight was determined after drying 48 h ($70^{\circ}C$).

Orography of each site was characterized by exposition, inclination and measurements of the horizon (using a horizontoscope). These variables were used to calculate the cumulative potential direct solar insolation during the growing season from April to September (based on an algorithm by Volz 1958). Fifteen samples of the top soil (0–15 cm depth) evenly distributed on the plot area were collected with a soil corer (1 cm diameter) from each site after biomass harvest and pooled. Dry soil samples were sieved to 2 mm, visible plant remains were removed using tweezers. Soil pH was determined in a 1 M KCl solution. Soil extracted with 1 M calcium-acetate-lactate (CAL) solution was analysed for phosphorus photometrically, and potassium by atomic absorption spectrometry. To determine total nitrogen (N_t) and carbon (C_t) concentrations, soil was ground and analysed with an elemental analyser. Concentrations of soil carbonate were determined volumetrically.

Data analysis

Plant trait matrix

A trait matrix for all species was created. We used 14 candidate traits summarized in Table 1. Data were largely

compiled from literature (Kutschera and Lichtenegger 1982, 1992, Rothmaler 2002), and databases ('LEDA trait database': Kleyer et al. 2008; 'Ecological database of the British Isles', <www.ecoflora.co.uk>: Fitter and Peat 1994) and completed with our own measurements. Nevertheless, for some species that occurred with low abundances in the respective samples reliable information for potential rooting depth (7%) and specific leaf area (4% of species in total) was not available. In these cases we used the mode of the trait across all species. All traits were assigned to categories to treat them equally for the following reasons. Firstly, quantitative values cannot be derived for morphological traits, e.g. type of the root system, or species life history. Secondly, quantitative values of several traits are known to vary in response to species growth conditions, e.g. specific leaf area, plant height (Dyer et al. 2001). The inclusion of quantitative values would require trait measurements at all sites that would have been impossible for several traits (e.g. rooting depth, N_2 fixation rates). Thus, the usage of ordered trait categories acknowledges the uncertainty about precise trait values in the investigated grasslands.

In the following we give an overview of the statistical methods. Detailed information can be found in the Supplementary material Appendix 1.

Aggregated trait values

Aggregated trait values for all 14 traits were calculated separately for each site using relative species cover as a

surrogate of species' relative abundance according to the equation

$$T = \sum_{i=1}^S p_i t_i$$

where S is the number of species in the community, p_i are the relative abundances of species and t_i are species-specific trait values.

Functional diversity

The matrix of plant functional traits for all species occurring in the vegetation relevés also served as a basis for the description of the functional diversity of communities. We used Rao's quadratic diversity (FD_Q) as a measure of functional diversity, which can be interpreted as the average dissimilarity of two randomly chosen individuals of the community. Functional diversity FD_Q is defined as

$$FD_Q = \sum_{i=1}^S \sum_{j=1}^S p_i p_j d_{ij}$$

where S is the number of species in the community, p_i and p_j are the relative abundances of species i and j , and d_{ij} describes the functional dissimilarity between species i and j . It incorporates functional traits of species as well as their relative abundances thus comprising information about functional richness and functional evenness of a community (Mouillot et al. 2005). Different dissimilarity measures have

Table 1. List of functional traits compiled from literature.

	Trait	Abbreviation	Trait categories
1	Vegetative spread	clonal	3 (0) no lateral spread (1) over short distances (e.g. short stolons, rhizoms) or formation of dividualls (2) over longer distances (e.g. creeping stems, above- and belowground stolons)
2	Height of vegetative plant	h_{veg}	5 (1) up to 10 cm, (2) up to 20 cm, (3) up to 30 cm, (4) up to 40 cm, (5) >40 cm average height
3	Height of flowering plant	h_{flower}	4 (1) up to 20 cm, (2) up to 50 cm, (3) up to 90 cm, (4) >90 cm average height
4	Canopy structure	structure	4 (1) whole phytomass near the ground (2) main part of phytomass near ground, but minor part along the stem (3) equal parts of phytomass near the ground and along the stem (4) main part of the phytomass equally distributed along the stem
5	Leaf area	$leaf_{area}$	5 (1) nanophyllous (20–200 mm ²) (2) microphyllous (2–6 cm ²) (3) submicrophyllous (6–20 cm ²) (4) mesophyllous (20–100 cm ²) (5) macrophyllous (100–500 cm ²)
6	Leaf inclination	$leaf_{incl}$	3 (1) vertical (=60–90°), (2) ascending (=30–60°), (3) horizontal (=0–30° deviation from a horizontal plane)
7	Specific leaf area	SLA	5 (1) <15 mm ² mg ^{−1} , (2) 15–20 mm ² mg ^{−1} , (3) 20–25 mm ² mg ^{−1} , (4) 25–30 mm ² mg ^{−1} , (5) >30 mm ² mg ^{−1}
8	Depth of the root system	$root_{depth}$	5 (1) up to 20 cm, (2) up to 40 cm, (3) up to 60 cm, (4) up to 100 cm, (5) >100 cm
9	Type of the root system	$root_{type}$	3 (1) long-living primary root system (beet- or stake-like tap roots) (2) secondary fibrous roots in addition to the primary root system (3) short-living primary root system, extensive secondary root system
10	Life cycle	life	3 (1) annual, (2) biennial, (3) perennial
11	Seasonality of foliage	foliage	3 (0) deciduous, (1) partly deciduous (most foliage dies off in winter), (2) evergreen (all-season with foliage)
12	Start of flowering period	f_{start}	4 (1) before May, (2) May, (3) June, (4) July
13	Duration of flowering period	$f_{duration}$	4 (1) 1 month, (2) 2 months, (3) 3 months, (4) more than 3 months
14	N_2 fixation capacity	legume	2 (0) no, (1) yes

been used in the calculation of FD_Q , but we will restrict attention to the squared Euclidean distance in multidimensional trait space for two reasons: The resulting diversity measure FD_Q is additive with respect to plant traits and it relates the diversity of a community to a common measure of variability of plant traits, the abundance-weighted variance of individual traits (Supplementary material Appendix 1). All traits were standardized to unit variance before calculating FD_Q .

Weighting of traits

Besides selection of traits for the calculation of functional diversity a main source of arbitrariness lies in the relative weighting of traits. Usually the traits are normalized to cover the same range [0,1] or standardized to have mean = 0 and variance = 1 (Legendre and Legendre 1998). These approaches are often justified by a lack of prior knowledge about the relative importance of the different traits and lead to a seemingly fair equal weighting of all traits. However, it is very unlikely that all selected traits contribute in a comparable manner to the functional diversity of a community. If greater importance of particular traits is known a priori, this previous knowledge can be incorporated. Otherwise, viewing functional diversity primarily as an explanatory variable, the arbitrariness in weighting could be fully conceded and each functional trait could be assigned a weight to be estimated from the data (Weigelt et al. 2008, Supplementary material Appendix 1).

Linear modelling

The representation of FD_Q as a weighted sum of variances of individual plant traits allows for the estimation of these weights within the linear regression setting where the variance of each incorporated functional plant trait corresponds to one explanatory variable. The weighted combination of the different plant traits into FD_Q introduces a restriction on the regression coefficients; they must all have the same sign. Estimation of the trait weights therefore relies on least squares procedures with box constraints. If the estimation procedure results in zero weights for some traits, inclusion of these traits into the calculation of functional diversity would not increase its predictive power with respect to aboveground community biomass. To make the weights identifiable, the weights of the most important trait is fixed to 1. Estimated weights for other traits can then be interpreted as relative importance of diversity with respect to those traits for the aboveground biomass of the community. Embedded in the linear regression setting, functional diversity FD_Q can be combined with other predictors. Incorporating abiotic factors, abundance-weighted aggregated trait values as well as functional diversity FD_Q as predictor variables can help to understand the relative contributions of these different groups of variables based on competing hypotheses to explain biodiversity–ecosystem functioning relationships.

Model selection

Estimating the relative contribution of abiotic effects, direct effects of particular functional traits of species and func-

tional diversity to aboveground biomass now amounts to variable selection in a multiple linear regression setting. Although correlations between different predictor variables prevent an unequivocal attribution of effects to single variables, selection of a parsimonious model capable of describing the observed differences in aboveground biomass protects against overfitting and helps to identify important explanatory variables. Among the several existing model selection criteria cross-validation, where the data set is repeatedly split into a training data set for model fitting and an assessment data set used to estimate the predictive power of the fitted model, is intuitively appealing because it focuses on prediction error, does not impose any distributional assumptions on the nature of the errors and does not require repeated testing of statistical significance. We therefore selected best models based on minimum prediction error estimated by leave-one-out cross-validation, where the prediction error is estimated by successively predicting aboveground biomass at each grassland site based on a model fitted on all remaining sites. We used the leaps and bounds algorithm of Furnival and Wilson (1974) to search for the 20 best-fitting models (largest R^2) at each level of complexity (i.e. number of predictor variables) and subsequently calculated cross-validation estimated prediction errors for all of these models.

We report best models separately for each possible combination of the three types of predictor variables – abiotic factors, aggregated trait values and functional trait diversity. Values of Akaike's information criterion (AIC), a closely related model selection criterion but based on likelihood theory, is given for comparison. The statistical significance for each predictor variable was additionally assessed based on a randomization test. For this test the matrix of explanatory variables was kept fixed but the values of the response variable were randomly permuted 1000 times. Hierarchical models were compared using sequential F-tests. Data analyses were performed using R (<www.R-project.org>).

Results

Species richness effects on aboveground community biomass

Species richness varied between 7 and 31 species per m^2 sample area. In total 112 plant species were recorded. Aboveground biomass ranged from 182 to 592 $g_{dw} m^{-2}$ with a mean of 424 $g_{dw} m^{-2}$. Aboveground biomass slightly decreased with increasing species richness, but this relationship was not statistically significant ($R^2 = 0.100$, $p = 0.064$, Fig. 1).

Effects of abiotic variables

Basic descriptive statistics of environmental variables are summarized in Table 2. Among the three classes of predictor variables the effect of abiotic factors was most pronounced. Soil nitrogen concentration in top-soil was the most important single predictor, accounting for more than

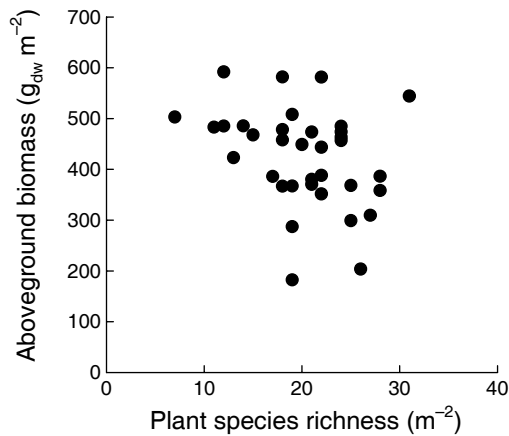


Figure 1. Relationship between plant species richness (m^{-2}) and aboveground biomass ($\text{g}_{\text{dw}} \text{m}^{-2}$).

40% of the total variability in aboveground biomass (Fig. 2a, $R^2=0.419$). The selected best abiotic model contained soil nitrogen and carbonate content as predictors, together explaining about 50% of the total variability ($R^2 = 0.483$). Although the amount of direct solar radiation over the growing season was also strongly positively correlated with aboveground biomass ($r = 0.577$, $p < 0.001$) it has not been included in one of the best models probably because of its strong correlation with the best predictor total nitrogen content ($r = 0.701$, $p < 0.001$).

Adding species richness to the best abiotic model incorporating nitrogen and carbonate content as predictors did not result in a significant model improvement ($F_{1,31} = 0.012$, $p = 0.912$). There was a significant negative correlation between species richness and nitrogen content (Fig. 2b, $r = -0.566$, $p < 0.001$). This was probably an indirect effect caused by the positive correlation between aboveground biomass and soil nitrogen content ($r = 0.647$, $p < 0.001$).

Effects of functional trait diversity

When the diversity of the plant communities was quantified with FD_Q , i.e. the functional diversity with respect to the considered plant traits, aboveground biomass was negatively

related to diversity. The best model solely based on diversity of functional traits explained about 30 % of the total variability in aboveground biomass ($R^2 = 0.295$, Table 3) and identified diversity with respect to leaf area and the duration of the flowering period as most important predictors.

Effects of aggregated traits

When only aggregated traits were considered as predictors of aboveground community biomass, six different traits were included in the best model (Table 3). These traits were related to aboveground space use (distribution of phytomass in the vertical profile, plant height), belowground space use (rooting depth), life history, phenology (start of flowering) and net assimilation rate (specific leaf area). Although the percentage of explained variability ($R^2 = 0.541$) was higher than for the pure abiotic model, the predictive power was smaller as indicated by the estimated cross-validation prediction error.

Model comparison

Assessment of the predictive performance of the models in different combinations of the three classes of predictor variables resulted in a best model that incorporated abiotic effects, effects of aggregated traits and trait diversity effects (Fig. 3, Table 3). This finding emphasizes that all three groups of predictor variables contributed to the effect on aboveground community biomass. Soil nitrogen concentration in top-soil was selected as single important abiotic variable being positively related to aboveground biomass (Table 4). A combination including characteristics as leaf distribution across all strata of the vertical canopy profile, a deep root system, high specific leaf area and the prevalence of a perennial life cycle were chosen as aggregated traits in the best model (Table 4). Contrary to the negative effects of functional diversity in the pure trait diversity model in the global model effects of functional trait diversity turned out to be positive, with diversity in life history, leaf area, and vegetative height of species present in the community having significant effects on aboveground biomass. The estimated relative weights for leaf area and vegetative height

Table 2. Summary (mean, standard deviation (SD), coefficient of variation (CV), minimum (min) and maximum (max)) of species richness, aboveground biomass and site characteristics of 35 investigated grassland sites.

Variable	mean	SD	CV	min	max
Species richness (m^{-2})	20	5	27.0	7	31
Aboveground biomass ($\text{g}_{\text{dw}} \text{m}^{-2}$)	423.9	96.6	22.8	182.0	591.6
Soil carbonate (%) (CO_3)	12.5	7.4	59.6	0.4	26.8
pH(KCl)	7.10	0.12	1.6	6.57	7.26
Soil carbon (mg g^{-1}) (C_t)	53.2	14.4	27.0	23.8	85.8
Soil carbon (mg g^{-1}) (C_{org})	28.2	8.9	31.6	12.6	43.4
Soil nitrogen (mg g^{-1}) (N_t)	3.9	0.9	24.4	1.8	5.6
$\text{C}_{\text{org}}:\text{N}$	13.8	2.6	18.9	10.2	19.5
Soil phosphorus (mg g^{-1}) P(CAL)	0.099	0.073	73.3	0.014	0.249
Soil potassium (mg g^{-1}) K(CAL)	0.173	0.105	60.7	0.056	0.448
Potential insolation ($\text{kJ cm}^{-2} \text{d}^{-1}$)	2.70	0.79	0.3	0.30	3.47

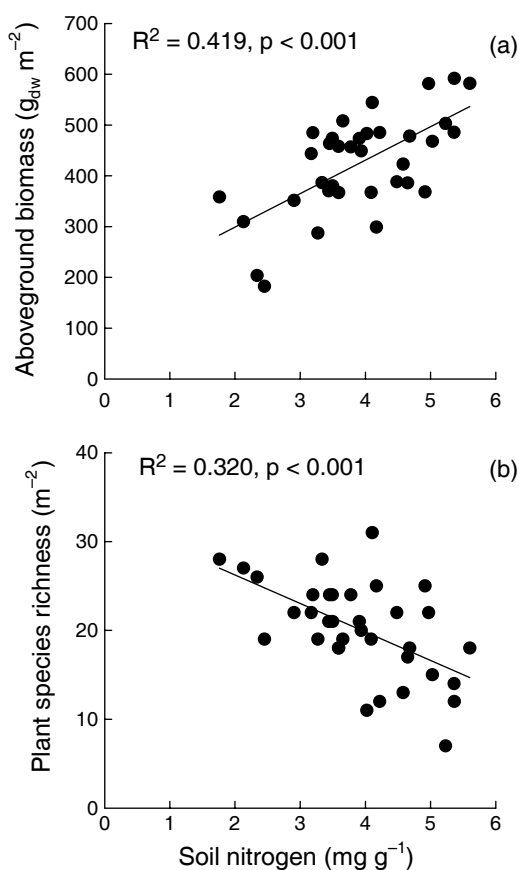


Figure 2. Relationship between soil nitrogen content (mg g⁻¹) and aboveground biomass (g_{dwt} m⁻²) (a), and plant species richness (m⁻²) (b).

were smaller than 1, so that diversity in species life cycles apparently was the most important aspect in functional trait diversity of the communities (Table 4). The fact that the second and third best model differed from the best one by only one included variable indicated the relative stability of the variable selection process even in the presence of substantial correlation between the different predictor variables. When the submodels of the selected best model were hierarchically compared using sequential F-tests, the addition of abiotic factors was always statistically significant, thus underscoring the role of soil nitrogen concentration as the single best predictor.

Discussion

Species richness has been suggested to peak at intermediate productivity (Al-Mufti et al. 1977) although not only maximum species richness but also maximum variation in species richness occurs at intermediate productivity levels in natural ecosystems (Moore and Keddy 1989, Grace 1999, Schaffers 2002, Kahmen et al. 2005). However, the unimodal relationship was found more consistently in across-community type comparisons, while no consistent

relationships have been observed within community types (reviewed by Waide et al. 1999, Mittelbach et al. 2001). A number of observational studies (Vermeer and Berendse 1983, ter Heerdt et al. 1991, Gough et al. 1994) and fertilization experiments (reviewed by DiTommaso and Aarssen 1989) have supported Grime's (1973) hypothesis that higher resource availability favours competitive exclusion and leads to a negative species richness–productivity relationship at high resource levels. In our study, species richness and aboveground community biomass varied largely independently (Fig. 1), although sites with low species richness had the highest aboveground biomass and aboveground biomass varied greatly in more diverse grasslands.

Observational studies on biodiversity–ecosystem functioning relationships in natural ecosystems have been questioned because of uncontrolled co-varying environmental factors (Lawton et al. 1998). The high proportion of variability explained by abiotic factors, in particular soil nitrogen (Fig. 2a), revealed the overwhelming influence of extrinsic factors. Total soil nitrogen concentrations are related to soil organic matter mineralization rates and nitrogen availability in case of no phosphorus deficiency (Marschner 1995, Janssens et al. 1998). Nevertheless, plant traits selected in a pure analysis of aggregated traits accounted for a similar proportion of variability in aboveground community biomass than the pure analysis of abiotic factors. Aggregated values of traits known to be related to competitive dominance in herbaceous vegetation under high resource availability (plant height, rooting depth and canopy structure; Gaudet and Keddy 1988) and high relative growth rates (specific leaf area; Hunt and Cornelissen 1997) were included as best predictors in the model. Therefore, the collinearity between abiotic factors and aggregated trait values that led to only a minor model improvement when we combined analyses of abiotic factors and aggregated trait values was not surprising in our data set where soil nitrogen concentration was the most important abiotic driver of aboveground biomass production. The selected traits confirmed that higher resource availability favours competitive superior, highly productive species and may exclude other less-competitive subordinate species (Grime 1998). However, this mechanism is obviously not sufficient to explain variability in aboveground community biomass at high species richness. In our data pure effects of functional trait diversity were negatively related to aboveground biomass and had a lower explanatory power than pure abiotic effects or pure effects of aggregated trait values. One possible explanation for the apparent negative trait diversity effect could be that it reflects an indirect abiotic effect favouring the dominance of highly competitive species under high resource availability. Therefore, an isolated consideration of trait diversity effects may be misleading.

Although we observed significant effects of each group of predictor variables, i.e. abiotic factors, aggregated trait values and functional trait diversity, the combination of these variable groups led to a considerable increase of explained variability in aboveground community biomass.

Table 3. Summary of statistical models.

Model class	Model score	CV	AIC	R ²	Parameters included in the model		Trait diversity
					Abiotic factors	Aggregated traits	
Abiotic effects	1	5522.17	403.17	0.483	N _t CO ₃		
	2	5696.90	403.97	0.501	N _t CO ₃ P(CAL)		
	3	5737.01	404.43	0.464	N _t C _{org} :N		
Effects of aggregated traits	1	6461.36	407.03	0.541		life structure h _{flower} SLA root _{depth} f _{start}	
	2	6554.32	406.87	0.516		life structure h _{flower} root _{depth} f _{start}	
	3	6617.65	407.16	0.539		life structure leaf _{incl} h _{flower} root _{depth} f _{start}	
Effects of trait diversity	1	8128.20	414.04	0.295			(-) leaf _{area} f _{duration}
	2	8691.58	418.04	0.210			(-) structure leaf _{area}
	3	8935.80	418.50	0.152			(-) leaf _{area}
Abiotic + aggregated trait effects	1	4536.20	395.36	0.652	N _t	structure SLA root _{type} f _{start}	
	2	4686.25	397.34	0.610	N _t	structure SLA f _{start}	
	3	4696.17	397.71	0.582	N _t	structure SLA	
Abiotic + trait diversity effects	1	5031.95	402.43	0.522	N _t CO ₃		(-) f _{start}
	2	5155.93	400.92	0.516	N _t		(+) SLA
	3	5185.32	403.81	0.503	N _t C _{org} :N		(-) f _{start}
Aggregated trait + trait diversity effects	1	5292.69	398.45	0.661		h _{veg} h _{flower} SLA root _{depth} f _{start}	(+) h _{veg} SLA
	2	5300.21	401.18	0.589		h _{veg} SLA root _{depth} f _{start}	(+) SLA
	3	5381.33	400.58	0.618		h _{veg} h _{flower} SLA root _{depth} f _{start}	(+) SLA
Abiotic + aggregated trait + trait diversity effects	1	3737.28	387.58	0.765	N _t	life structure SLA root _{depth}	(+) life leaf _{area} h _{veg}
	2	4011.53	388.48	0.745	N _t	life structure root _{depth}	(+) life leaf _{area} h _{veg}
	3	4156.33	390.28	0.731	N _t	life structure SLA root _{depth}	(+) life leaf _{area}

Results on models including different combinations of predictor variable groups (abiotic factors, aggregated traits, functional trait diversity) are shown. Within each model category models are ordered according to minimum estimated cross-validation prediction error (CV). Values of Akaike's information criterion (AIC) and R² are given for comparison. The last columns show abiotic variables and plant traits selected in these models. For abbreviations of abiotic factors and plant traits see Table 1 and 2.

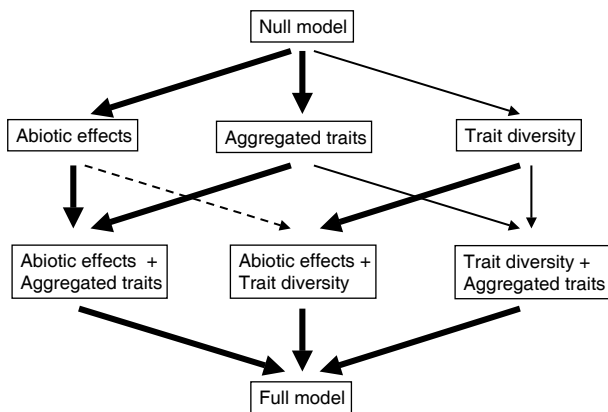


Figure 3. Hierarchical model comparison for submodels of the selected best model incorporating abiotic effects, effects of aggregated traits and functional trait diversity effects as predictors for aboveground biomass. Models are compared using sequential F-tests. The style of the arrows indicates statistical significance of model improvements - dashed line: $p > 0.05$, thin solid line: $p < 0.05$, thick solid line: $p < 0.01$.

Similar to models where we included pure effects of each variable group, soil nitrogen content was the most important environmental factor in the full model. Vertical leaf distribution, rooting depth, specific leaf area and plant longevity being indicative for species competitive dominance were included as important aggregated traits. However, in contrast to the model of pure functional diversity effects, diversity in life history, leaf area and vegetative plant height now had positive effects on aboveground biomass. Although the proportion of additional explained variation in aboveground community biomass was small, this result clearly underpins that even under circumstances where abiotic factors and the closely interacting dominance of particular functional traits have large impacts their combination with functional diversity may best explain variation in aboveground biomass.

So far, studies that included plant functional traits as explanatory variables for community biomass were restricted either to the use of aggregated traits (Garnier et al. 2004, 2007, Louault et al. 2005, Vile et al. 2006) or the calculation of one or several indices of functional diversity (Petchey et al. 2004, de Bello et al. 2006). Only

few studies in natural ecosystems used more complex approaches and involved abiotic and biotic influences (Thompson et al. 2005, Mokany et al. 2008). To our knowledge there exist only one study that applied a stepwise procedure to model effects of abiotic factors, aggregated trait values and trait value distribution (diversity of individual traits) sequentially (Díaz et al. 2007). Our approach is similar, but differs in two important aspects. Firstly, following their strict stepwise procedure in the combined analysis of abiotic and trait factors Díaz et al. (2007) only included significant variables from separate analyses of single predictor variable groups. The analysis of single predictor variable groups in our data set showed that the importance of some traits may be hidden by correlated abiotic factors. As all three groups of predictor variables are based on established ecological hypotheses an equitable treatment of these predictor variable groups is more appropriate. In our case an apparent negative effect of functional trait diversity was reversed in the combined analysis. Secondly, our approach is more flexible in the inclusion of several functional traits. Díaz et al. (2007) simply averaged diversity between traits to assess the simultaneous effects of several traits. Implicitly this approach assumes an equal importance of all candidate traits. In contrast, our method allows for a weighting of different functional traits and therefore may help to identify their relative importance.

Our study shows that the separate consideration of competing hypotheses is not sufficient for a mechanistic understanding of ecosystem productivity. The proposed method may contribute to exploration of patterns consistent with these different hypotheses, especially in natural communities.

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Table 4. Summary of the best model based on the three classes of predictor variables.

Predictor variables		Coefficient	Relative weight	t	p
Abiotic:	intercept	−4448.64		−4.03	0.020
	N _t	851.07		5.83	< 0.001
	life	3520.97		3.41	0.054
	structure	489.62		3.27	0.055
	SLA	237.24		1.50	0.407
Aggregated traits:	root _{depth}	458.80		2.96	0.085
	life	359.38	1.00	3.97	0.021
	leaf _{area}	30.49	0.29	3.01	0.085
	h _{veg}	34.48	0.31	1.93	0.240

Detailed results of the multiple regression analysis including abiotic factors, aggregated traits and trait diversity are shown. For traits selected for FD_Q, relative weights are estimated according to the method described in the Supplementary material Appendix 1. p-values are based on a randomization test.

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Supplementary material (available online as Appendix O17711 at www.oikos.ekol.lu.se/appendix). Appendix 1