

Plant trait responses to the environment and effects on ecosystem properties

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Abstract

A combined analysis of plant trait responses to the environment, and their effects on ecosystem properties has recently been proposed. In this study, we related the trait composition of plant communities to soil nutrients and disturbance as environmental drivers and to productivity, decomposition and soil carbon as ecosystem properties. We surveyed two sites, one comprising intensively grazed and fertilized grasslands, the other consisting of semi-natural grassland and open heathland. Species abundance and trait values of 49 species were recorded in 69 plots, as well as parameters describing soil resources, land-use disturbances, and ecosystem properties. Our main goal was to test whether the average or the diversity of the trait values of the vegetation had stronger effects on ecosystem properties (mass ratio *vs.* diversity hypothesis). Structural equation modeling was used to perform a simultaneous analysis of trait responses and effects. Specific leaf area and leaf nutrient contents were always negatively correlated with stem dry matter content and canopy height, indicating greater investments in supportive and nutrient-conserving tissue as plants increased in size. In the agricultural site, disturbance was the single most important factor decreasing plant height, while leaf traits such as specific leaf area and leaf nutrient contents increased with soil resources in heathlands. Productivity was directly or indirectly driven by leaf traits, and investments in structural tissue increased standing biomass and soil carbon. Different environmental drivers in the two sites produced opposing leaf trait effects on litter decomposition. Ecosystem properties were explained by the community mean trait value as predicted by the mass ratio hypothesis. Evidence for effects of functional diversity on productivity and other ecosystem properties was not detected, suggesting that diversity–productivity relationships depend on the length of the investigated environmental gradients. We conclude that changes in community composition and dominance hierarchies deserve the most attention when ecosystem properties must be maintained.

Zusammenfassung

Eine kombinierte Analyse der Reaktion von Pflanzenmerkmalen (traits) auf die Umwelt und ihrer Auswirkungen auf Ökosystemfunktionen wurde kürzlich vorgeschlagen ('response-effect framework'). In der vorliegenden Studie wenden wir diese Analyse auf zwei landwirtschaftliche Gebiete, welche sich in der Nutzungsintensität unterscheiden, und folgende Ökosystemprozesse an: oberirdische Biomasse, spezifische Nettoprimärproduktion (SANPP), Streuzersetzung und Bodenkohlenstoff. Dafür wurden die Frequenz und die trait-Werte von 49 Arten in insgesamt 69 Plots aufgenommen. Darüber hinaus wurden Parameter erhoben, welche Bodenwasser und -nährstoffe, Landnutzung und Ökosystemeigenschaften beschreiben. Wir haben zudem getestet, ob der durchschnittliche trait-Wert oder die Diversität der trait-Werte aller Arten einer Gemeinschaft größere Effekte auf Ökosystemprozesse zeigt ('mass ratio' versus 'diversity' Hypothese). Strukturgleichungsmodelle wurden verwendet, um eine simultane Analyse des 'response-effect framework' zu untersuchen. Der Gesamtdatensatz wurde in zwei Gruppen

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eingeteilt: die eine bestehend aus intensiv gedüngten Weiden und Grasflächen, die andere aus naturnahem Grasland und offener Heide. In beiden Datensätzen waren die Blattmerkmale negativ korreliert mit der Stängeltrockenmasse und der Wuchshöhe, was auf einen eher konservierenden Umgang mit Ressourcen hindeutet. Auf den landwirtschaftlich geprägten Plots war Störung der wichtigste Umweltfaktor der zu einer Abnahme der Wuchshöhe führte, während die Bodenressourcen die Blatteigenschaften, z.B. spezifische Blattfläche und Blattnährstoffgehalte in den Heidegebieten geprägt haben. Die Biomasseproduktivität war direkt oder indirekt angetrieben von den Blattmerkmalen, wobei verstärkte Investitionen in die Pflanzenstruktur zu einer Erhöhung der stehenden Biomasse und Bodenkohlenstoffgehalte führten. Die unterschiedlichen Landnutzungen hatten gegensätzliche Effekte der Blatteigenschaften auf die Streuzersetzung zur Folge. Die gemittelten trait-Werte aller Arten einer Gemeinschaft hatten den größten Einfluss auf die Ökosystemeigenschaften, wie durch die ‘mass ratio’ Hypothese vorhergesagt. Belege für Effekte der funktionellen Diversität auf die Produktivität und andere Ökosystemeigenschaften wurden nicht gefunden, was darauf hindeutet, dass Diversitäts-Produktivitäts-Beziehungen von der Ausdehnung (Länge) der untersuchten Umweltgradienten abhängen. Deshalb verdienen Änderungen in der Artenzusammensetzung und in der Dominanzhierarchie von Pflanzengemeinschaften große Aufmerksamkeit bei der Betrachtung von Ökosystemeigenschaften.

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Keywords: Disturbance; Ecosystem function; Functional diversity; Landuse; Leaf economics spectrum; Mass-ratio hypothesis; Path analysis; Litter decomposition; Productivity; Structural equation model

Introduction

Current research in plant functional traits uses two different approaches providing valuable insights into the mechanisms of ecosystem function. First, extensive study on trait response to environmental drivers and biotic interactions has been reported (e.g. Garnier et al. 2004). Second, investigations addressed how ecosystem properties including primary productivity and litter decomposition depend on functional traits (e.g. Kremen & Ostfeld 2005). The response–effect framework (Lavorel & Garnier 2002; Suding et al. 2008) offers a combined analysis of trait responses to the environment and the subsequent effects on ecosystem properties, but the methodology has rarely been applied in natural landscapes (Pakeman 2004). This remains a notable disparity (Lavorel et al. 2011). In the present study, we perform a simultaneous analysis of trait responses and effects in an agricultural region characterized by land-use intensification.

In agricultural landscapes, ecosystem processes and properties such as primary productivity, standing biomass, and litter decomposition translate directly into ecosystem services, including forage and crop yields, and associated nutrient balance (Díaz et al. 2007a; Lavorel et al. 2011). Therefore, quantified relationships between environmental conditions, plant traits, and ecosystem properties are particularly relevant for agricultural landscape management. One central aim was to study these response–effect relationships, particularly for aboveground biomass (AGB), specific above ground net primary productivity (SANPP), litter decomposition (LITTER), and total soil carbon (CARBON) of grasslands and heathlands, managed for agriculture and conservation, respectively. Farmers manipulate these ecosystem properties by selecting soils with appropriate water resources, by changing the nutrient status of the soil, and by applying disturbances such as tilling, mowing or grazing. Therefore soil nutrients, soil water holding capacity and disturbance intensity are considered relevant environmental

drivers affecting ecosystem properties in agricultural landscapes. These effects can be direct, for example increasing tillage and fertilization improve decomposition of organic carbon by enhancing microbial activity (DeGryze et al. 2004). The response–effect framework, however, assumes that most links between the abiotic environment and carbon-related ecosystem properties are indirect and operate through changes in the trait composition of plant communities, which in turn depend on gains and losses of species, *i.e.* changes in biodiversity. Traits related to plant growth and carbon gain are likely candidates to simultaneously respond to environmental drivers and affect ecosystem properties of the carbon cycle. For instance, specific leaf area (SLA) is associated with net assimilation and plant growth rates (Reich, Walters, & Ellsworth 1997) while leaf dry matter content (LDMC) is tied to plant nutrient retention (Poorter & Garnier 1999). Leaf nitrogen content (LNC) and leaf phosphorus content (LPC) are correlated with protein concentrations involved in photosynthesis (Evans 1989) as well as leaf growth and defense strategies (Reich et al. 2008). Global (Wright et al. 2004) and local (Lienin & Kleyer 2011) datasets reported these leaf traits as highly correlated, indicating a ‘leaf economics spectrum’ that runs from resource conservation to rapid resource acquisition and turnover in leaves. Freschet, Cornelissen, Logtestijn, and Aerts (2010) proposed that the ‘leaf economics spectrum’ can be expanded to a whole plant economics spectrum as stem and root dry matter show a strongly coordinated pattern with leaf traits. Another trait associated with growth and carbon gain is plant height. It is a major determinant for a plant’s ability to compete for light but requires increasing investments in structural tissues, such as stems and branches (Westoby, Falster, Moles, Vesk, & Wright 2002; Moles et al. 2009), which should decrease plant growth rates.

Here, we hypothesize that ecosystem processes such as biomass, litter and soil C accumulation are associated with

resource conservation and height attaining strategies in plants as well as with low soil resources and disturbance intensities (Lavorel & Grigulis 2012). On the other hand, high soil resources and increasing land use intensity should favor rapid resource acquisition by plant leaves and lower plant height, which in turn increases carbon turnover in terms of annual productivity and decomposition, whereas effects on standing biomass and soil carbons stocks should be negative.

Evidence from experiments indicates that plant species richness has positive effects on multiple ecosystem properties (e.g. Isbell et al. 2011). Consequently, we ask if multiple ecosystem properties and multiple environmental factors are linked via recurring key traits, or if each ecosystem property is affected by different traits (Hooper et al. 2005).

However, the diversity of traits responding to environmental drivers and affecting ecosystem properties is only one facet of functional diversity. Another aspect refers to trait value diversity within communities, and two hypotheses were generated. The mass ratio hypothesis states that the functional traits of the most abundant species in a community determine ecosystem properties (Grime 1998). To address this hypothesis, the trait values of all species in a community are averaged, then weighted by species relative abundance (termed CWM: community weighted mean; Díaz et al. 2007b). According to the ‘diversity hypothesis’, organismal diversity in a community, and species’ functional traits should influence ecosystem properties through complementary resource use, among other factors (Tilman et al. 1997). Increased functional diversity (FD) should lead to heightened niche packing along a resource use axis, therefore a highly diverse community will have more substantial effects on biogeochemical pools and fluxes (Hooper 1998). Empirical evidence has been reported for both theories (e.g. Vile, Shipley, & Garnier 2006). Mokany, Ash, and Roxburgh (2008) for instance demonstrated that functional traits of dominant species had the greatest effect on ecosystem properties. Díaz et al. (2007b) included abiotic factors, aggregated trait values, and FD in a single analysis and described differential effects on standing biomass, productivity, and litter decomposition. The fact that both hypotheses are normally tested separately does not mean that they are mutually exclusive. Rather, community weighted means and functional diversity of traits may exhibit an additive influence in response–effect frameworks.

To specify these hypotheses in greater detail, we first devised an initial model based on published knowledge. We then used structural equation modeling (SEM) to evaluate the initial model. SEM can be considered as a method that seeks to create a connection between empirical data and theoretical ideas (Grace, Anderson, Olff, & Scheiner 2010). We performed our survey in two sites, one consisted of intensively grazed and fertilized grasslands classified as ‘agriculture’, while ‘heath’ was comprised extensively grazed and unfertilized semi-natural grassland and open heathlands.

Materials and methods

Study sites

Two field sites were located in Northwest Germany, approximately 25 km apart from each other (52°55′N, 8°15′E; 52°55′N, 7°56′E) (Appendix A). The climate is characterized as oceanic, with dominant westerly winds. Mean annual rainfall is 740 mm, and mean annual temperature is 8.7 °C. Elevation ranges from 19 m to 44 m a.s.l. Soils are primarily sandy on moraine sediments.

We applied a random stratified design to select 69 non-contiguous plots (4.5 m × 4.5 m) across both sites. Sampling was conducted in 2007 and 2008. The plots selected were stratified by broad categories of land-use intensity and soil moisture. The ‘agriculture’ site ranged from intensively and extensively used grassland to fallow land (29 plots) and the ‘heath’ site from semi-natural grasslands (dry soils) to shrub/heathlands (well-drained and dry soils; 40 plots).

A common feature of both sites was the ‘Plaggen’ cultivation, a historic land use practiced from the Middle Ages to the 18th century. In this land use system, the top soil including the litter layer was removed from forests, used as bedding for cattle, and after being enriched with slurry, spread on arable fields for fertilization. As an outcome of these land use practices, forests almost vanished, and open heaths and even denuded soils became predominant. This land use system was abandoned with the availability of mineral fertilizer. Today, remaining heathlands are extensively managed and confined to small areas (Behre 2008) whereas the majority was converted to fertilized pastures and fields.

Environmental parameters

In each plot, soil samples were obtained from each soil horizon (typically three or less) down to a depth of 60 cm using a 100-cm³ soil sample ring, air-dried, and sieved using a 2 mm sieve. Field and lab measured variables included bulk density, soil solution pH, soil texture, soil density (Schlichting, Blume, & Stahr 1995), available soil potassium (K), and phosphorus (P) per unit mass (Table 1). K and P were extracted with ammonia-lactate solution. K was measured with a flame photometer, P with a Continuous Flow Analyzer (Murphy & Riley 1962; Skalar Analytic, Netherlands). Soil texture and organic carbon content were used to estimate soil water holding capacity (WHC) following AG Boden (2005).

Plots were ranked on a disturbance gradient using an index which was calculated as the product of the percentage of biomass removal per disturbance event (F) with the disturbance return interval per year (I), summarized over all disturbances (i) that represent the land management of a plot (e.g. cutting, grazing, ploughing):

$$D = \sum F_i \times I_i$$

Table 1. Abbreviations and units of environmental (A), trait (B), and ecosystem property (C) variables.

	Abbreviation	Type of variable/unit	'Agriculture' site				'Heath' site			
			Mean	SD	Min	Max	Mean	SD	Min	Max
(A) Environmental variables										
Disturbance index	DISTURBANCE	Relative ^a	1.13	0.44	0.14	1.80	0.42	0.17	0.06	0.70
Soil potassium content	Soil K	kg/ha ^a	64.78	10.99	37.54	84.00	92.00	33.57	50.61	168.14
Soil phosphorus content	Soil P	kg/ha ^a	300.25	304.70	89.05	1237.88	141.94	195.30	4.02	642.49
pH value	pH	log-scale	4.66	0.57	3.50	5.70	3.66	0.51	3.00	4.43
Soil water holding capacity	WHC	mm	119.92	21.50	40.42	149.27	95.58	31.04	53.79	148.90
(B) Trait variables										
Canopy height	HEIGHT	cm	28.26	9.44	16.93	53.80	22.63	6.29	12.11	36.92
Specific leaf area	SLA	mm ² /mg	24.10	1.62	20.96	26.38	12.18	6.30	6.44	22.56
Leaf dry matter content	LDMC	mg/g	299.46	100.55	215.22	568.50	512.70	206.99	238.17	708.40
Leaf nitrogen content	LNC	%	22.87	1.79	19.43	26.45	17.68	2.97	13.73	24.15
Leaf phosphorus content	LPC	%	2.72	0.33	2.06	3.40	1.30	0.75	0.63	2.49
Leaf C/N ratio	LC/N	Ratio	19.81	2.54	16.66	26.37	28.36	5.86	19.45	36.13
Stem dry matter content	SDMC	mg/g	311.93	59.24	242.25	430.78	459.83	80.47	319.75	547.00
Functional dispersion	FDis	—	1.01	0.22	0.38	1.43	1.25	0.38	0.49	1.80
(C) Ecosystem properties										
Aboveground biomass	AGB	g/m ²	409.76	138.75	215.48	731.12	494.54	292.15	159.66	1067.14
Specific aboveground net primary productivity	SANPP	g/kg/month	0.07	0.04	0.01	0.15	0.07	0.05	0.01	0.19
Rate of litter mass loss	LITTER	%	65.02	11.87	37.32	89.44	42.33	20.05	15.74	85.19
Total soil organic carbon concentration	CARBON	t/ha	202.93	179.76	41.77	697.25	164.11	70.70	65.19	297.30

^aTrait log₁₀-transformed for analysis. Mean values, standard deviation, minimum and maximum values for each variable are displayed for each dataset.

In areas grazed by cattle or sheep, plots were fenced to exclude grazing. Biomass removal by grazing was quantified by harvesting 1-m² inside and outside the enclosure. Harvest differences were expressed as percentage of aboveground biomass removal.

Species selection and trait measurements

Frequencies of plant species at each plot were recorded with a 1 m × 1 m frame. Nomenclature followed Jäger and Werner (2002). Traits of the most abundant species (total of 49 species) were measured for ten individuals of each species as follows (Table 1): specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf C/N ratio (LC/N), stem dry matter content (SDMC), and canopy height of an individual plant (HEIGHT). Trait measurements and chemical analyses from all samples obtained in the laboratory followed standard protocols (Knevel, Bekker, Kunzmann, Stadler, & Thompson 2005).

Ecosystem properties

Total aboveground standing biomass (AGB) was harvested in March and August (minimum and maximum yearly values, respectively) on 0.5-m² per plot for each date. Specific aboveground net primary productivity (SANPP) was calculated as follows:

SANPP

$$= \frac{\log_e(\text{live biomass in August}) - \log_e(\text{live biomass in March})}{t_{\text{August}} - t_{\text{March}}}$$

where t_{August} and t_{March} are the harvest dates, and \log_e expresses the natural logarithm to the base e

SANPP expresses primary productivity on a per gram of green biomass basis instead of a ground area basis (Garnier et al. 2004), and describes the net increase in a community aboveground biomass per unit time (here: per month).

Litter mass loss (or decomposition rate) was determined in a litterbag experiment. Fresh plant material was collected in autumn 2007, and left to decompose for 12 months in the field on the soil surface in 1 mm mesh litterbags (four replicates per plot, 2 g litter each). The recovered material was cleaned, oven dried, and weighed. The rate of litter mass loss was calculated relative to its initial mass. In addition, total soil carbon was measured for the upper 60 cm of soil.

Statistical analysis

For each plot, community weighted means of each trait were calculated by weighing the trait value of a species by its frequency, and averaging the weighted trait values

across all species of a community selected for trait measurements. As a functional diversity index, we calculated the functional dispersion (FDis) of all traits. FDis is the mean distance in multidimensional trait space of individual species to the centroid of all species in the community. FDis accounts for species abundance, and is by construction unaffected by species richness. For more details see Laliberté and Legendre (2010).

Leaf traits (SLA, LDMC, LNC, LPC, LC/N) and soil parameters (Soil P, Soil K and pH) were converted into aggregate variables ('LEAFTRAITS' and 'NUTRIENTS', respectively) via principal component analyses (PCA). The first principal component score was generated as a new/aggregate value. The first PCA component for leaf traits accounted for 55.13% ('agriculture') and 72.25% ('heath') of the variance in the five trait variables. The first PCA component for soil variables accounted for 61.03% ('agriculture') and 66.92% ('heath') of the variance in the three soil parameters. LEAFTRAITS summarized the leaf economics spectrum, which ranged from leaves exhibiting acquisition properties with high SLA, LNC, and LPC and low LDMC and LC/N values to conservative leaves with low SLA, LNC, and LPC and high LDMC and LC/N values (Wright et al. 2004). LEAFTRAITS increased with SLA and decreased with LDMC.

We applied path modeling to quantify the response–effect framework. Path modeling can be considered a special approach to structural equation modeling (SEM; Grace 2006), where only single indicators are applied to each of the variables. SEM results are dependent on the correct specifications of theoretical underlying relationships among variables prior to analysis (Shipley 2000). SEM can be used in a confirmatory or exploratory mode. If used in a confirmatory mode, the theoretical model is tested to examine if the model adequately fits the data. In this study, we used an exploratory mode where an initial theoretical model was separately applied to the 'agriculture' and 'heath' datasets.

The initial response–effect model

The initial path-model (Fig. 1, variables explained in Table 1) specifies the hypothesized relationships between environmental variables (NUTRIENTS, DISTURBANCE, and WHC) influencing traits (SDMC, HEIGHT, LEAFTRAITS, and FDis), which determined ecosystem properties (AGB, SANPP, LITTER and CARBON). The environmental variables were considered exogenous variables with no incoming arrows and all other variables were endogenous variables, assumed to depend on the exogenous variables.

We assumed a positive relationship between disturbance regimes (DISTURBANCE) and nutrient availability (NUTRIENTS). Fertilizer application is more pervasive in intensively used sites, such as agricultural landscapes. Soil water holding capacity (WHC) should exhibit a negative correlation with DISTURBANCE and NUTRIENTS, because we expect that land use concentrates on soils with lower

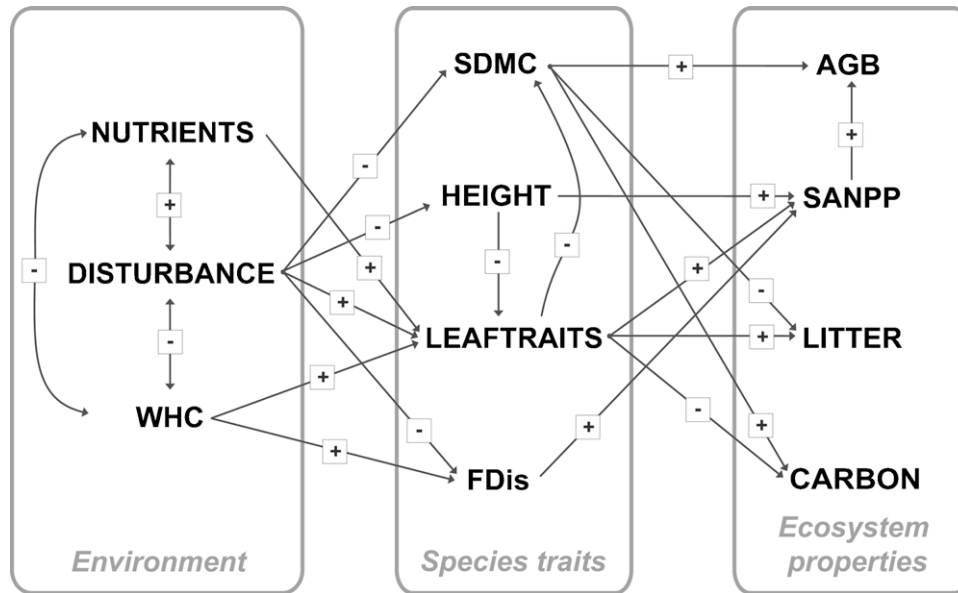


Fig. 1. Initial path model structure showing the hypothesized relationships between plant species traits, the environment and ecosystem properties. 'LEAFTRAITS' and 'NUTRIENTS' are the first principal component scores of correlated leaf traits (SLA, LDMC, LNC, LPC, LC/N) and soil parameters (Soil P, Soil K and pH), respectively. Single-headed arrows represent assumed direct effects; double-headed arrows represent correlations. Expected positive relationships are indicated by '+', negative relationships by '-'. For names and abbreviations see Table 1.

WHC, avoiding stagnant soils under the humid conditions of Northwest Germany. The model core comprised of plant traits that respond to soil resources and disturbances, and affect components of the carbon and/or nitrogen cycles. Stem dry matter content (SDMC) is often correlated with LDMC (Freschet et al. 2010), therefore the relationship between LEAFTRAITS and SDMC should be negative.

LEAFTRAITS, SDMC, and plant canopy height (HEIGHT) entered the model as community weighted means. As a measure of FD, we chose the functional dispersion of these traits (FDis, Laliberté & Legendre 2010). We expected that increasing NUTRIENTS, WHC, and DISTURBANCE would favor plants with acquisitive leaf traits, *i.e.* high LEAFTRAITS values. DISTURBANCE should negatively affect HEIGHT and SDMC, because frequent biomass removal favors non-woody plants of relatively small stature (Garnier et al. 2004; Lienin & Kleyer 2011). Frequent biomass removal represents a strong environmental filter, therefore we assumed that increasing DISTURBANCE reduces the diversity of viable plant strategies in a community, and consequently negatively affects FDis. Alternatively, higher WHC should result in a broader range of viable functional strategies, due to fewer restrictions on water use ('physiological tolerance', Currie et al. 2004).

Our second set of initial paths focused on how plant communities affect the ecosystem through specific traits. An increase in SANPP was expected with LEAFTRAITS due to the correlation of SLA with relative growth rate, whereas plant height should have an opposite effect on SANPP, due to additional investments in structural tissue. FDis was expected

to affect SANPP positively via niche complementary (Díaz et al. 2007a). LITTER and CARBON are mainly controlled by leaf characteristics. For example, species with low LDMC and high leaf nutrient values produce rapidly decomposing litter (Kazakou, Vile, Shipley, Gallet, & Garnier 2006). Therefore, LEAFTRAITS should increase LITTER, and be negatively correlated to CARBON, however SDMC should increase CARBON and AGB, while decreasing litter decomposition (De Deyn, Cornelissen, & Bardgett 2008; Freschet et al. 2010).

Based on modification indices and residuals, the initial model was altered by removing or adding paths to improve the fit between the model and the data from each site. This was achieved by maintaining the overall initial relationships (as described above). This approach allowed assessment and identification of the specific paths contingent on management. The best-fit model was selected by aiming to achieve the following: (i) a non-significant χ^2 value with an associated high *P*-value; (ii) a root mean square error of approximation (RMSEA) with values <0.05; and (iii) a Comparative Fit Index (CFI) with values >0.90 (Byrne 2010). The χ^2 test of model fit determined whether the fit between model and data was adequate and is recommended since a non-significant result is a strong indication of an adequate fit between model and data. RMSEA and CFI, which take sample size into account, are recognized as one of the most helpful criteria in structure modeling (Grace 2006).

Additional model interpretation was facilitated by 'direct effects' and 'total effects', which are the sum of direct and indirect pathways from the predictors. Statistical analyses were conducted using the computer software R to calculate

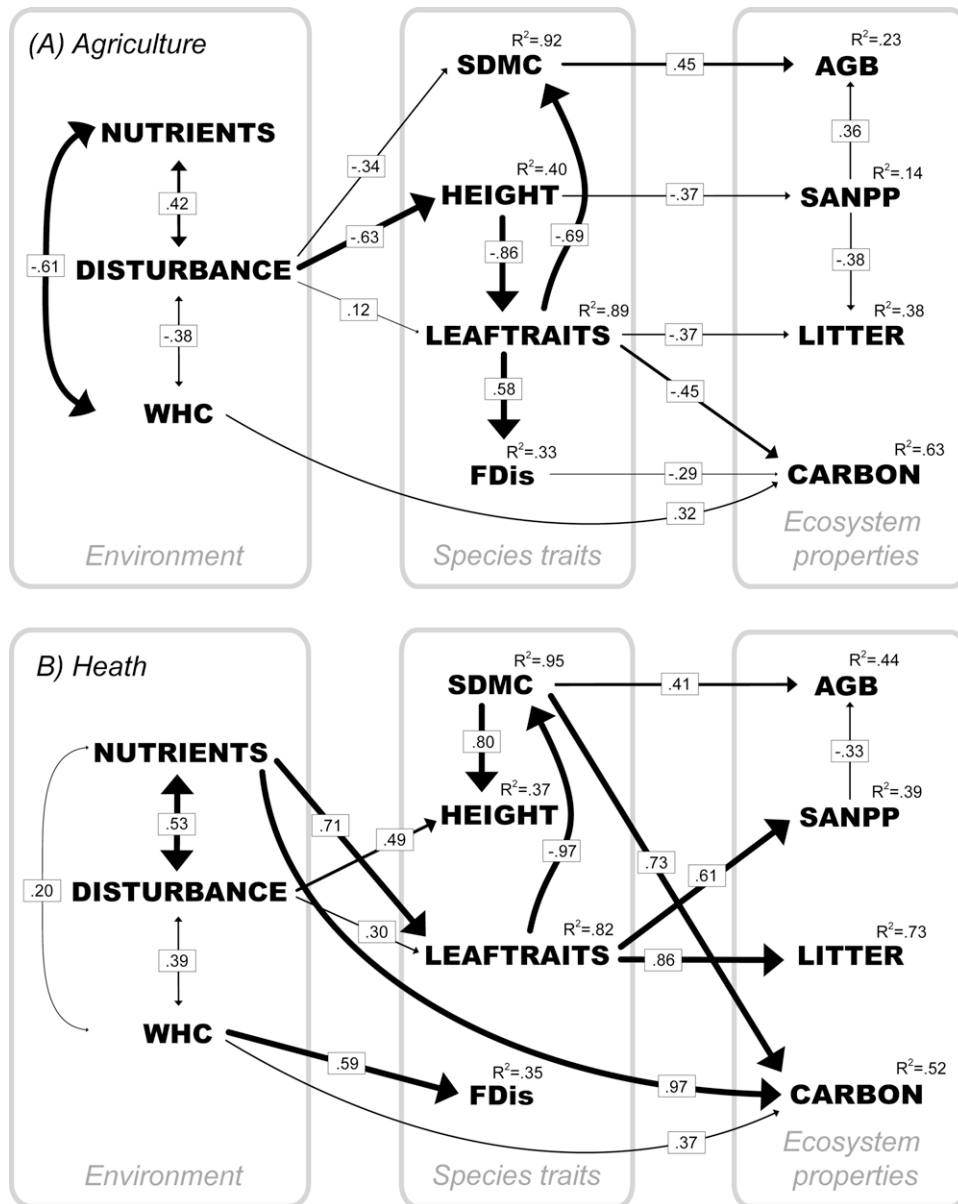


Fig. 2. Final structural equation model with standardized direct effects for datasets ‘agriculture’ (A) and ‘heath’ (B). Leaf traits (SLA, LDMC, LNC, LPC, LC/N) and soil parameters (Soil P, Soil K and pH) were converted into aggregate variables (‘LEAFTRAITS’ and ‘NUTRIENTS’, respectively). Single-headed arrows represent direct effects; double-headed arrows represent correlations. Positive effects are indicated by ‘+’ and negative effects by ‘−’. Arrow widths are proportional to the standardized direct effects. The R^2 values represent the total variance explained as a result of all predictors pointing to that variable.

CWM; and the package “FDis” within R was used to generate FDis (R Development Core Team 2011). Amos 18 (Arbuckle 2010) was employed to conduct path analysis and SEM for model evaluation.

Results

Differences between ‘agriculture’ and ‘heath’ sites

The pastures, meadows and field margins of the ‘agriculture’ site had on average higher soil phosphorus, water

holding capacity, pH, and disturbance intensity values than the ‘heath’ site (Table 1). Soil potassium was the only variable that exhibited a higher value in ‘heath’. Correspondingly, ‘agriculture’ plant communities showed increased canopy height, SLA, LNC, LPC, and decreased SDMC and LDMC values relative to ‘heath’. However, AGB, SANPP, rate of litter mass loss, and soil carbon were not significantly different between both sites.

SEM modifications

The initial model (Fig. 1) did not produce an adequate fit for the ‘agriculture’ data. Results suggested the deletion of

several non-significant paths (WHC → LEAFTRAITS and FDis, NUTRIENTS → LEAFTRAITS, DIST → FDis, SDMC → LITTER and CARBON, LEAFTRAITS → SANPP and FDis → SANPP). Adding paths from WHC to CARBON, HEIGHT to LEAFTRAITS, LEAFTRAITS to FDis, and FDis to CARBON improved model fit. The resulting ‘agriculture’ model exhibited good consistency with the data ($P=0.46$, RMSEA=0.02, CFI=0.99; see Fig. 2 for standardized direct effects), and explained 23% of the variation in AGB, 14% of the variation in SANPP, 38% of the variation in LITTER, and 63% of the variation in CARBON.

The initial ‘heath’ model did not produce adequate fit. Similarly, we removed non-significant pathways from the model (DISTURBANCE → SDMC and FDis, WHC → LEAFTRAITS, SDMC → LITTER, FDis → SANPP and HEIGHT → SANPP). Modification indices suggested the addition of two direct paths from NUTRIENTS to CARBON and WHC to CARBON. The resulting stable model was consistent with the data ($P=0.19$, RMSEA=0.07, CFI=0.98; see Fig. 2 for standardized direct effects), and explained 44% of the variation in AGB, 39% of the variation in SANPP, 73% of the variation in LITTER, and 52% of the variation in CARBON.

Our description of the final models will be primarily restricted to direct effects, but considers standardized total effects where necessary for model interpretation (Appendix A).

Environment–trait–ecosystem property relationships

Trait–trait relationships were largely consistent with the initial model. In both sites, increasing values of leaf traits, *i.e.* higher SLA and lower LDMC, covaried with lower SDMC. Increased canopy height required an increase in SDMC, and concomitantly lower SLA and LNC, and higher LDMC (~lower leaf trait values). In our initial model, a correlation between FDis and traits calculated as community-weighted means was not detected. However, in the ‘agriculture’ model, FDis increased with positive leaf trait values and decreased with plant height (total effect), indicating that grassland communities consist, on average of small, fast-growing acquisitive species with higher variation in trait values. The ‘agriculture’ plant community traits were primarily controlled by disturbance intensity; however, soil nutrients affected the ‘heath’ communities. FDis was controlled by water holding capacity only in heathlands. Most paths from traits to ecosystem properties in the ‘heath’ communities were consistent with the initial model, *e.g.* leaf traits positively affected SANPP and litter decomposition rates. A limited number of relationships between traits and ecosystem properties conformed to the initial model for the ‘agriculture’ communities, for either the path or path direction. For example, leaf traits were not related to SANPP,

although we assumed high SLA, LNC, LPC, and low LDMC would increase SANPP. Furthermore, litter decomposition rates decreased instead of increased with higher leaf trait values, and showed a positive relationship with canopy height (total effect). The only paths consistent with the initial model and ‘heath’ data were a negative leaf trait relationship with soil carbon, a positive SDMC relationship with AGB, and a negative canopy height relationship with SANPP. Results of the initial model indicated FDis should positively affect SANPP, which was not supported by the final models.

Both models included indirect links between environmental variables and ecosystem properties. The ‘agriculture’ model detected a positive correlation between soil carbon and water holding capacity. In the ‘heath’ model, soil nutrients and water holding capacity directly affected soil carbon.

Discussion

This study provided further evidence that plant-related ecosystem properties are influenced by plant traits (*e.g.* Chapin et al. 2000). Furthermore, traits depend on environmental conditions, which add a functional element to the long-standing biodiversity–ecosystem functioning debate (Tilman et al. 1997; Naeem et al. 2000; Wardle et al. 2000). Results also indicated direct environment–ecosystem links, but according to the number and strength of significant paths, environment–trait–ecosystem controls were more cohesive. Trait–trait correlations within plants remained consistent across both sites, confirming our initial model. A negative relationship between the leaf economics spectrum (Wright et al. 2004) and SDMC and canopy height was detected, indicating increased investments in supportive and conservative tissue as plants grew and matured (Freschet et al. 2010; Lienin & Kleyer 2011).

Responses of this general functional pattern to the environment and its effect on ecosystem properties were markedly shaped by land-use intensity. In our initial model, we assumed that soil nutrients and disturbance intensity should cumulatively influence leaf traits, and that canopy height and SDMC should respond to disturbance intensity, that is, more frequent disturbances lead to smaller plants (Tilman 1988; Kühner & Kleyer 2008). However, in the agricultural site the main environmental gradient affecting trait responses was disturbance, and the nutrient gradient had no influence, probably because all plots had been fertilized. In contrast to that, the nutrient and water holding capacity gradient determined to a considerable extent trait responses in the unfertilized heathland, which was managed with overall light sheep grazing. In the ‘heath’ model, SDMC and leaf traits were highly correlated, and were key traits that influenced all ecosystem properties. In contrast to this result, the ‘agriculture’ model showed the absence of any obvious key trait. Instead, each trait affected another ecosystem property (with the exception of functional dispersion). Consequently, this study revealed context-dependent

results regarding whether a few key traits or diverse traits influenced ecosystem properties.

Nutrient-driven relationships in the ‘heath’ model

As expected, and described for the initial model, leaf traits influenced the rate of productivity (SANPP), litter decomposition, and soil carbon in the ‘heath’ model. These relationships were identified in an overall nutrient-poor environment (Table 1), where relatively little variation in soil nutrients was responsible for trait responses and effects. Aboveground biomass was negatively correlated with leaf traits (indirect effects, Appendix A), and positively correlated with SDMC, indicating biomass accumulation in dry, nutrient-poor sites inhabited by plants exhibiting a resource-conservation strategy, according to the high leaf C/N ratios and dry matter content (e.g. Pakeman, Leps, Kleyer, Lavorel, & Garnier 2009). Litter decomposition in heathlands occurs gradually, resulting in slow soil carbon cycling and increased soil organic carbon (Aerts & Chapin 2000; Tjoelker, Craine, Wedin, Reich, & Tilman 2005).

Disturbance-driven relationships in the ‘agriculture’ model

Some trait–ecosystem paths in the ‘agriculture’ model were not consistent with the initial model. Disturbance intensity increased with soil nutrient availability and decreased with water holding capacity, *i.e.* farming and fertilization were concentrated on drier sites, and moister sites were less intensely farmed or abandoned. These correlations added indirect effects to the model. For example, almost no direct effect by disturbance on leaf traits was observed, however, a correlation with soil nutrient availability yielded a positive indirect effect, as SLA increased with high soil nutrients (Freschet et al. 2010). That said, a concurrent decrease of LDMC and SDMC with increasing disturbance intensity was observed.

Cumulatively, disturbance and increasing soil nutrient availability favored smaller plants with acquisitive leaves, which facilitated productivity, *i.e.* high SANPP, during shorter intervals between disturbance events. However, aboveground standing biomass accumulated in less disturbed sites, with plants exhibiting high investments in supporting tissue.

Inconsistent with the ‘heath’ model, leaf traits had negative effects on litter decomposition, which we did not expect. This effect may be explained by decreased litter decomposition at drier and open sites due to reduced microbial activity, although high disturbance and fertilization on these sites favored plants with low leaf dry matter content, which typically shows enhanced decomposition (DeGryze et al. 2004; Kazakou et al. 2006).

Diversity effects on ecosystem properties

The results showed that ecosystem properties were best explained by the average trait value of all species of a community weighted by their abundance, as predicted by the mass ratio hypothesis (Grime 1998). Evidence for the species diversity hypothesis (e.g. Tilman et al. 1997) was not revealed by our study, most likely because of a scaling effect. Environmental gradients control species occurrence patterns by strong selective pressure on responsive traits, sieving different subsets of the total range of trait expressions in the species pool of a landscape. Consequently, the distribution of trait values in each community converges around a mean describing each subset (Grime 2006). Over a relatively large gradient such as that observed in this study, differences between community means affect ecosystem properties more heavily than within-community trait dispersion, which is congruent with Grime’s (1998) mass ratio hypothesis. This is particularly relevant when the trait values are weighted by abundance, and therefore emphasize the effect of traits of the most abundant species on ecosystem properties (Díaz et al. 2007b). However, the importance of within-community functional dispersion to explain productivity may increase when environmental gradients shorten (Schwilk & Ackerly 2005). In a recent global synthesis of biodiversity–ecosystem functioning experiments, Hooper et al. (2012) found that species losses had to reach high levels (41–60%) to complement nutrient enrichment effects on productivity. All abiotic conditions including disturbance being equal, it is unlikely to find such variations in species richness in local communities of our study sites. This may explain why changes in environmental conditions and resulting changes in functional trait composition are stronger predictors than trait dispersion within communities. However, the relationship between functional and species diversity is not always straightforward, and the question of intra- versus inter-community trait diversity effects on productivity should deserve further attention, requiring more studies aiming at a simultaneous analysis of trait responses and effects.

Conclusions

This is one of the first studies showing trait responses to environmental drivers and effects on ecosystem properties in a simultaneous analysis (Lavorel et al. 2011; Minden & Kleyer 2011; de Bello et al. 2010). Two different land-use systems with common history were compared, and results showed that trait–trait relationships remained consistent, however environmental drivers exhibited marked effects on how the trait pattern affected carbon related ecosystem properties. Our results indicated that trade-offs and allometries between traits defined the general spectra in the functional organization of plants. Plant positions in these spectra were sorted by land-use intensity, which then resulted in specific effects on ecosystem properties, particularly

litter decomposition. Productivity was directly or indirectly influenced by the leaf economics spectrum, whereas standing biomass increased with investments in structural tissue. Most responses and effects were context-depending, suggesting that differences in land use intensity result in specific effects on ecosystem properties. The results further reinforce that traits of the most abundant species have the greatest effects on ecosystem properties following Grime's (1998) mass ratio hypothesis. Functional diversity had hardly any effect on ecosystem properties. These results suggest that the relevance of diversity-productivity relationships decreases with increasing length of environmental gradients. Therefore, changes in community composition and dominance hierarchies following environmental change deserve the most attention when ecosystem properties in natural systems must be maintained.

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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.baae.2012.05.002>.

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