Consistent increase in herbivory along two experimental plant diversity gradients over multiple years

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Abstract. Research on the functional importance of biodiversity, motivated by global species loss, has documented that plant species richness affects many plant-related ecosystem functions. Less is known about the effects of plant species richness on functions related to higher trophic levels, such as the consumption of biomass by animals, that is, herbivory. Previous studies have shown positive, neutral, or negative effects of plant species richness on herbivory. In the framework of a grassland biodiversity experiment (the Jena Experiment), we investigated herbivory (the proportion of leaf area damaged and the amount of leaf biomass consumed by arthropod herbivores) along two experimental gradients of plant species richness ranging from 1 to 60 species (Main Experiment) and from 1 to 8 species (Trait-Based Experiment) biannually for five and three years, respectively. Additionally, plant functional diversity, based on traits related to plant growth, was manipulated as the number of functional groups in a community (Main Experiment) or a gradient of functional trait dissimilarity (Trait-Based Experiment). Herbivory at the level of plant communities ranged from 0% to 31% (0 and 33.8 g/m^2) in the Main Experiment and 0% to 8% (0 and 13.7 g/m^2) in the Trait-Based Experiment, and it was on average higher in summer than in spring. For both experimental gradients and all years investigated, we found a consistent increase in damaged leaf area and consumed biomass with increasing plant species richness. As mechanistic explanations for effects of plant species richness, we propose changes in plant quality and herbivore communities. The presence of specific plant functional groups significantly affected herbivory, likely related to traits affecting plant defense and nutritional value, but we found little evidence for effects of plant functional diversity. The general positive relationship between plant species richness and herbivory might contribute to effects of plant species richness on other ecosystem functions such as productivity and nutrient mineralization and can cascade up the food web also affecting higher trophic levels.

Key words: biodiversity ecosystem functioning (BEF); biodiversity; biodiversity experiment; consumers; functional diversity; functional groups; grassland; legumes; plant species richness; the Jena Experiment; trophic interactions.

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INTRODUCTION

The global loss of species in recent centuries (Butchart et al. 2010) has raised questions about the functional importance of biodiversity (Schläpfer and Schmid 1999). Over 20 yr of research have demonstrated that biodiversity is of critical importance for ecosystem functioning, as a decline in biodiversity is typically associated with a lower performance and greater temporal variability in performance in many ecosystem functions (e.g., Balvanera et al. 2006, Allan et al. 2013). However, most studies investigating the effect of plant species loss on ecosystems focused on plant-related ecosystem variables like primary productivity, nutrient cycling, and invasion resistance (Hector et al. 1999, van Ruijven and Berendse 2005, Roscher et al. 2011b, Reich et al. 2012). While studies at the producer level have made an important contribution to demonstrating the functional importance of biodiversity, more studies at higher trophic levels and on related ecosystem processes are needed for an understanding of how biodiversity affects whole ecosystems (Duffy et al. 2007). For example, even the well-studied effects of plant species richness on plant productivity can be underestimated when not considering removal of biomass by heterotrophs (Seabloom et al. 2017).

Plant diversity has been demonstrated to affect abundance and diversity of invertebrates (Scherber et al. 2010, Haddad et al. 2011, Borer et al. 2012, Hertzog et al. 2016). Consequently, plant diversity can also affect ecosystem functions mediated by these consumers (Scherber et al. 2010, Ebeling et al. 2014a) and multi-trophic interactions can be stabilized by high plant diversity (Haddad et al. 2011, Ebeling et al. 2012). Herbivory, defined as the consumption of living plants or plant parts, is an interaction that is particularly important for a better understanding of multi-trophic effects of plant diversity because herbivory connects plant primary productivity with higher trophic levels in food webs (Wirth et al. 2008). Effects of plant diversity on predator communities (e.g., abundance and diversity) are likely driven by plant diversity-induced changes in herbivory and herbivore communities, which serve as a food resource for predators (Hertzog 2017). Furthermore, herbivory can cause important feedback effects such as changes in plant community composition and

diversity (Brown and Gange 1999) and increased speed of nutrient cycling (Belovsky and Slade 2000, Nitschke et al. 2015).

In contrast to the positive effects of plant species richness on abundance and diversity of herbivores (Haddad et al. 2001, Vehviläinen et al. 2007, Unsicker et al. 2008, Borer et al. 2012), effects of plant species richness on herbivory rates remain less clear. A literature search yielded 33 studies on the effects of terrestrial plant diversity on herbivory that were conducted mostly in grassland and forests ecosystems (Table 1). Roughly half of these studies found an increase in herbivory with plant species richness, while the other half showed negative, or in a few cases non-significant effects of plant species richness on herbivory (Table 1). In general, studies that investigated herbivory on individuals of particular plant species tended to find reduced herbivory with increasing plant diversity. This finding has been confirmed in agricultural systems, where the mixing of plant species (e.g., monocultures vs. two-species mixtures) reduced losses due to consumption by pest species on the focal crop (Risch 1983, Andow 1991). However, ecological studies often aim at investigating the potential contribution of herbivory to element cycling that is linked to herbivory of the whole plant community rather than of single species. These studies observed mixed effects of plant species richness on herbivory on the plant community level. Overall, there was stronger evidence for positive (nine out of 14 studies) than for negative or neutral effects (Table 1).

It has been argued that plant functional diversity could be a better predictor of herbivory by providing a more mechanistic understanding of effects of plant species loss on herbivory (Hillebrand and Matthiessen 2009, Cadotte et al. 2013). Indirect evidence for an importance of plant functional diversity for herbivory comes from studies that revealed effects of the presence of individual functional groups—the presence of legumes increased and the presence of grasses decreased herbivory (Scherber et al. 2006a, b, Sobek et al. 2009, Loranger et al. 2014)—and from a number of plant functional traits affecting herbivory (Loranger et al. 2012, 2013, Schuldt et al. 2012). In summary, the relationship between plant diversity and herbivory remains ambiguous due to studies with contrasting

Table 1. Overview of published studies investigating relationships between plant diversity and herbivory.

Ref.	Type	Habitat	Species richness range	Herbivory estimate	Basis for estimate	Comm.	Relation.
1	Obs.	Forest	German deciduous forests	Leaf damage (insects)	1 Beech species	No	Neg.
2	Meta.	Forest	1 vs. several	Leaf damage	Many species	Yes	Neg.
3	Exp.	Grassland	1 vs. 16	Leaf damage (specialists)	1 Legume species	No	Neg.
4	Exp.	Forest	1 vs. 5	Leaf damage	1 Shorea species	No	Neg.
5	Obs.	Savanna	Serengeti	Consumed biomass	Community	Yes	Neg.
6	Exp.	Grassland	1, 2, 3, 4, 6, 9	Infestation by aphids	Community	Yes	Neg.
7	Exp.	Montane grassland	18–45	Leaf damage	Many plants	Yes	Neg.
8	Meta.	Forest	1 vs. several	Leaf damage	1 Birch species	No	Neg.
9	Exp.	Grassland	1–4 (manipulated evenness)	Infestation (spittlebugs)	1 species	No	Neg.
10	Exp.	Forest	0–6	Leaf damage	1 Quercus species	No	Neg.
11	Exp.	Forest	German forests	Leaf damage	2 species	No	Neg.
12	Exp.	Grassland	1, 2, 4, 6	Leaf damage	6 polycarpous perennial species	Yes	Neg.
13	Exp.	Grassland	English grasslands	Leaf damage	5 species	No	Neg.
14	Exp.	forest	1–5	Probability pest attack	Community	Yes	None
15	Exp.	Grassland	3, 6, 12	Leaf damage (mollusks)	3 species	No	None
1	Obs.	Forest	German deciduous forests	Leaf damage (insects)	2 maple species	No	None
16	Obs.	Forest	Managed French forests	Leaf damage	1 Oak species	No	None
17	Exp.	Grassland	1, 2, 4, 8, 16, 60	Leaf damage	*Plantago lanceolata*	No	None
18	Exp.	Grassland	1 vs. 60	Leaf damage	5 forb species	No	Neg. (1) Pos. (4)
3	Exp.	Grassland	1 vs. 16	Leaf damage (generalists)	1 legume species	No	Pos.
19	Exp.	Grassland	1, 2, 3, 4, 8, 12	Leaf damage	Community	Yes	Pos.
20	Exp.	Forest	1 avs. 3	Leaf damage	1 Rosea tree	No	Pos.
21	Exp.	Forest	3, 6, 18	Leaf damage	2 Conyza species	No	Pos.
22	Exp.	Grassland	1, 2, 4, 8, 16, 60	Leaf damage	all planted species	Yes	Pos.
23	Exp.	Forest	25–69	Leaf damage	10 tree species	Yes	Pos.
8	Meta.	Forest	1 vs. several	Leaf damage	Oak and Alder	No	Pos.
24	Exp.	Grassland	1, 2, 4, 6, 8, 11	Number grazed plants	Community	Yes	Pos.
25	Exp.	Grassland	1, 2, 4, 8, 16, 60	Leaf damage	1 species	No	Pos.
26	Exp.	Grassland	1, 2, 4, 8, 16, 60	Leaf damage	Community	Yes	Pos.
27	Exp.	Forest and grassland	Koffer scientific reserve	Leaf damage	27 species	Yes	Pos.
28	Exp.	Grassland	1, 2, 4, 8, 16, 60	Leaf damage	Community	Yes	Pos.
29	Exp.	Forest	25–69	Leaf damage	10 tree species	Yes	Pos.
30	Exp.	Forest	25–69	Leaf damage	10 tree species	Yes	Pos.

Notes: The column "Ref(erence)" identifies the study. "Type" indicates whether the study was an experiment or observational study. "Habitat" categorizes the studied ecosystem. "Species richness range" quantifies the levels of plant diversity in the study. If only a location is stated, the study investigated the natural range in species richness at that location. "Herbivory estimate" describes what was used as a measure for herbivory, and "basis for estimate" describes the study unit on which the potential effect of plant species richness was measured. "Comm(unity)" indicates whether the herbivory was measured for plant communities or individual species. Finally, "Relation(ship)" shows which kind of relationship was found between plant diversity and herbivory. Study references: 1: Sobek et al. (2009); 2: Jactel and Brockerhoff (2007); 3: Lau et al. (2008); 4: Massey et al. (2006); 5: McNaughton (1985); 6: Petermann et al. (2010); 7: Unsicker et al. (2006); 8: Vehviläinen et al. (2007); 9: Wilsey and Polley (2002); 10: Alalouni et al. (2014); 11: Vockenhuber et al. (2013); 12: Lanta (2007); 13: Silvertown (1980); 14: Castagneyrol et al. (2014); 15: Hanley (2004); 16: Yguel et al. (2011); 17: Mraja et al. (2011); 18: Lipowsky et al. (2011); 19: Mulder (1999); 20: Plath et al. (2012); 21: Prieur-Richard et al. (2002); 22: Scherber et al. (2006*b*); 23: Schuldt et al. (2010); 24: Wang et al. (2010); 25: Scherber et al. (2006*a*); 26: Loranger et al. (2014); 27: Dinnage (2013); 28: Ebeling et al. (2014*a*); 29: Schuldt et al. (2014); 30: Schuldt et al. (2015).

results (Table 1) and effects of functional diversity are currently largely unexplored. In addition, studies on herbivory where plant species richness has been manipulated have often been conducted within a single year and shortly after the onset of the experiment. Considering the strong temporal dynamics in plant community composition and resulting productivity across years (Reich et al. 2012, Meyer et al. 2016), it is of utmost importance to also consider the cascading temporal effects on higher trophic interactions, such as herbivory as otherwise results could be biased by transient dynamics or temporal variability in herbivory.

Here, we address the temporal changes in invertebrate herbivory rates in response to plant species richness and functional trait diversity. Specifically, we investigated herbivory responses to plant species richness and plant functional trait diversity at the plant community level in two biodiversity experiments during both spring and summer over several years. Following past studies, we hypothesized that higher plant species richness, functional diversity, and the presence of legumes would increase herbivory, while the presence of grasses would decrease herbivory.

Methods

Study site and experimental design

The study was conducted in the framework of "The Jena Experiment," one of the largest long-term biodiversity experiments worldwide, which is situated on a 10 ha large area in the floodplain of the Saale river in Jena, Germany (50°57′3.06″ N, 11°37′29.98″ E, 130 m asl). Climatic conditions are characterized by mean annual temperatures of 9.9°C and precipitation of 610 mm (Hoffmann et al. 2014). The field site was used as a highly fertilized arable field for growing vegetables and cereals before the establishment of the Jena Experiment in 2002 (Roscher et al. 2004). The species pool of the Jena Experiment comprises 60 plant species typical of semi-natural species-rich mesophilic grasslands (Molinio-Arrhenateretea meadows according to Ellenberg 1988). All experimental plant communities were sown with constant total densities with equal proportions of all species in the mixtures, mown twice a year in late May and August, and weeded three times a

year in spring, summer, and autumn to maintain the biodiversity gradients. Experimental plots were not fertilized. The Jena Experiment consists of various biodiversity experiments established on the same field site. For the current study, we used the plant- and functional diversity gradients of the so-called Main Experiment (Roscher et al. 2004) and the Trait-Based Experiment (Ebeling et al. 2014b). Also, all 60 plant species have been established as monocultures.

The Main Experiment was established in 2002 on 82 plots of 20 × 20 m size (reduced to 6 × 5 m in 2009) and manipulates plant species richness and plant functional diversity, based on plant functional groups. To account for a gradient in soil texture with distance from the river, the Main Experiment was established in a block design. The diversity gradient was created by sowing plant communities with random subsets of the species pool of a defined species richness level on a logarithmic scale (1, 2, 4, 8, 16, and 60) and with 16 replicates at each richness level from one to eight, 14 replicates at species richness 16, and four replicates at species richness 60. In addition to species richness, functional diversity was manipulated by varying the number of functional groups present in a community. Plant species were assigned to four functional groups—grasses, legumes, small herbs, and tall herbs—based on a cluster analysis of seventeen plant traits spanning aboveground and belowground morphology, phenology, and the capacity of N_2 fixation (Roscher et al. 2004). The number of plant functional groups was varied from one to four functional groups in species mixtures independently of species richness in a full-factorial design. There were the limitations that monocultures can contain only one functional group, two-species mixtures contained only one or two functional groups, and all 60-species mixtures contained all four functional groups because these mixtures were comprised of the complete species pool (Roscher et al. 2004).

The Trait-Based Experiment manipulates plant species richness and functional diversity, derived from continuous plant functional traits (Ebeling et al. 2014b). The Trait-Based Experiment was established in 2010 on a total of 138 plots of 3.5 × 3.5 m in size and used a subset of 20 plant species from the full 60-species pool that excludes legumes because their importance for grassland

communities was already well documented at the time (Mulder et al. 2002, Temperton et al. 2007). Plant species were described by six traits related to spatial and temporal resource acquisition as analyzed using a principal component analysis (Ebeling et al. 2014b). The resulting two main axes describe the major gradients in functional similarity. The first axis separates species according to their resource use along a spatial gradient (light, water, nutrients) and the second axis along a temporal gradient (phenology). Three partially overlapping species pools of eight species each were defined based on the results of the principal components analysis (PCA). Pool 1 covered the entire PCA axis 1, thus representing species with different spatial resource use niches. Pool 2 covered the entire PCA axis 2, thus representing species with different temporal resource use niches. Both pools contain only species at intermediate values of the respective orthogonal axis. In contrast, pool 3 comprised the extreme species on the two PCA axes and thus maximized both spatial and temporal functional diversity (Ebeling et al. 2014b). Each pool was divided into four sectors from which two species were selected per sector. The range and distance of sectors, which are covered by the species in mixtures, define the level of functional diversity, which is described by the functional diversity Jena index (FD_{Jena}) that ranges between one and four. $FD_{Jena} = 1$ means that species in a mixture are from the same sector, $FD_{Jena} = 2$ that species are from neighboring sectors, $FD_{Jena} = 3$ that species are from sectors separated by one sector in between, and $FD_{Jena} = 4$ that species are from the first and the last sectors, representing maximal functional diversity. For a particular plant community, species were selected randomly from the appropriate sectors. Overall, all possible combinations of species richness (levels 1, 2, 3, 4, and 8 species) and functional diversity (levels 1, 2, 3, and 4) were realized within each pool (Ebeling et al. 2014b). The Trait-Based Experiment was located in a previously unused stripe at the eastern edge of the field site and divided into three spatial blocks.

Herbivory measurements

Large vertebrates were excluded from the experimental site by a fence such that herbivory was only caused by invertebrates (though there was occasional grazing by voles). Herbivory was measured during the biomass harvest twice a year, typically at the end of May for spring and the end of August for summer. In the Main Experiment, herbivory was measured in 5 yr, and in the Trait-Based Experiment in 3 yr from 2010 and 2012 to 2014, respectively.

Sampling of plant communities.—The standing biomass in plant communities was harvested for every sampled year from each plot, in both the Main Experiment and the Trait-Based Experiment, each spring (late May) and summer (late August). From each plant community, one biomass sample was taken at a random position (same coordinates in all plots) by cutting all vegetation in an area of 20 × 50 cm at 3 cm height above the ground. Biomass samples were divided into weed, dead (detached completely brown and wilted tissue), and target biomass. The target biomass, that is, all biomass of the sown species forming the diversity gradient, was sorted to species level. Because of the patchy distribution of plants in the plant community and the extinction of several species over time, not all species sown in a given mixture were presented in the biomass sample. For each target species present in the sorted biomass samples, usually, 30 fully developed leaves (only 20 in 2012 and 2013) were sampled randomly for herbivory measurements. Only leaves undamaged by the harvesting procedure were used except for a few species growing in rosettes close to the ground, such as *Plantago media*, where cutting of the biomass practically always damages the leaves. For these species, only leaf fragments estimated to be larger than one-third of the original leaf (in the case of doubt comparison with a complete leaf of similar width) were taken for herbivory estimates. Leaves were chosen randomly by blindly drawing a leaf from the species sample and mixing the remaining biomass between draws. In the case of leaves connected to stems, the leaf situated closest to where the stem was picked was chosen. For species with fewer than the target number of leaves in the sample, all available leaves were measured. The leaf area of all sampled leaves (i.e., the area left after feeding of the herbivores including petioles) was measured with a leaf area meter (LI-3000C Area Meter, LI-COR Biosciences, Lincoln, Nebraska, USA). The biomass of each species sample per plot

(including the measured leaves) was oven-dried (70°C/48 h) to determine dry weight.

Estimating herbivory damage.—The proportion of leaf area removed by herbivores was not estimated directly (e.g., Johnson et al. 2016) because of the expected low levels of herbivory and the large range of up to two orders of magnitude in the size of leaves in the biomass. To exemplify, average leaf size in Spring 2010 in monocultures was 0.72 cm^2 for *Festuca rubra* and 66.44 cm^2 for *Cirsium oleaceum* (range between 16.1 and 127.9 cm^2 in this sample). Instead, herbivore damage (i.e., the leaf area damaged by herbivores in mm^2) was estimated visually by comparing the damaged leaf area to a series of circular and square templates ranging in size from 1 to 500 mm^2. Herbivory damage included four different herbivory damage types: chewing, sap sucking, leaf mining, and rasping damage. For each leaf, a single value of the total area damaged by all types of herbivory was estimated (Loranger et al. 2014). We did not estimate the damaged area for each type of damage separately because of the high number of leaves that needed to be processed (about 10,000 leaves per experiment and sampling campaign). Estimates of herbivory damage did not include missing sections of leaf blades attributable to the harvest (e.g., straight, fresh cuts) and holes in leaf blades surrounded by dead, brown tissue, often shading off into yellow surrounding tissue, which were accompanied by gray-brown spots with a likewise yellow corona. These characteristics are symptoms of a leaf spot disease caused by bacterial or fungal infections causing necrosis where dry, dead tissue can break off leaving holes (Greenwood and Halstead 2009). Likewise, missing tips of grass blades (Poaceae) were not included in the estimates of herbivory damage, if the adjacent area was yellow- or brownish-colored indicating senescence or infection.

Calculating herbivory rates.—Herbivory rates ($h_{ik,}$ i.e., proportion of leaf area damage) for each plant species i in a mixture k was calculated by dividing the estimated area damaged by herbivores ($A_{d,ik}$) by the original leaf area without damage. To obtain the total leaf area before herbivore feeding, we summed the leaf area remaining after feeding by herbivores ($A_{m,ik}$) that was measured with a leaf area meter and the leaf area removed by chewing herbivores. Only the leaf area removed by chewing herbivores was added because areas damaged by sap sucking, leaf mining, and rasping herbivores cast a shadow detectable by the area meter and are thus already included in the measured leaf area (Loranger et al. 2014). The area removed by chewing damage was unknown for plants in the community samples of varying diversity because only one value of total leaf area damaged by all types of herbivores was estimated. To estimate the leaf area removed by chewing herbivores, we used a species-specific correction factor (c_i) that estimated the proportion of herbivory damage caused by chewing herbivores (chewing damage divided by total herbivory damage; values between 0 and 1).

$$h_{ik} = \frac{A_{d,ik}}{\left(A_{m,ik} + c_i A_{d,ik}\right)}$$

The correction factor c_i was calculated separately for spring and summer from data from monoculture measurements in 2010 and 2011, where all four herbivory damage types were estimated separately. For one small herb species in summer, which we failed to sample in monocultures (*Ajuga reptans*), the average proportion of chewing damage of the plant functional group small herbs was used as a correction factor. For each plant species in each plot, the estimated leaf area damaged by herbivores was multiplied by this correction factor to obtain the area missing due to chewing damage.

A community-level herbivory rate h_k was calculated by summing the species-specific herbivory rates weighted by their respective relative leaf biomass:

$$h_k = \sum_{i=1}^{s} \frac{h_{ik} B_{ik}}{B_k}$$

where B_{ik} is the dry mass of the leaves of species i in community k, B_k the total leaf dry mass, and s the number of species in the community k. Aboveground plant biomass values for each plant species in each plot, year, and season (measured as described above) were converted to leaf biomass by multiplying with the quotient of leaf area ratio (LAR*) and specific leaf area (SLA) as described below. Estimates of herbivory were robust against using the correction factor (c_i) and

estimating its values from the proportions of herbivory types in monocultures (Appendix S2).

In <5% of the species/plot combinations, herbivory damage estimates were missing due to the logistic difficulties of coordinating two teams conducting the large biomass and herbivory sampling campaigns within a few days. When measurements of all species in a plot were missing, this plot was removed from the analysis. In cases where only values of single species were missing, we used the monoculture herbivory rate of the respective species to substitute for the missing plot-specific measurement.

Calculating consumed biomass.—Herbivory rates were converted into estimates of consumed plant biomass in three steps. First, the total leaf biomass of a species in a plot was estimated from the species-specific aboveground biomass that included the biomass of leaves, stems, and inflorescences, using the ratio of leaf biomass to total aboveground biomass. This ratio was calculated as the aboveground LAR* (i.e., leaf area per aboveground plant biomass) divided by the SLA (i.e., leaf area per leaf biomass). These variables were available for all plant species based on measurements in the monocultures on the field site of the Jena Experiment (Gubsch et al. 2011a, Roscher et al. 2011a, Lipowsky et al. 2015). Second, the leaf biomass of each species in each mixture was multiplied by the respective herbivory rate to obtain the leaf biomass consumed from this species in gram dry weight per square meter. Third, the total biomass removed from a particular plant community was calculated by summing the consumed leaf biomass over all plant species in the community (Loranger et al. 2014). For those species where plot-specific trait information was available from the Main Experiment, calculated values of removed biomass using plot-specific data did not systematically differ in a sensitivity analysis from values calculated based on monoculture trait values (Appendix S3).

Statistical analysis

Statistical analyses were performed using R version 3.2.2 (R Development Core Team 2014). We build separate linear mixed-effects models for the Main Experiment and the Trait-Based Experiment with either herbivory rates or consumed biomass as the response variable. For the Main Experiment, we tested the effect of year (as a factor), season (May or August biomass harvest), sown plant species richness, and the number of plant functional groups in each plot. The explanatory variables were fitted in this order along with all possible interactions. Plot nested within block was included as a categorical random effect to account for spatial and year as a continuous random effect to account for temporal non-independence of the data. For the Trait-Based Experiment, similar models with the same random-effect structure were fitted with species pool, year, season, sown plant species richness, and FD_{Jena}, (in this order) and all possible interactions as fixed effects. Models were assessed using the lme function from the nlme package (Pinheiro et al. 2012). Type I models were fit using maximum likelihood with a α-level of 0.05. Starting with full models, stepwise model simplification of the fixed effects was used to derive minimal adequate models based on log likelihood ratio tests between nested models (ANOVA command in R). Explanatory variables resulting in non-significant P-values when comparing between a model with and without the respective variable were removed from the models starting with the highest order interactions. We applied reciprocal transformations (adding a constant of 1 to the raw data to avoid division by zero) to herbivory rates and the consumed biomass values to ensure normality of errors and homoscedasticity in the models, as assessed by diagnostic plots. After this transformation, the data fulfilled the prerequisites of the model best compared to other more commonly used transformations. To test for the influence of the presence of individual functional groups in the Main Experiment, we added the presence of functional groups together with two-way interactions with seasons and with year to the minimum adequate model for the Main Experiment (Loranger et al. 2014). This was done in separate models for all four functional groups followed by removal of non-significant terms.

Results

The average herbivory rates ranged from 0% to 31.24% in the Main Experiment and 0% to 8.01% in the Trait-Based Experiment. Between 0 and 33.77 g/m^2 of plant biomass were consumed in the Main Experiment and 0 and 13.72 g/m^2 in the Trait-Based Experiment.
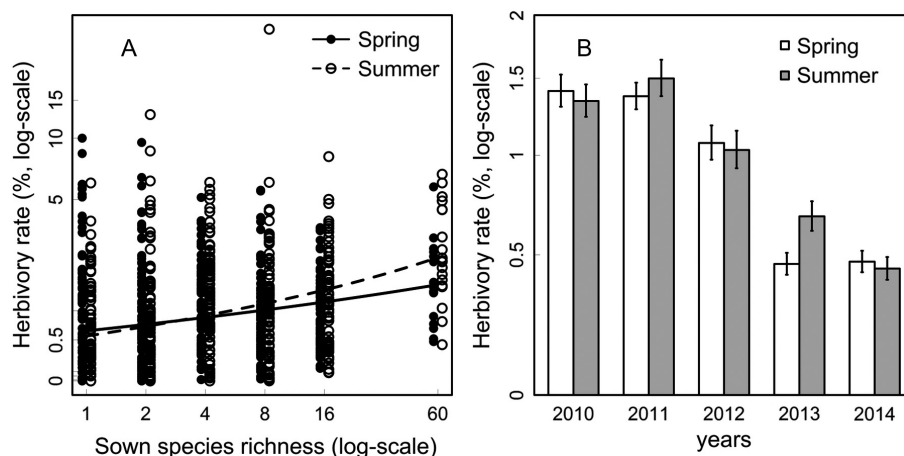
Fig. 1. Effects of sown species richness (A) and year (B) on herbivory rates in the Main Experiment. Both effects interacted significantly with season. Only significant effects as detailed in Table 2 are shown. Lines are predictions from the minimum adequate model. Bar plots show means with standard errors. The main effect of season and the effects of the presence of individual functional groups are shown in Appendix S1: Fig. S1.

Main Experiment

Herbivory rates increased with higher plant species richness from 0.82% in monocultures to 1.82% in the sixty plant species mixtures. The increase was stronger in summer than in spring (Fig. 1A, Table 2). While the effect of plant species richness was independent of year (Table 2), the average herbivory rate differed among years, with higher herbivory rates in the earlier than later years (Fig. 1B). The number of plant functional groups did not affect herbivory rates (Table 2). However, the presence of individual plant functional groups had significant effects, none of which interacted with year (Table 3). The presence of legumes increased herbivory rates by more than a third (Appendix S1: Fig. S1A). In contrast, herbivory rates were lower if grasses were present in the mixtures (Appendix S1: Fig. S1B). This effect was stronger in summer than in spring. Herbivory rates increased by almost a third in the presence of small herbs (Appendix S1: Fig. S1C). For tall herbs, there was a strong interaction with season (Appendix S1: Fig. S1D). While herbivory rates were lower in plant species mixtures with tall herbs in spring, they were higher in species mixtures with tall herbs in summer (Appendix S1: Fig. S1D).

Consumed biomass increased with sown plant species richness (Fig. 2A, Table 2) and with increasing number of plant functional groups in a

Table 2. Results for the Main Experiment.

Explanatory variable	Herbivory rates		Consumed biomass	
	df	F	df	F
Year	**4, 691**	**102.7*****	**4, 696**	**45.64*****
Season	1, 691	1.670	**1, 696**	**44.73*****
Sown species richness (SR)	**1, 76**	**10.73****	**1, 75**	**67.02*****
No. functional groups (FG)	1, 75	$(2.182)^{10}$	**1, 75**	**6.558***
Year × season	**4, 691**	**3.025***	4, 686	$(0.300)^7$
Year × SR	4, 682	$(0.409)^6$	4, 682	$(0.203)^6$
Season × SR	**1, 691**	**8.502****	1, 695	$(0.443)^{11}$
Year × FG	4, 687	$(1.591)^9$	4, 691	$(0.767)^{10}$
Season × FG	1, 686	$(1.079)^8$	1, 690	$(0.081)^8$
SR × FG	1, 74	$(0.513)^7$	1, 74	$(0.284)^9$
Year × season × SR	4, 674	$(0.954)^4$	4, 673	$(0.375)^3$
Year × season × FG	4, 678	$(1.309)^5$	4, 678	$(0.431)^5$
Year × SR × FG	4, 669	$(0.536)^2$	4, 669	$(0.271)^2$
Season × SR × FG	1, 673	$(0.388)^3$	1, 677	$(0.065)^4$
Year × season × SR × FG	4, 665	$(0.151)^1$	4, 665	$(0.052)^1$

Notes: Given are summary statistics for linear mixed-effects models testing the effects of sown species richness, number of functional groups, year, season, and all interactions on herbivory rates or consumed biomass for a period of 5 yr. The minimum adequate model for each response variable is given. Significance explanatory variables are indicated by symbols: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and emphasized in bold. Terms in parentheses were non-significant and have been removed during model simplification in the order giving by superscript numbers.

Table 3. Results for the Main Experiment.

Functional group (FG)	Legumes		Grasses		Small herbs		Tall herbs	
	df	F	df	F	df	F	df	F
Herbivory rates								
Presence FG	**1, 75**	**17.20*****	**1, 75**	**11.36****	**1, 75**	**9.450****	1, 75	0.662
Presence FG × year	4, 686	(1.604)[1]	4, 686	(1.802)[1]	4, 687	(1.703)[2]	4, 686	(1.210)[1]
Presence FG × season	1, 690	(3.472)[2]	**1, 690**	**10.67****	1, 686	0.7164[1]	**1, 690**	**6.297***
Consumed biomass								
Presence FG	**1, 74**	**16.04*****	**1, 74**	**34.87*****	**1, 74**	**6.717***	1, 74	(1.826)[3]
Presence FG × year	4, 69	(0.388)[1]	4, 691	(0.838)[1]	4, 692	(0.910)[2]	4, 692	(0.247)[2]
Presence FG × season	**1, 695**	**4.730***	**1, 695**	**9.851****	1, 691	(0.376)[1]	1, 691	(0.006)[1]

Notes: Given are summary statistics for linear mixed-effects models testing the effect of the presence of individual functional groups in a plant community on herbivory rates and consumed biomass. The effects of the different functional groups were tested in separate models by adding their presence and its interactions with year and with season to the minimum adequate models given in Table 2.

Significance explanatory variables are indicated by symbols: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and emphasized in bold. Terms in parentheses were non-significant and have been removed during model simplification in the order giving by superscript numbers. Akaike's information criterion (AIC) of the minimal adequate models were: herbivory rates AIC = −504.2, consumed biomass AIC = −295.9. The final model AICs for herbivory rates are as follows: legumes, −518.2; grasses, −522.1; small herbs, −511.3; tall herbs, −507.2. The final model AICs for consumed biomass are: legumes, −311.5; grasses, −329.8; small herbs, −300.3; tall herbs, −295.9.

species mixture (Fig. 2B) independent from year or season (Table 2). As for herbivory rates, consumed biomass was higher in earlier than in later years (Fig. 2C) and higher in summer than in spring (Fig. 2D). The presence of individual plant functional groups in the community affected also the amount of consumed biomass (Table 3). For species mixtures with legumes, consumed biomass was twice as high as without them (Appendix S1: Fig. S2A). The effect of legumes was slightly stronger in spring. The effect of grasses on consumed biomass strongly depended on season (Appendix S1: Fig. S2B). In summer, the presence of grasses had a positive effect and in spring a negative effect on consumed biomass. Consumed biomass was twice as high in species mixtures with small herbs compared to those without them (Appendix S1: Fig. S2C). Tall herbs had no significant effect on consumed biomass (Table 3).

Trait-Based Experiment

Herbivory rates in the Trait-Based Experiment were affected by sown plant species richness (Fig. 3A), the species pool (Fig. 3B), and the year (Table 4; Appendix S1: Fig. S3). The effect of sown plant species richness interacted with year, showing stronger effects on herbivory in 2012 and 2014 than in 2013 (Fig. 3A). With regard to species pools, herbivory rates were higher in species mixtures from pools 1 and 3 than in species mixtures from pool 2 (Fig. 3B). For 2012 and

2014, the herbivory rate was higher than in 2013 (Appendix S1: Fig. S3).

The amount of consumed biomass increased with increasing sown plant species richness especially in summer (Fig. 4A, Table 4). Effects of pool, year, and season interacted significantly causing idiosyncratic differences between the individual measurements (Fig. 4B) but also showing significant main effects (Table 4). Regarding the different species pools, most biomass was consumed in species mixtures from pool 1, less from pool 2, and least from pool 3 (Appendix S1: Fig. S4A). Generally, consumed biomass was higher in 2012 and 2014 than in 2013 (Appendix S1: Fig. S4B), and more biomass was consumed in summer than in spring (Appendix S1: Fig. S4C).

Discussion

We found consistent positive effects of plant species richness on herbivory rates and consumed biomass over different experiments, seasons, and years. These results strengthen the evidence for a positive effect of plant diversity on herbivory that previously emerged from a single year of measurements in the Main Experiment (Loranger et al. 2014). In contrast to plant species richness, plant functional diversity (number of functional groups in the Main Experiment and manipulated functional diversity, FD_{jena}, in the Trait-Based Experiment) had no effect on herbivory rates and only
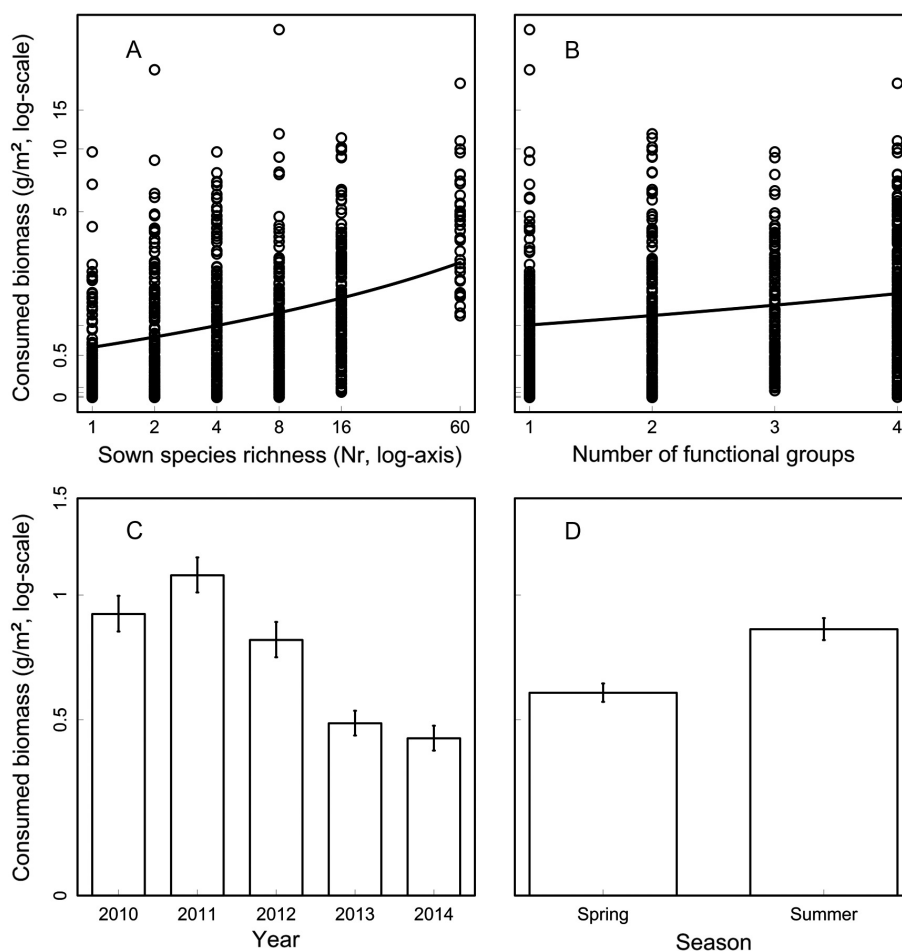
Fig. 2. Effects of sown species richness (A), number of functional groups (B), year (C), and season (D) on consumed biomass in the Main Experiment. Only significant effects are shown as detailed in Table 2. Lines are predictions from the minimum adequate model. Bar plots show means with standard errors. The effects of the presence of individual functional groups are shown in Appendix S1: Fig. S2.

weak effects on consumed biomass. However, the presence of specific plant functional groups in the Main Experiment had strong effects. Legumes and small herbs increased herbivory rates and consumed biomass while the presence of grasses decreased herbivory rates. For consumed biomass, the effect of grasses was dependent on the season, where the presence of grasses resulted in reduced biomass consumed during the spring, but lead to increased biomass consumption in summer.

Comparison to other studies on biodiversity–herbivory relationships

Our results add to a growing number of studies that document an increase in herbivory with

higher plant species richness in grasslands (Mulder 1999, Scherber et al. 2006a, b, Lau et al. 2008, Wang et al. 2010, Dinnage 2013, Ebeling et al. 2014a, Loranger et al. 2014) and forests (Prieur-Richard et al. 2002, Vehviläinen et al. 2007, Schuldt et al. 2010, 2014, 2015, Plath et al. 2012). This finding of increased herbivory with increasing plant species richness contrasts with early ecological theory predicting that the abundance of specialized herbivores (assumed to cause most damage) decreases with plant diversity, due to the lower density of the preferred host plant species in a diverse plant community (the "resource concentration hypothesis"; Root 1973). However, more recent studies have shown that
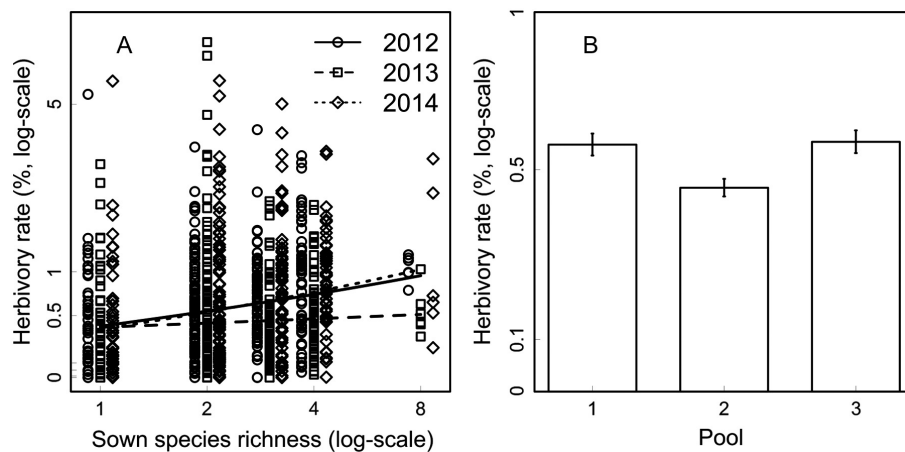
Fig. 3. Effects of sown species richness interacting with year (A) and pool (B) on herbivory rates in the Trait-Based Experiment. Only significant effects are shown as detailed in Table 4. Lines are predictions from the minimum adequate model. Bar plots show means with standard errors. The main effect of year is shown in Appendix S1: Fig. S3.

the dependence of herbivory on host plant density can be more complex, depending on herbivore behavior (Hambäck and Englund 2005). Differing results in studies that found no or negative effects of plant species richness on herbivory (Table 1) can be explained by (1) whether herbivory was investigated on plant species or community level, (2) transient dynamics in non-equilibrium communities, and (3) different methodologies used. Most studies which found negative effects of plant species richness on herbivory investigated herbivory on individual species rather than at the community level (Table 1). For studies that focus on species-specific herbivory, it is important to note that plant species differ drastically in their susceptibility to herbivory (Turcotte et al. 2014) depending on their functional traits (Loranger et al. 2012, Schuldt et al. 2012). As a result, the effect of plant species richness on herbivory experienced by an individual plant species can vary greatly between plant species even within the same study (Vehviläinen et al. 2007, Lau et al. 2008, Sobek et al. 2009, Lipowsky et al. 2011). A further complication may arise that herbivory of a single species not only depends on its own traits but also on the traits of the species in the surrounding community (Loranger et al. 2013), making the results obtained from individual species even more variable. In contrast, on a community scale, all

species-specific variations can add up to a positive net effect of plant species richness on herbivory, as has been demonstrated for plant productivity (Hector et al. 2010).

Second, transient dynamics can occur when herbivory is investigated in communities that undergo large shifts in community composition either because of successional dynamics (Schuldt et al. 2015) or plant community assembly processes in young, artificially established plant communities (discussed in detail in Loranger et al. 2014). The herbivore community may take time to assemble, in particular when experimental communities (e.g., grasslands) are created on a site where another land-use type was present beforehand (e.g., arable field, as in the case of the Jena Experiment). As more diverse plant communities harbor more diverse communities of herbivores (Hertzog et al. 2016), the process of community assembly is likely to take longer as more species need to colonize the plant communities. Consequently, the time since an experiment was established before the measurements of herbivory may alter the relationship between plant species richness and herbivory by affecting realized plant and herbivore species compositions.

Finally, differences in the plant diversity–herbivory relationships among studies can also be caused by the use of different methodologies and variables, for example, infestation rates (Wilsey

Table 4. Results for the Trait-Based Experiment.

Explanatory variable	Herbivory rates		Consumed biomass	
	df	F	df	F
Pool	**2, 132**	**3.203***	**2, 132**	**4.870****
Year	**2, 677**	**12.00****	**2, 655**	**27.58****
Season	1, 676	$(2.311)^{27}$	**1, 655**	**30.26****
Sown species richness (SR)	**1, 132**	**15.04****	**1, 132**	**29.28****
Functional diversity (FD$_{Jena}$)	1, 131	$(0.422)^{26}$	1, 131	$(0.173)^{22}$
Pool:year	4, 670	$(2.130)^{24}$	4, 665	0.822
Pool:season	2, 674	$(2.839)^{25}$	**2, 665**	**4.382***
Year:season	2, 664	$(0.184)^{18}$	**2, 665**	**3.833***
Pool:SR	2, 127	$(0.297)^{20}$	2, 126	$(0.101)^{16}$
Year:SR	**2, 677**	**4.409***	2, 660	$(1.447)^{19}$
Season:SR	1, 666	$(0.082)^{19}$	**1, 665**	**4.471***
Pool:FD$_{Jena}$	2, 129	$(1.969)^{23}$	2, 129	$(0.291)^{18}$
Year:FD$_{Jena}$	2, 667	$(0.358)^{21}$	2, 663	$(1.942)^{21}$
Season:FD$_{Jena}$	1, 669	$(0.956)^{22}$	1, 662	$(1.644)^{20}$
SR:FD$_{Jena}$	1, 126	$(0.018)^{17}$	1, 128	$(0.061)^{17}$
Pool:year:season	4, 660	$(1.798)^{16}$	**4, 665**	**5.839****
Pool:year:SR	4, 650	$(0.947)^{13}$	4, 646	$(0.692)^{11}$
Pool:season:SR	2, 641	$(0.131)^{8}$	2, 643	$(0.296)^{8}$
Year:season:SR	2, 658	$(0.814)^{15}$	2, 650	$(0.521)^{12}$
Pool:year:FD$_{Jena}$	4, 654	$(0.675)^{14}$	4, 656	$(1.390)^{15}$
Pool:season:FD$_{Jena}$	2, 643	$(0.034)^{9}$	2, 652	$(0.714)^{13}$
Year:season:FD$_{Jena}$	2, 645	$(0.452)^{10}$	2, 641	$(0.095)^{7}$
Pool:SR:FD$_{Jena}$	2, 124	$(0.036)^{7}$	2, 124	$(0.380)^{9}$
Year:SR:FD$_{Jena}$	2, 648	$(0.748)^{12}$	2, 654	$(1.238)^{14}$
Season:SR:FD$_{Jena}$	1, 647	$(0.302)^{11}$	1, 645	$(0.229)^{10}$
Pool:year:season:SR	4, 631	$(0.668)^{4}$	4, 637	$(0.815)^{6}$
Pool:year:season: FD$_{Jena}$	4, 635	$(0.344)^{5}$	4, 631	$(0.537)^{4}$
Pool:year:SR:FD$_{Jena}$	4, 625	$(0.193)^{2}$	4, 627	$(0.324)^{3}$
Pool:season:SR: FD$_{Jena}$	2, 629	$(0.468)^{3}$	2, 625	$(0.005)^{2}$
Year:season:SR: FD$_{Jena}$	2, 639	$(1.309)^{6}$	2, 635	$(0.457)^{5}$
Pool:year:season: SR:FD$_{Jena}$	4, 621	$(1.039)^{1}$	4, 621	$(0.452)^{1}$

Notes: Given are summary statistics of linear mixed-effects models testing the effects of sown species richness, FD$_{Jena}$, pool, year, season, and all interactions on herbivory rates or consumed biomass for a period of 3 yr. The minimum adequate model for each response variable is given.

Significance explanatory variables are indicated by symbols: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and emphasized in bold. Terms in parentheses were non-significant and have been removed during model simplification in the order giving by superscript numbers.

and Polley 2002, Petermann et al. 2010), probability of pest attack (Castagneyrol et al. 2014), percent biomass loss (McNaughton 1985), leaf damage (most studies in Table 1), or leaf damage by specific groups of organisms (Hanley 2004, Lau et al. 2008, Sobek et al. 2009). We included all standing herbivory damage that we could identify on leaves including multiple herbivore groups, for all species in all plots. The comprehensiveness of this approach, the long time series, and the size of the dataset presented here give additional weight to the evidence that an overall increase in herbivory with increasing plant species richness is a general ecological phenomenon rather than an exception.

Potential mechanisms

Mechanisms for effects of plant species richness on herbivory.—Three types of mechanisms could explain the increase in herbivory with plant species richness: changes in plant quantity, in plant quality, and in invertebrate communities along the gradient of plant species richness. First, high plant biomass attracting more herbivores at higher plant species richness as a mechanistic explanation of the observed increase in herbivory can be neglected given that the proportion of removed leaf area (herbivory rates) was on average low (0.5% in the Trait-Based and 0.9% in the Main Experiment) exceeding 10% only in a low number of plots. Consequently, the quantity of available plant biomass is unlikely to limit herbivore abundance in our experiment. Second, changes in plant quality with plant species richness could cause the observed increase in herbivory as often nitrogen-rich plant species, like legumes, are preferentially consumed by invertebrate herbivores (Joern and Behmer 1997, Loranger et al. 2012, 2013, 2014, Kula and Hartnett 2015). While plant community-level C:N in the Jena Experiment tended to increase (Abbas et al. 2013), leaf nitrogen concentrations did not change with plant species richness (Gubsch et al. 2011a, Roscher et al. 2011a, Lipowsky et al. 2015). Thus, nutritional quality is an unlikely determinant of herbivory rates along the diversity gradient. A potential explanation for increased consumption of herbivores at high plant diversity is a feeding adaptation shown by generalist herbivores to resources of low or heterogeneous quality called dietary mixing. This behavior achieves a balanced and beneficial diet by feeding on combinations of different host plants, thereby increasing performance (Unsicker et al. 2008). Third, changes in the invertebrate herbivore community with increasing plant species richness could explain the observed increase in herbivory with plant
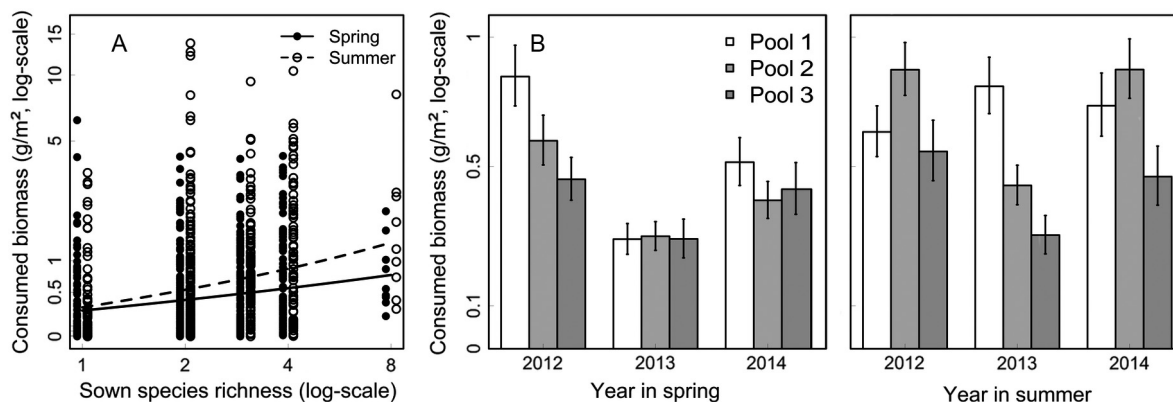
Fig. 4. Effects of sown species richness interacting with season (A) and year interacting with pool and season (B) on consumed biomass in the Trait-Based Experiment. Only significant effects are shown as detailed in Table 4. Lines are predictions from the minimum adequate model. Bar plots show means with standard errors. Significant main effects contained in the three-way interaction are shown in Appendix S1: Fig. S4.

species richness. The amount of biomass consumed by invertebrate herbivores should increase with higher abundance and, potentially, diversity of invertebrate herbivores (Ebeling et al. 2014a). That herbivore abundance and diversity increase with plant species richness has repeatedly been shown (Haddad et al. 2009, Scherber et al. 2010, Hertzog et al. 2016), and structural equation modeling has shown that both an increase in herbivore abundance and in species richness can be linked to increases in rates of herbivory (Ebeling et al. 2014a, Hertzog 2017). These changes, together with shifts in herbivore community composition, might be partially caused by or interact with changes in plant quality and also by biotic interactions with natural enemies (Oedekoven and Joern 2000). Unfortunately, there are little empirical data so far to analyze which species and which individual herbivore cause a particular amount of damage, to distinguish between various mechanisms. New molecular approaches used to study predator feeding behavior (Sheppard and Harwood 2005) may unravel this in future when adapted to track the interactions between particular plants and particular herbivores through the gradient of plant diversity.

Mechanisms for plant functional group effects on herbivory.—The strong effects of single plant functional groups on herbivory, found in our study, confirm findings of earlier experiments (Unsicker et al. 2006, Vehviläinen et al. 2007, Lau et al. 2008, Sobek et al. 2009, Loranger et al. 2014). In

general, herbivory increased in the presence of legumes and small herbs and decreased in the presence of grasses. The positive effect of legumes can be explained by the preference of invertebrate herbivores for nitrogen-rich plant tissue (Loranger et al. 2012). That is because legumes contain high concentrations of nitrogen and also increase nitrogen intake and concentrations of neighboring plants (Spehn et al. 2002, Temperton et al. 2007, Gubsch et al. 2011b, Lipowsky et al. 2015). Negative effects of the presence of grasses are most likely due to silica in the grass foliage (Massey and Hartley 2009), which is an important trait decreasing community-level herbivory (Loranger et al. 2013). Silica strocks in communities containing grasses in the Jena Experiment have been found to be twice as high as stocks in communities without grasses (Schaller et al. 2016). The surprisingly strong positive effect of the presence of small herbs on herbivory might be explained by the strong effect of the presence of this functional group on herbivore abundances in the Jena Experiment (Hertzog et al. 2016).

Mechanisms for weak effects of functional diversity on herbivory functional diversity is argued to be generally a better predictor of ecosystem functions than species richness because measures of functional diversity are directly based on functional traits that are the ultimate reason for differences between species and diversity effects (Cadotte et al. 2011). However, in our study, we found no (FD_{Jena} in the Trait-Based

Experiment) or only weak (number of functional groups in the Main Experiment) effects of functional diversity on herbivory. To understand the missing effect of functional diversity on herbivory, it is important to note that both experiments were explicitly designed to investigate effects of plant functional diversity based on traits known to affect the plant community itself, that is, plant resource use complementarity, productivity, and phenology (Roscher et al. 2004, Ebeling et al. 2014*b*), that is, traits that may or may not relate to interactions between plants and herbivores. As the explanatory potential of any measure of functional diversity depends critically on the traits used to calculate it (Cadotte et al. 2011), the use of traits that are little relevant for herbivory when quantifying functional diversity can explain why we found limited effects of functional diversity but strong effects of plant species richness.

Mechanisms for temporal changes in herbivory.— There was temporal variability in the relationship between herbivory and plant species richness as well as in the average level of community herbivory. In contrast to many other ecosystem functions that have been demonstrated to show increasingly strong effects of plant species richness over time (Meyer et al. 2016), the slope of the relationship between herbivory and plant species richness did not differ between years (Main Experiment) or showed temporal variation without a trend over time (Trait-Based Experiment) in our study. In the longer running Main Experiment, we observed a tendency for a decline in average levels of herbivory over years that becomes especially apparent when results presented here are compared with much higher herbivory rates of 2.87% measured on average in the Main Experiment in August 2004 (Scherber et al. 2006*b*). Changes in plant quality over time might explain this decline. A high nutrient availability shortly after the conversion from an agricultural field to experimental plots decreased strongly between the first and the second years of the experiment and after that remained at a low level for nitrogen and further declined for phosphorus (Oelmann et al. 2011*a*, *b*). However, also in early years, large variability in herbivory rates has been documented (0.65% in August 2003; 0.46% in May 2004; Scherber et al. 2006*b*) between or even within years (e.g., 2004) that is likely caused by strong environmental fluctuations or

extreme events affecting the invertebrate populations, for example, winter temperatures and rainfalls. The exceptionally low herbivory in the Trait-Based Experiment in 2013 can be best explained as the consequence of a heavy flooding of the field site of the Jena Experiment during 4 weeks in June 2013. While positive effects on plant biomass were recorded shortly after the flood (Wright et al. 2015), local herbivore population likely suffered from the flood (McMullen and Lytle 2012). Resulting lower invertebrate abundances at the field site after the flood in 2013 (Ebeling et al., *in press*) likely contributed to the observed low herbivory.

Implications

Effects of herbivory on plant species richness.— Herbivory can stabilize or destabilize plant species richness. Effects of herbivory on plant species richness depend on the feeding behavior of the herbivores (Hulme 1996, Olff and Ritchie 1998) but also interact with growth conditions of the plants (Borer et al. 2014). If rare plant species are preferentially consumed, for example by specialists, the competitive advantage of dominant plant species is strengthened, which would lead to a decrease in plant species richness (Olff and Ritchie 1998). On the other hand, if generalist herbivores feed proportionally to the abundance of plant species in the community or if herbivores feed preferentially on dominating competitive species, the abundance of dominant species is reduced and plant species richness stabilized (Hulme 1996). In the Jena Experiment, the proportion of mono and oligophagous herbivores was found to be generally high compared to polyphagous herbivores and increased further with higher plant species richness (A. Ebeling, M. Rzanny, M. Lange, N. Eisenhauer, L. R. Hertzog, S. T. Meyer, and W. W. Weisser, *unpublished manuscript*). If, as a consequence, herbivory destabilizes, plant species richness needs to be investigated further. Effects could also be neutral if a diverse community of specialized herbivores feeds on all occurring plant species with comparable rates or even positive if specialized herbivores of abundant plant species occur in higher densities, thereby removing more biomass compared to rarer plant species. At higher productivity, like in the diverse plots of the Jena Experiment where plant species richness can be reduced by

competition for light, positive effects of herbivory can be especially strong, because competition can be alleviated by herbivores opening the vegetation structure (Borer et al. 2014).

Herbivory as a mechanism contributing to plant species richness effects.—Increased herbivory not only may result from higher plant species richness but also may contribute to the effect of plant species richness on other ecosystem functions. For example, plant species richness increases plant productivity (Marquard et al. 2009). While higher herbivory decreases plant productivity measured as standing biomass (Coupe and Cahill 2003), herbivory can also fasten nutrient cycling and increase mineralization (Belovsky and Slade 2000, Nitschke et al. 2015) because feces are generally faster metabolized than plant litter. These effects might be especially important in mown systems, such as our experiment, where nutrients are regularly removed with the mown plant biomass. In contrast, nutrients contained in plant biomass consumed by herbivores return to the soil in the form of frass and carcasses. Thereby, herbivory contributes to higher nitrogen availability in the soil and thus, potentially, higher plant productivity (Hunter 2001, Nitschke et al. 2015). Such effects of herbivory on plant productivity should be stronger at high diversity, since herbivory increased with plant species richness, potentially contributing to the effect of plant species richness on plant productivity. Also, the relationship between plant species richness and plant productivity is even stronger than estimated based on measures of standing plant biomass when also taking the biomass consumed by higher trophic levels into account (Seabloom et al. 2017).

Cascading effects of plant species richness in trophic networks.—Herbivores, as plant consumers, connect primary productivity to higher trophic levels in the food web like, for example, predators (Wirth et al. 2008). Therefore, changes in herbivory with increasing plant species richness might also cascade to higher trophic levels. High herbivore abundance would increase the supply of resources in the form of herbivores serving as prey. In fact, increasing abundances at higher plant species richness have been documented for both invertebrate herbivores and predators (Haddad et al. 2009, Hertzog et al. 2016). Likely, these higher predator abundances contribute to higher predation rates and thus herbivore suppression at higher plant species richness (Hertzog 2017). This cascading effect would counteract increasing herbivory. Without these dampening feedbacks in the food web, the increase in herbivory with plant species richness would likely be stronger than the increase documented here. To test for this effect requires manipulating, besides plant species richness, the abundance and diversity of herbivores, and their natural enemies independent from each other, which is not possible by simple insecticide application (Siemann et al. 2004).

Conclusions

In conclusion, we have shown consistently positive effects of plant species richness on plant community herbivory and consumed biomass in a well-established long-term grassland biodiversity experiment. This positive effect of plant species richness was consistent over two independent diversity gradients and up to 5 yr of measurements strengthening the evidence that an increase in herbivory at higher plant species richness is the rule rather than the exception. The next step in analyzing the role of biodiversity in primary producers for herbivory is linking the effects of changes in herbivory to plant species richness-induced changes in the arthropod community and to investigate how increasing herbivory might contribute as a mechanism to effects of plant species richness on other ecosystem functions.

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