Plant diversity increases predation by ground-dwelling invertebrate predators

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Abstract.   Global declines in biodiversity have raised concerns over the implications of diversity loss for the functioning of ecosystems. Plant diversity loss has impacts throughout food webs affecting both consumer communities and ecosystem functions mediated by consumers. Effects of plant diversity loss on communities of invertebrate predators have been documented, yet little is known about how these translate into variations in predation rates. We measured predation rates along two plant diversity gradients in grassland experiments manipulating species richness and functional diversity. Measurements were conducted at two different heights (ground and vegetation) and in two different seasons (spring and summer), using three different types of baits. Our results show that overall predation rates increase with plant species richness, but effects are seasonally variable and are much more pronounced on the ground than in the vegetation. Plant functional diversity did not consistently affect predation rates in our experiments. Potential mechanistic explanations for an effect of plant diversity on predation include higher complementarity between predator species or reduced intraguild predation with increasing structural complexity at higher plant diversity. These results underline the importance of high local plant diversity for natural pest control.

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INTRODUCTION

Positive effects of local plant diversity on ecosystem functions such as plant productivity, nutrient cycling, or decomposition are a consensus among the scientific community (Hooper et al. 2005). Furthermore, changes in plant diversity can affect the structure, composition, and stability of whole food webs (Scherber et al. 2010, Haddad et al. 2011), consequently also affecting related ecosystem functions. Understanding how diversity affects ecosystem functioning within but also between trophic levels is a prerequisite to fully evaluate how diversity loss affects multiple ecosystem functions (Hines et al. 2015).

Linking shifts in consumer communities and the ecosystem function they mediate to changes in plant diversity is more complex than for directly plant-associated functions (Duffy 2002, Ives et al. 2005). Therefore, these relationships have been less intensively studied (Cardinale et al. 2012). Yet, there is growing evidence for higher consumer-related functioning with higher plant diversity for herbivory (Meyer et al. 2017) and pollination (Ebeling et al. 2008). In contrast, no study has so far measured predation rates caused by diverse predator communities (i.e.,

hundreds of species) along plant diversity gradients. That is surprising because changes in predation rates with plant diversity are likely. Numerous studies have reported changes in predator density and diversity along gradients of plant diversity (Haddad et al. 2009, Letourneau et al. 2011, Hertzog et al. 2016), and any change in consumer communities can be a mechanistic cause of changes in predation rates (Ebeling et al. 2014a). Several potentially counteracting mechanisms have been proposed to link plant diversity, predator communities, and predation rates. Consequently, predictions of the direction and magnitude of the effect of plant diversity on predation rates are difficult. Predation may increase or decrease depending on whether interactions between predator species are complementary, synergistic, or antagonistic (Letourneau et al. 2009). The link between predator diversity and top-down control has been intensively studied due to its importance in natural pest control; however, different meta-analyses on this topic found contrasting results (Letourneau et al. 2009, Griffin et al. 2013, Katano et al. 2015). The prevailing lack of empirical data diminishes the chance of successful management aiming at increasing pest control via natural enemies (Landis et al. 2000).

Predation rates have been shown to vary (1) globally, along a latitudinal gradient following the shifts in organismic diversity (Roslin et al. 2017); (2) seasonally (Winder et al. 1994), as seasonal shifts in predator identity (Douglass et al. 2008), prey community composition (Wilby and Thomas 2002), and vegetation structure (Finke and Denno 2002) affect predation rates; and (3) spatially, as predation rates may differ between the ground and the vegetation layer (strata), for example, because of the variation in the abundance of some important and voracious predator groups such as ground beetles that only forage on or near the ground (Miller et al. 2014). Therefore, when studying the determinants of predation rates, an important element is to take these variations and context dependency into account (Tylianakis and Romo 2010).

Predation rates under field conditions can be assessed using different methods (Letourneau et al. 2009). Many biological control studies have extensively studied predator–prey interactions using cages to set up treatments with various predator or prey communities (Cardinale et al.

2003), but the systems are often reduced to a few dominant interacting species (see, e.g., Table 1 in Janssen et al. [2006]). However, natural communities are highly diverse with potentially hundreds of predator species and as a consequence much higher potential for direct or indirect interactions affecting ecosystem functioning (Snyder et al. 2005). For a high level of replication in complex and diverse systems, the Rapid Ecosystem Function Assessment has been proposed as a toolbox of methods that measure proxies for ecosystem functions in an easy-to-use, simple, and cost-effective way (Meyer et al. 2015). For predation, sentinel prey methods are frequently used (Meyer et al. 2015, Lövei and Ferrante 2017). These methods fix live, dead, or even artificial prey items (baits) with glue or needles to sampling locations. Because prey is fixed, it cannot run away reducing the need for permanent observation. After exposure, sampling locations are surveyed and complete or partial removal of the prey items is noted as an indication of predation events. In case of artificial prey items, marks left during predation attempts can be evaluated during checking to determine groups of predators (Meyer et al. 2015).

Different prey items may show different predation rates (Lövei and Ferrante 2017) and be attractive to different groups of predators. This potential bias can be used to an advantage when estimating predation rates using different types of baits as sentinel prey to record predation rates from a broad range of potential predators. We used three different types of commonly used baits: pea aphids (Östman et al. 2003), mealworms (Rouabah et al. 2014), and dummy caterpillars made from plasticine (Sam et al. 2015), all being common sentinel prey items used to assess predation rates (Lövei and Ferrante 2017).

Here, we measured predation rates in two experiments manipulating both taxonomic diversity (species richness) and functional diversity. Using different diversity experiments, we could test whether the observed patterns are robust to variation in the length of the diversity gradient and the age of the gradient. To test for additional context dependency, we measured predation rates in two different seasons (spring and summer) and in two different strata (on the ground and in the vegetation). Specifically, we tested (1) whether predation rates increase at higher plant species richness and/or plant functional diversity

and (2) how strongly the plant diversity–predation relationship depends on the context, concerning season, stratum, prey type, and age of the plant community.

MATERIALS AND METHODS

Experimental field site

The study was conducted in 2014 in a grassland biodiversity experiment (The Jena Experiment) situated in the floodplain of the river Saale in Jena (Thuringia, Germany, 50°55′ N, 11°35′ E, 130 m above sea level). The mean annual air temperature at the site is 9.9°C, and yearly precipitation is 610 mm (Hoffmann et al. 2014). Two plant diversity experiments have been established at the field site (see Appendix S1: Fig. S1 for a representation of the spatial distribution of the plots). The first one, called the Main Experiment, was established in 2002 and included at the time of the study 80 plots of 6 × 7 m (Roscher et al. 2004). The plots were sown with combinations of grassland plant species from a species pool of 60 species commonly found in Molinio-Arrhenatherea meadows that naturally occur in the area of the field site. The plots formed a gradient of species richness with 1, 2, 4, 8, 16, and 60 sown species, each level being replicated 16 times except for the 16-species (14 replicates) and the 60-species mixtures (four replicates). Two monocultures were abandoned in 2009 due to poor performance, reducing the number of plots from 82 to 80. The experiment also manipulated functional diversity of the plant communities by varying the number of plant functional groups (grasses, small herbs, tall herbs, and legumes) sown into the plots in a full-factorial design. Limitations of the design were 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). Species composition was randomly drawn for each plot constrained by plant species number and the number and identity of the plant functional groups. To control for the effect of varying soil texture at the field site, a block design was implemented where four blocks were established parallel to the river. The second plant diversity gradient, called the Trait-Based Experiment (TBE), was established in 2010 and consisted of 138 plots of 3.5 × 3.5 m (Ebeling et al. 2014b). The aim of this experimental gradient was to directly manipulate the trait composition of the plant community to better understand the links between biodiversity and ecosystem processes. In this experiment, six plant traits (maximum height, leaf area, rooting depth, root density, growth start, and flowering start) were used to characterize the plants of the species pool of The Jena Experiment using a Principal Component Analysis. Three pools of eight species each (excluding legumes) were chosen from the PCA in which the first two axes represented traits related to spatial and temporal resource acquisition, respectively. Species pool 1 manipulated functional diversity based on the first axis (spatial resource acquisition), species pool 2 selected species along the second axis (temporal resource acquisition), and species pool 3 maximized functional diversity along both axes, covering the four corners of the trait space. Within each of these species pools, functional diversity was defined as the distance between the species grouped in sectors along the PCA axes and ranged between 1 and 4 (Ebeling et al. 2014b). In addition to the gradient in functional diversity, the TBE also includes a gradient in plant species richness ranging from 1 to 8 sown species. As in the Main Experiment, blocks were established to control for variation in environmental conditions. All plots in both experiments were manually weeded three times per year to maintain the species mixtures. Also, the field site was mown twice a year in late spring and summer as is the common practice for unfertilized meadows in the region. The realized species richness was tightly correlated with sown species richness (see Table 2 in Marquard et al. [2009]). The matrix between all plots consisted of frequently mowed standard meadow.

Predation assessment

We measured predation rates using three different types of baits: pea aphids, mealworms, and plasticine dummies. Data were collected in two seasons (spring and summer of 2014) before the two peaks in standing biomass. On seven days during each season (between 12 and 23 May and between 11 and 22 August), baits were exposed at ten specific positions per plot with a distance of 50 cm between them (see Appendix S1: Fig. S3). Baits were exposed in the morning between 9 am

and noon and recovered the next day after 24 h of exposure. The type of bait placed at each position was randomized and different on each day. For example, on the first day of the measurement, the bait at position 3 could have been a mealworm, while on the second day the bait would have been a dummy. At the end of each season, a total of 10 aphids, 20 dummies, and 40 mealworms were exposed per plot (see Appendix S1: Table S1, Fig. S1). Dummies and mealworms were placed in two strata, both on the ground and in the vegetation; aphids were placed only on the ground because of a limited number of aphids available. Baits exposed in the vegetation were put on a plant shoot at approximately half the maximum height of the selected shoot. As baits were fixed and could not move (i.e., sentinel prey), opportunistic scavengers such as slugs may attack or consume baits in our experiments in addition to actively hunting predators.

Pea aphid baits.—Pea aphids (*Acyrthosiphon pisum* (Harris, 1776), hereafter aphids) were cultivated on broad beans (*Vicia faba*) in a climate chamber at 20°C with 50% air humidity. Aphid colonies were reared continuously throughout the experiments by frequently transferring winged adults to new un-colonized plants. Plants were covered with a transparent plastic foil to avoid the dispersal of individuals. Every day in the morning, we glued fourth-instar or adult individuals (largest individuals in the colonies of at least 1 mm in size) to white labels using waterproof glue (Pattex 100% Kleber; Henkel & Cie, CH-4133 Pratteln). After exposure, we recorded whether aphids were removed from the label or not. Partially remaining aphids were counted as removed. In total, we exposed 4400 aphid baits.

Mealworms baits.—Mealworms (larvae of the beetle *Tenebrio molitor* (Linnaeus 1775)) were bought from a nearby pet shop and stored at 7°C in a fridge for a maximum of 15 d to keep mealworms in a larval stage. We used only medium- and large-sized mealworms (minimum size 3 cm, maximum size 5 cm). The mealworms were pinned with insect needles (0.35 × 38 mm; Bioform, Nürnberg, Germany) either to the ground or to plant shoots. As for the aphids, we recorded whether mealworms were removed or not. In cases where mealworms were only partly consumed, we counted this as removed for the binary analysis. In total, we exposed 17,600 mealworm baits.

Plasticine dummy baits.—We used green plasticine (Staedtler Noris Club, Nürnberg, Germany) to form dummies: plain cylinders of 0.6 × 2 cm in size to vaguely resemble lepidopteran larvae (Meyer et al. 2015). Dummies were pinned either on the ground or in the vegetation using insect needles (0.35 × 38 mm). After exposure dummies were checked for predation marks using a stereo microscope with a five times magnification. Predation marks were classified into broad categories of predators based on the large collection of photographs from Low et al. (2014) and our photographs that were taken at the field site. We used five categories of marks (Appendix S1: Fig. S4): (1) rasping marks (gastropods), (2) mandibular marks (biting insects), (3) teeth marks (rodent), (4) beak marks (bird), and (5) stylet (predatory bugs) or ovipositor marks (e.g., by parasitic Hymenoptera). In total, we exposed 8800 dummy baits. Each dummy was scored for each predator type independently as showing any marks or not (binary variables).

Additional cage experiment.—We observed many birds on the field site in May 2014 together with exceptionally high predation rates on the exposed mealworms. As the effect of the diversity gradient is certainly different between a large mobile vertebrate predator and invertebrate predators, we conducted an additional cage experiment to exclude vertebrates as potential predators. In 2015, between 18 and 22 May, we selected a subset of 16 plots across the diversity gradient in the Main Experiment with 1, 4, 16, and 60 sown plant species (four replicates each) to expose ten mealworms per plot each day. Half of the mealworms were individually protected from birds by a cage made of green plastic mesh (mesh size 10 × 10 mm) covered with a transparent plastic roof. The cages were fixed to the ground. Baits were replaced every day between 09:00 and 11:00 am, and after 24 h of exposure, removal rates were assessed. The position of the baits with cages was randomized between the days of the experiment. For example, on the second day, the bait at position number 5 was caged, and on the fourth day, the bait at the same position was uncaged.

Data analysis

All mealworms and dummies for which not even the needle was found after one day of exposure were considered to be lost. These baits were

not included in the calculation of the respective proportions of predated baits. In total, 13 dummies (<1% of the total) and 2299 mealworms (13% of the total) have been lost. The latter were likely due to heavy bird predation in spring (see *Additional cage experiment*) when occasionally birds might have removed also the needles with which mealworms were pinned. For aphids, no plastic labels were lost so that for all exposed aphids their status could be determined. To allow comparability in the results between the dummies and the other two types of baits, we combined all types of predation marks into an indicator of total predation (i.e., marks of any type as a binary variable; 0/1). In addition, we investigated the potential effect of including opportunistic scavengers on our results by analyzing predation on dummies excluding rasping marks caused by gastropods.

In both plant diversity experiments, data were aggregated across the replicates within plots separately for each type of bait, season, and stratum (ground vs. vegetation). The number of removed or attacked baits was computed. This number was divided by the number of recovered baits to derive the proportion of removed or attacked baits. This proportion, weighted by the number of recovered baits, was used as the response variable in our models. The effect of plant species richness and plant functional diversity on the proportion of predated baits was tested using generalized linear mixed models for the two experiments and the two strata separately. Models were fitted using the function *glmer* implemented in the library lme4 v1.1 (Bates et al. 2015) in R v3.2 (R Core Team 2015). A binomial distribution with a logit link was used. Models included a random effect for plots nested within blocks to account for any block- and plot-level random deviations. In addition, we included an observation-level random effect to account for overdispersion (Harrison 2014). For the Main Experiment, the models contained as fixed effects the type of baits (aphids, dummies, or mealworms), the season, plant species richness, and plant functional diversity (i.e., the number of plant functional groups) in that order. Three-way interactions between the two measures of plant diversity each and type of baits and season were included. For the TBE, equivalent models were fit including as fixed effects the type of bait (aphids, dummies, or mealworms), the season, the pool,

plant species richness, and plant functional diversity (i.e., FDjena) in that order. A three-way interaction between plant species richness and type of bait and season was included as well as an additional four-way interaction between FDjena, type of bait, season, and pool as the effect of functional diversity might differ between the different plant species pools. Plant species richness was log-transformed to improve model fit. To assess the significance of individual fixed-effect terms, we sequentially reduced the models starting from the most complex interaction terms up to single main effects and computed at each step a likelihood ratio test (LRT) statistic. This value represents the increase in model deviance as the model is gradually reduced. The significance of the LRT statistics was assessed using a chi-square distribution. The sequence in which terms were dropped from models was based on the order in which the variables were included in the models starting with the most complex interactions. We chose this method because it is an extension of classical analysis of deviance used for generalized linear models also using variation in deviance and chi-square tests to assess the significance of terms (Nelder and Baker 1972). Marginal and conditional R^2 of the models were computed using the approach described in Nakagawa and Schielzeth (2013). As the logit transformation used to model the predation rates is a nonlinear transformation, we compute the effect sizes by comparing the change in the back-transformed predicted values at the endpoints of the diversity gradients. For example, if the model predicts predation rates of 30% for the monocultures and 70% for the 60-species mixtures, we report an increase of 40 percentage points (pp) in the predation rates along the species richness gradient.

For the caging experiment, we aggregated all observations per plot and similarly computed the proportion of removed mealworm. To analyze the effect of caging on the relationship between plant species richness and predation rates, we used a generalized linear model with a binomial distribution and a logit link. The variables in the model were the caging status of the baits (caged/uncaged), plant species richness, and the interaction between these variables. We assessed the significance of the terms using an analysis of deviance with a chi-square test (Nelder and Baker 1972) as above.

RESULTS

Average predation rates and effects of season and heights

In the Main Experiment, 99% of aphid, 90% of mealworm, and 100% of dummy baits could be assessed after one day of exposure. On average, predation rates on aphids were highest with 60%, followed by predation rates on mealworms (53%) and dummies (19%). In the TBE, 99% of aphids, 86% of mealworms, and 99% of dummies were recovered, and average predation rates showed similar values to the Main Experiment (63% on aphids, 56% on mealworms, and 16% on dummies). Predations rates strongly differed between seasons. Predation rates on aphids and mealworms were significantly higher in May than in August. They decreased on average by 24 pp from 72% to 48% and by 35 pp (from 71% to 36%), respectively, from May to August in the Main Experiment (Appendix S1: Table S2), and by 33 pp (from 79% to 49%) and 48 pp (from 82% to 34%) in the TBE (Appendix S1: Table S2). Predation rates on dummies increased slightly by 7 pp (from 15% to 22%) from May to August in the Main Experiment, while they stayed unchanged at 15% in the TBE. Predation rates also differed between strata. Predation rates on mealworms and dummies in the Main Experiment were 36 pp (70% vs. 34%) and 21 pp (30% vs. 9%) higher on the ground than in the vegetation (Appendix S1: Table S2). Similarly, in the TBE, predation rates were 33 pp (71% vs. 38%) and 17 pp (24% vs. 7%) higher on the ground than in the vegetation for mealworms and dummies, respectively. Aphid baits were only exposed on the ground in both experiments. Regarding the identity of predator groups that we could identify based on the attack marks left in the dummies, biting insects and gastropods were the main group of predators with 52% and 46% of the dummies with attack marks showing marks from these two groups in the Main Experiment and 53% and 35% in the TBE, respectively. Intermediate proportions of marks were caused by rodents (Main: 10%; Trait-based: 8%). Less than 0.1% of the total observed predation marks were attributed to the other types of predators: birds, predatory bugs, and parasitic Hymenoptera.

Plant species richness effects on predation rates

Our models explained between 26% and 43% of the observed variation in predation rates (Appendix S1: Table S5), which is a relatively large fraction of the variance given that our models did not include any variables describing the predator communities. While baits exposed in the vegetation showed generally very low lower predation rates (see *Average predation rates and effects of season and heights*) without significant main effects of plant species richness, plant species richness had significant main effects on predation rates across all three types of baits and in both diversity experiments for baits exposed on the ground while for baits in the vegetation no significant main effects were found (Fig. 1, Table 1). Effects of plant species richness for baits exposed on the ground interacted with the type of dummy used for the experiment and with season. In summer, The plant species richness effects were consistently positive across all types of baits and both experiments ranging from an increase of 10 pp (from 18% in monocultures to 28% in eight-species mixtures) in the TBE for dummies to 29 pp from 44% in monocultures to 73% in the 60-species plots for mealworms in the Main Experiment. In contrast, in spring differences in strength and direction of plant species richness effects were observed (Fig. 1, Table 1). For aphids and dummies, predation rates increased with plant species richness also in May by 48 pp (from 48% in the monocultures to 96% in the 60-species mixtures) and 20 pp (from 37% in monocultures to 57% in eight-species mixtures) for aphids and by 20 pp (from 19% to 39%) and 10 pp (from 18% to 28%) for dummies and for the Main Experiment and the TBE, respectively. In the Main Experiment, plant diversity effects increased predation rates on aphids by 48 pp in May (from 48% in the monocultures to 96% in the 60-species mixtures) and 28 pp in August (from 38% to 66%). In the TBE, predation rates on aphids increased by 20 pp from monocultures to eight-species mixtures in both seasons (from 37% to 57% in May and from 70% to 90% in August). In contrast, predation rates on mealworms were positively affected in August but negatively affected by plant species richness in May but in both diversity gradients. Specifically, in May predation rates on mealworms declined along the plant species richness gradient by 51 pp (from 74% to 23%) in the vegetation and 12 pp (from 92% to 80%) on the ground in the Main
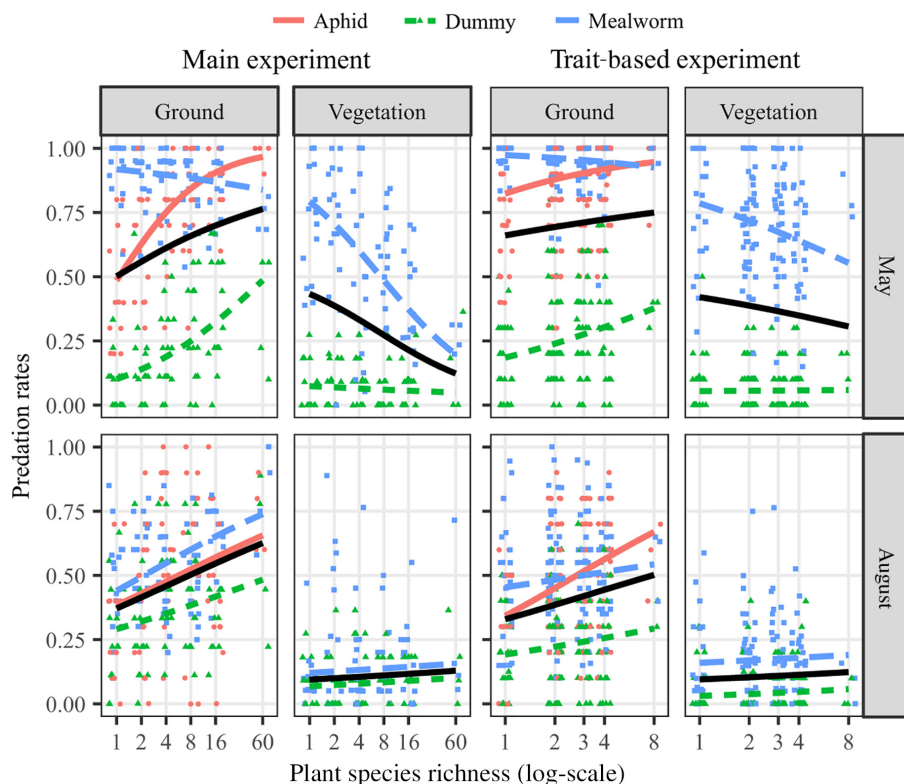
Fig. 1. Predation rates across the two plant species richness gradients: Main Experiment and Trait-Based Experiment, in two different strata (ground and vegetation), and in two different seasons (August and May). The colors indicate the different types of baits used in the experiment. Colored lines represent fitted regression curves from full generalized linear mixed models (see Table 1), and the thick black lines represent the average effect across the different types of baits.

Experiment and by 19 pp (from 75% to 56%) in the vegetation and 10 pp (from 92% to 82%) on the ground in the TBE.

Effects of excluding vertebrate predators on predation rates on mealworms

Because we observed large numbers of birds on the field site in May, the impact of vertebrate predation was tested in a separate experiment that excluded vertebrate predators using cages and compared patterns to uncaged controls. Plant species richness increased the predation rates on mealworms inside of cages, while it decreased predation rates on mealworms outside of cages (Fig. 2, Table 2).

Functional diversity effects on predation rates

Functional diversity had no significant main effects on predation rates across all three types of

baits, in both diversity experiments and for both baits on the ground and in the vegetation (Table 1). Also, no significant interactions between functional diversity and other explanatory variables were found. Plots of the fitted regression between predation rates and functional diversity are given in Appendix S1: Figs. S6 and S7.

Sensitivity analysis for the inclusion of scavenging slugs

Excluding gastropod marks from the estimates of predation rates on dummies weakened the relationship between plant species richness and predation rates on the ground. In the Main Experiment, the increase in predation rates with plant species richness became a nonsignificant trend (Appendix S1: Fig. S5, Table S3). In the TBE, the increase in predation rates with plant species richness remained significant, also when

Table 1. Generalized linear mixed model results for the relationships between predation rates and the type of baits, plant species richness, functional diversity (FunDiv), pools (only for the Trait-Based Experiment [TBE]), and season separately for each stratum (ground and vegetation) in the Main Experiment and in the TBE.

Explanatory variables	df	Main experiment		Trait-Based experiment	
		Ground	Vegetation	Ground	Vegetation
Bait type	2	189.3***	98.9***	438.4***	265.1***
Season	1	54.7***	51.1***	340.0***	207.4***
Pool	2	–	–	13.2**	3.0
Plant species richness (PSR)	1	33.4***	1.5	14.0***	0.1
Functional diversity (FunDiv)	1	0.0	2.4	0.0	0.0
Season:Pool	2	–	–	5.8	3.1
Season:PSR	1	0.3	9.1**	0.1	2.3
Season:FunDiv	1	1.5	0.6	0.0	1.5
Pool:FunDiv	2	–	–	5.8	0.5
Season:Type	2	119.9***	61.7***	257.8***	132.6***
Type:Pool	2	–	–	21.6***	5.3
Type:PSR	2	34.6***	5.5*	13.7**	1.3
Type:FunDiv	2	5.9	0.1	1.0	0.2
Season:Pool:FunDiv	2	–	–	0.8	2.4
Type:Season:Pool	4	–	–	9.5*	16.4***
Type:Season:PSR	2	26.7***	3.1	10.5**	0.0
Type:Season:FunDiv	2	0.2	0.0	1.6	0.5
Type:Pool:FDjena	5	–	–	3.5	0.6
Type:Season:Pool:FDjena	3	–	–	6.7	0.8

Notes: The models were sequentially simplified starting from the interactions up to a null model (intercept-only) one term at a time following the inverse row order. The significance of the terms was assessed using a likelihood ratio test comparing between two nested models with or without the focal term. The P-values were based on a chi-square test. Asterisks represent the significance level of the terms with *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

excluding marks caused by gastropods (Appendix S1: Fig. S5, Table S4).

Discussion

Our experiment has demonstrated an increase in invertebrate predation with higher plant species richness, an effect that was most pronounced on the ground. This increase emerged from both experiments and all three bait types, despite variation between seasons. The strongest seasonal effect was shown by predation rates on mealworms in May which declined with plant species richness. An additional experiment excluding vertebrate predators revealed that this deviation from the general pattern was due to vertebrate predators (mainly birds) which were present in high abundance at the field site only at this time of the year. We speculate that these predators were impaired by the increasing plant cover with plant richness leading to the observed decline in predation rates with plant richness. Inside cages, also predation rates on mealworms increased consistently with plant species richness. As a significant proportion of dummies showed marks from gastropods, we tested for the potential effect of these opportunistic scavengers on our analysis by excluding gastropods. We found that the positive effect of plant species richness on predation rates in the Main Experiment was weakened, while results from the TBE stayed significant. Therefore, results should be interpreted carefully as different groups of predators (and scavengers) might show different responses to plant species richness. Another caveat inherent with the use of sentinel prey is the fact that some predators use movement cues to detect their prey (Howe et al. 2009). Because of these limitations, estimates of predation rates using sentinel prey may not accurately reflect absolute levels of predation in natural communities but can estimate adequate proxies to contrast predation rates across environmental gradients (Gonzalez-Gomez et al. 2006, Lövei and Ferrante 2017).

Season and stratum effects

Predation rates on mealworms and aphids varied strongly between seasons, with higher predation rates in spring compared to summer. Such
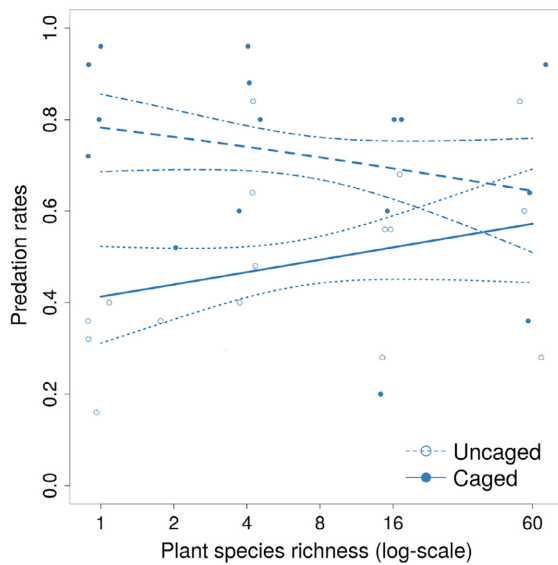
Fig. 2. Effect of removing vertebrate predation using cages on predation rates on mealworms across the plant species richness gradient in the Main Experiment in May. Points are the observed values and the solid lines the fitted regression curves from a generalized linear model (see Table 2) together with their 95% confidence intervals (dotted lines).

Table 2. Generalized linear model results for the relationship difference between predation rates on mealworm baits inside and outside of cages depending on plant functional group richness and plant species richness.

Explanatory variable	df	Deviance
Caged	1	45.6***
Plant species richness (PSR)	1	0.0
Functional group richness (FunRich)	1	0.0
Caged:FunRich	1	22.1***
Caged:PSR	1	4.1*

Notes: The *P*-values for the deviance were computed using a chi-square test. Asterisks represent the significance level of the terms with *$P< 0.05$ and ***$P< 0.001$.

changes can be caused by differences in the populations of predators between seasons and also by changes in the height of the vegetation (Solovyeva 2015). In our study, predation rates on mealworms were probably higher in May than in August due to the high activity of birds (as documented with the additional cage experiment), which feed their offspring during spring (Martin

1987). Higher predation rates on aphids in May than in August have already been reported in the literature and are thought to have a strong impact on aphid population dynamics reducing the risks of outbreaks (Winder et al. 1994).

In general, we found very low predation rates for both mealworm and dummy baits in the vegetation compared to baits on the ground. Likely explanations for these differences between the two strata are variations in the abundance of predators between the two strata, in the cues used by predators to detect their prey, and also in the hunting modes of occurring predators. For example, actively hunting carabids occur on the ground, while web-building spiders are important predators in the vegetation (Miller et al. 2014). The potentially complex interactions between bait types, season, and stratum require future studies of the predator communities and their changes in abundance, diversity, and behavior along plant diversity gradients to mechanistically understand these context effects.

Effects of plant species richness and functional diversity

We found that plant species richness had larger and more consistent effects on predation rates than plant functional diversity. This contradicts the hypothesis that functional diversity is a better predictor of ecosystem functioning than taxonomic diversity (McGill et al. 2006, Gagic et al. 2015). This might be due to two reasons. First, we used the opportunity of available experimentally created gradients in plant functional diversity to test their effects on predation in our study. However, the traits used to define these gradients such as spatial and temporal plant resource acquisition traits (Roscher et al. 2004, Ebeling et al. 2014b) may not be strongly linked to predation. We would expect that predation rates depend more on plant traits that relate to vegetation structure (Schmitz 2008). However, we decided against screening a number of plant traits for their explanatory potential for observed predation rates by creating measures of functional diversity a posteriori. Second, in our dataset, plant productivity increased with plant species richness but not with plant functional diversity. If plant diversity effects on predation were mediated by changes in aboveground productivity, predation rates would consequently respond more strongly

to plant species richness than to plant functional diversity (Hertzog et al. 2016).

Potential mechanisms of plant species richness effect on predation

Multiple mechanisms can potentially cause effects of plant species richness on predation rates. These are potentially counteracting, and our experiment does not allow us to test individual mechanisms explicitly, but based on our results, some mechanisms appear more relevant. We will briefly describe these in the following. First, the observed positive effect of plant diversity on predation may be caused by the increase in predator density with increasing plant diversity (Haddad et al. 2009, Hertzog et al. 2016) leading to higher predation through mass effects as documented in Ebeling et al. (2014a). Second, as predator diversity also increases with plant diversity (Hertzog et al. 2016), complementarity between predator species (Snyder et al. 2006, 2008), positive selection effects (Straub and Snyder 2006), or facilitation (Losey and Denno 1999) may lead to the observed patterns. Third, predator species may also show different levels of voracity along the richness gradient both through selection effects (Finke and Snyder 2010) and through compensatory feeding due to changes in prey quality (Abbas et al. 2014). Finally, plant diversity effects on predation may also be mediated by the increase in vegetation structural complexity which can cause changes in predation directly and indirectly by affecting prey and predator behavior, movement, and hunting efficiency (Brose 2003, Diehl et al. 2013). Higher predation rates at higher plant species richness could be caused by reduced intra-guild predation (Finke and Denno 2002), changes in temperature and humidity conditions affecting predator activity (Heck and Crowder 1991), or reduced foraging efficiencies of top predator, such as birds, reducing predation pressure on intermediate predators (Thompson et al. 2016).

Further experimental work using moving prey and predator individuals in combination with behavioral observations or using more sophisticated methods such as gut-content analysis (Roubinet et al. 2015, Tiede et al. 2016) would enable further insights into the mechanisms underlying the positive effects of plant diversity on predation rates reported here. Another interesting result from our field site is that omnivorous species tend to become more predatory along the plant diversity gradient (Ebeling et al. 2017). Resasco et al. (2012) reported similar patterns, namely that the trophic position of omnivorous ants increased with plant richness. This implies that shifts in omnivore feeding behavior can contribute to higher predation rates with increasing plant diversity.

Ecological and applied implications

Elevated predation rates may have various effects on prey and plant communities as well as on ecosystem functioning. Higher predation rates could reduce prey population sizes and affect interspecific competition between prey species (Chase et al. 2002, Chesson and Kuang 2008) leading to changes in prey community composition. An increased predation may also affect prey foraging behavior (Preisser et al. 2007) because with increasing predation pressure prey organisms might avoid foraging in potentially risky habitats (Schmitz 2008). For example, recent evidence showed that predators can affect decomposition rates of plant litter by increasing stress levels in their prey (Hawlena et al. 2012) which would in turn affect nutrient cycling. These effects induced by predators may cascade down to lower trophic levels affecting plant community biomass (Schmitz et al. 2000, Halaj and Wise 2001), plant community composition (Schmitz 2003), and plant fitness (Romero and Koricheva 2011). Via trophic cascades, an increase in predation suppressing herbivores could cause an increase in plants biomass (Borer et al. 2005). However, at our field site community-level herbivory increased with plant species richness (Loranger et al. 2014, Meyer et al. 2017). This increase in herbivory occurred despite the increased predation pressure documented here. Taken together, these results imply that without the increase in top-down control exerted on herbivores at higher plant diversity, consumed plant biomass would be even larger in diverse plant communities.

Effects of plant diversity on predation also have implications in an applied context. In agricultural systems, biological control of herbivorous pest species by natural enemies has been of long-standing interest (Stern et al. 1959). Research on biological control has emphasized ways to enhance natural enemy populations (Landis et al. 2000, Tscharntke et al. 2007) to

reduce the reliance on insecticides by increasing biological pest control. Our work shows that predation by invertebrate natural enemies increases with higher plant species richness in line with a meta-analysis showing higher herbivore suppression with a higher diversity of crop species (Letourneau et al. 2011). This evidence calls for management schemes that sustain natural enemy populations in agricultural landscapes by increasing plant and habitat diversity (Tscharntke et al. 2007) to sustain provisioning of the important ecosystem service of pest control.

Acknowledgments

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