

ECOLOGY

Biodiversity enhances the multitrophic control of arthropod herbivory

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Arthropod herbivores cause substantial economic costs that drive an increasing need to develop environmentally sustainable approaches to herbivore control. Increasing plant diversity is expected to limit herbivory by altering plant-herbivore and predator-herbivore interactions, but the simultaneous influence of these interactions on herbivore impacts remains unexplored. We compiled 487 arthropod food webs in two long-running grassland biodiversity experiments in Europe and North America to investigate whether and how increasing plant diversity can reduce the impacts of herbivores on plants. We show that plants lose just under half as much energy to arthropod herbivores when in high-diversity mixtures versus monocultures and reveal that plant diversity decreases effects of herbivores on plants by simultaneously benefiting predators and reducing average herbivore food quality. These findings demonstrate that conserving plant diversity is crucial for maintaining interactions in food webs that provide natural control of herbivore pests.

INTRODUCTION

Decades of experiments have revealed that biodiversity of primary producers is crucial for providing and maintaining ecosystem functions and services in planted and natural grasslands (1–3), which are increasingly critical as humans expand and intensify agriculture to feed our growing population (4, 5). Although biodiversity-ecosystem functioning research has mainly focused on the relationship between primary producer diversity and biomass production, evidence is mounting for the influence of plant diversity on higher trophic levels (6) and multiple associated ecosystem functions and services (2, 7–10). In light of global findings that terrestrial insect biomass may be in decline (11), it is imperative that mechanisms underlying changes in insect biodiversity and the services they provide are identified. An improved understanding of these mechanisms will enable more accurate forecasting of changes in insect-mediated ecosystem services, such as the natural control of herbivore pests (6, 12).

Earlier studies found that plant diversity increases arthropod biomass with particularly strong effects on predator numbers (10), suggesting that plant diversity may support predator abundance,

increasing predation on herbivores and reducing herbivory on plants. Recent analyses of complex food web models have also lent support to these conclusions by showing that increasing animal diversity and biomass yields higher plant primary production (13). Conversely, other experimental studies have found evidence for a stronger positive effect of plant diversity on arthropod herbivores compared with their predators (8, 14), leading to potential increases in herbivory in high-diversity plant communities (15). Reconciling these findings—disentangling the effects of plant quantity and quality (“bottom-up”) from those of predators (“top-down”) that simultaneously act on herbivores and determining the true, generalizable role of plant diversity in constraining herbivore impacts on plant biomass production—requires a unified measure of total herbivore impacts across manipulative plant diversity experiments.

Recent findings suggest that the positive effects of plant quality and quantity on herbivore energy gains may decline from low- to high-diversity plant communities due to the dilution of high-quality resources with increased nutrient heterogeneity (6). These results are consistent with the “resource concentration hypothesis” (16), which proposes that trophic efficiency decreases as resource diversity increases (17). However, plant diversity likely constrains herbivore performance by means other than just the dilution of nutrient concentrations, as predation rates have also been shown to increase at high levels of plant diversity (18, 19). This process is described by the “enemies hypothesis” (16), which proposes that higher plant species diversity will provide greater refuge for predators [e.g., (20)], leading to greater suppression of herbivores via top-down control (19). Given that both bottom-up and top-down forces operate simultaneously, increasing plant diversity likely reduces herbivore impacts on plants through these simultaneous multitrophic controls in food webs. Together, these processes yield four central predictions around the multitrophic control of herbivory in arthropod food webs. With increasing plant diversity, herbivores will experience (i) reduced per capita energetic gains from plants (Fig. 1A) and (ii) enhanced per capita predation rates (Fig. 1A) and will therefore face (iii) increasing net losses due to these simultaneous shifts in resources and predation with increasing plant diversity (Fig. 1A). Because of the predicted

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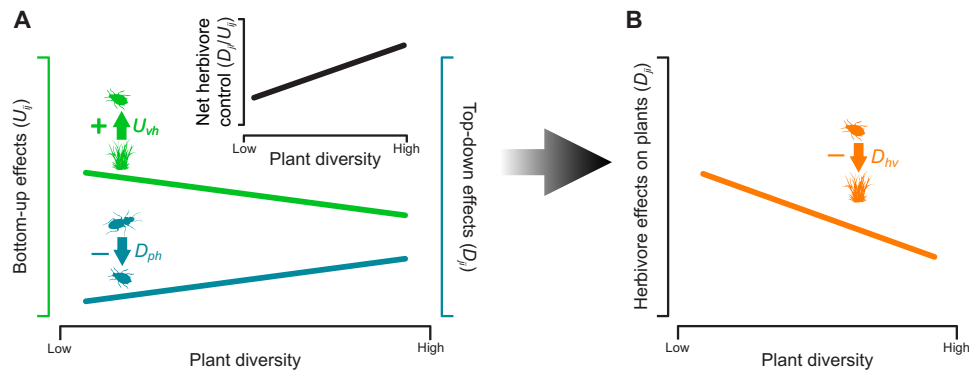


Fig. 1. Hypothesized effects of plant diversity on multitrophic control of herbivory. The simultaneous roles of the resource concentration hypothesis and enemies hypothesis in constraining herbivore impacts are described by (A) isolated bottom-up (U_{ij}) and top-down (D_{ji}) effects on herbivores, respectively, yielding the emergent net herbivore control (log ratio of top-down versus bottom-up effects). This is expected to drive a decline in (B) biomass-specific effects of herbivores on plants.

positive effect of plant diversity on net herbivore control, we expect (iv) a decline in arthropod herbivory per unit biomass of primary producers at high plant diversity (Fig. 1B).

We determine the role of plant diversity in controlling herbivore impacts on plant communities using a quantitative food web approach (21) to examine multitrophic arthropod data collected across 2 years from analogous grassland biodiversity experiments conducted on two continents, Europe (22) and North America (7). We constructed 487 functional group-level food webs (fig. S1 and table S1) from aboveground arthropod datasets (7, 22) by first grouping all species into functional feedings groups based on taxonomy and life history traits and then assigning trophic links based on known feeding relationships among these groups (see Materials and Methods). We then quantified energy fluxes along trophic links in each food web using a food web energetics approach (21, 23, 24) and quantified total fluxes of energy (i) through each food web, (ii) to herbivores, and (iii) to their arthropod predators, which also included fluxes to omnivores via herbivorous and predatory interactions, respectively. Using these energy fluxes, we quantified the top-down effects of predators and the bottom-up effects of plants on herbivores to estimate the net multitrophic control of herbivory in each food web. Last, to determine the emergent influence of plant diversity on arthropod herbivory, we quantified the top-down impact of arthropod herbivores on plant communities across the experimental plant diversity gradients by calculating herbivore feeding rate per unit biomass of primary producers (see Materials and Methods). This approach provides a unified measure of herbivory that assesses the impacts of herbivores proportional to the biomass production of plant communities of varying diversity.

RESULTS AND DISCUSSION

Plant diversity increases energy fluxes in grassland food webs

Increasing plant diversity resulted in higher overall energy flux through arthropod food webs with 95% more resource consumption in 16-species plant communities than in monocultures ($P < 0.001$; Fig. 2A and table S2). While the effect of increasing plant diversity on energy flux to herbivores was weaker (a 70% increase, $P < 0.001$; Fig. 2B and table S2), we found a particularly strong effect of plant diversity on total predation, with 162% greater energy flux to predators in 16-species plant communities compared to monocultures ($P < 0.001$;

Fig. 2C and table S2). Our initial results closely match those of recent findings from the Jena Experiment in Germany (25), despite using fundamentally different approaches to quantifying energy fluxes (21). However, unlike the study by Buzhdygan *et al.* (25), we use energy fluxes to quantify herbivore pest control via multitrophic mechanisms that represent so far unresolved competing hypotheses of plant diversity effects on herbivore control. The observed increases in energy flux in the arthropod food webs of the current study are likely driven, in part, by increased arthropod biomass and abundance with increasing plant diversity (fig. S2), as has been found in previous studies testing for plant diversity effects on arthropods (7, 8). It is, however, important to note that organismal biomass alone does not govern the energetic demands of biological communities; energy fluxes are collectively determined by variation in species composition, body size structure, and food web structure. Nevertheless, organismal biomass has been shown to be a key determinant (24) that is also sensitive to changes in primary producer biomass on which arthropod communities rely. Although the total biomass of herbivores and predators both responded similarly to increasing plant diversity (fig. S2), energy fluxes to predators increased more strongly from monocultures to 16-species plant communities than those to herbivores (Fig. 2, A and B, and table S2). This indicates that biomass is not a simple proxy for energy transfer and that approaches integrating information on metabolism, assimilation efficiency, and trophic interactions (e.g., 21, 23) yield unique insights into energy flux dynamics in multitrophic systems.

These findings corroborate those of some previous studies from grassland biodiversity experiments (9, 10), suggesting that arthropod predators benefit more strongly from increasing plant diversity than do herbivores. However, other studies have found opposite trends in organismal biomass for herbivores compared with predators across different biodiversity experiments [e.g., (9)]. We observed no marked differences in predator or herbivore biomass responses to plant diversity that could provide clear support for primacy of top-down or bottom-up processes (fig. S2). Despite apparent inconsistencies among previous studies (8–10) that measured responses in abundance or biomass, our results indicate that food web energetics across the systems analyzed in these previous studies are remarkably similar and demonstrate clearer differences in responses of herbivores versus predators to the experimental plant diversity gradients (Fig. 2). Our analyses reveal consistent shifts in energy

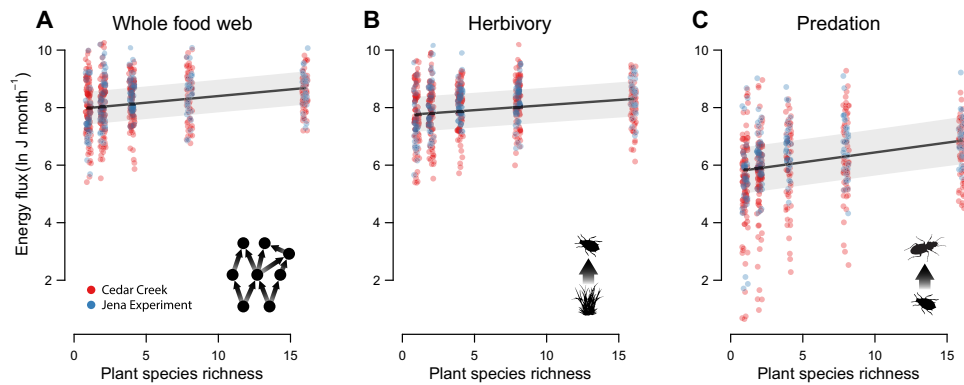


Fig. 2. Effects of plant diversity on food web energy fluxes. Plant diversity–energy flux relationships are shown for total summed energy flux (log-transformed) to all trophic groups in the arthropod food webs (A), to all herbivores (B), and to all predators (C). Trend lines show the partial effects of plant diversity from the linear mixed effects models (see table S2) after accounting for different years [\pm 95% confidence interval (CI)].

fluxes to herbivores and predators between the North American and German biodiversity experiments (Fig. 2 and table S3), suggesting that the effects of plant diversity on the energetic structure and functioning of food webs are general across different contexts.

Disentangling the multitrophic controls of herbivores in grassland food webs

The underlying mechanisms driving these different herbivore and predator responses (i.e., stronger positive plant diversity effects on predators versus herbivores) are not experimentally tested here. However, our results are consistent with the resource concentration hypothesis, whereby arthropod herbivores have lower chances of encountering preferred plant species in patches with higher plant diversity, thus reducing their likelihood of remaining in high-diversity patches (26, 27). In addition, within plant species, declines in tissue protein (nitrogen) levels have been found in plant communities with high species richness (28, 29), suggesting that host plants may be less nutritious at higher plant diversity. Note that we do not directly incorporate shifts in plant tissue stoichiometry in our calculations of energy flux and bottom-up effects, which would require quantitative knowledge of scaling relationships between stoichiometry and assimilation efficiency. Instead, our results arise from stoichiometric constraints on arthropod community structure, which is consistent with previous findings that resource stoichiometry influences arthropod diversity and biomass (30). At the same time, arthropod predators also benefit significantly from the increased habitat complexity of high-diversity plant communities, which has been suggested to reduce their risk of being detected and eaten by vertebrate predators (18).

In line with our predictions, with increasing plant diversity, we found an 11% decline in bottom-up effects of primary producers on the abundance of arthropod herbivores ($P = 0.018$; Fig. 3A and table S4) and a 25% increase in top-down effects of predators on herbivores from monocultures to 16-species plant communities, although this was statistically nonsignificant ($P = 0.105$; Fig. 3A and table S4). Moreover, our third prediction was strongly supported, as we found a significant positive effect of plant diversity on net herbivore control with an average 28% increase in the log ratio of top-down versus bottom-up effects on herbivores across the plant diversity gradients of both biodiversity experiments ($P < 0.001$; Fig. 3B and table S4). These results provide strong support (which are consistent across both experiments; table S5) for previous suggestions that primary

producer diversity could impose constraints on arthropod herbivore biomass (26, 27). However, unlike many previous attempts to quantify plant diversity effects on arthropod herbivores, by implementing a quantitative food web approach (21), our analyses integrate simultaneous mechanisms that control herbivory and thus provide new insight into the true role of plant diversity in controlling herbivores.

Plant diversity indirectly controls impacts of herbivores on plants

Our analytical approach also reveals that increasing multitrophic control on herbivores at higher plant diversity (via increased predation and reduced plant nutritional value) drives an overall decline in the biomass-specific impacts of herbivores on plant communities ($P < 0.001$; Fig. 3C and table S4), shedding light on earlier work that demonstrated greater reduction of biomass by arthropods with increasing plant diversity (31). In particular, we found a 44% reduction of herbivore feeding rates (estimated by energy flux from plants to invertebrate consumers), per gram of plant mass, from monoculture to 16-species plant communities. Thus, for every gram of plant biomass produced, plants lose just under half as much energy to arthropod herbivores when planted in high-diversity mixtures compared to when plants are grown in monocultures. Therefore, although overall energy loss to herbivores moderately increases in high-diversity plots (Fig. 2B)—which matches findings of previous studies [e.g., (17)]—the proportional loss of energy to herbivory is lower because high-diversity plant communities also produce more total biomass per unit area (32).

Our results seemingly contrast with earlier findings of higher loss of plant biomass with increasing plant diversity in the presence (versus absence) of the entire arthropod food web (31). However, quantification of plant community responses to food web interactions varied markedly and is difficult to compare. Seabloom *et al.* (31) assessed the impacts of the entire arthropod food web (without distinguishing trophic guilds) on total plant biomass, while our analyses specifically quantify the flux of energy, per unit biomass of plants, to arthropod herbivores (including plant-feeding omnivores). These differences point to two general implications of these contrasting results. First, our measure of herbivore impact is likely to detect herbivore effects on plant performance beyond those that manifest in short-term biomass production, such as tissue nutrient content (28). Second, while heavy sustained applications of broad-spectrum insecticides [as in the Seabloom *et al.* (31) study] may yield larger

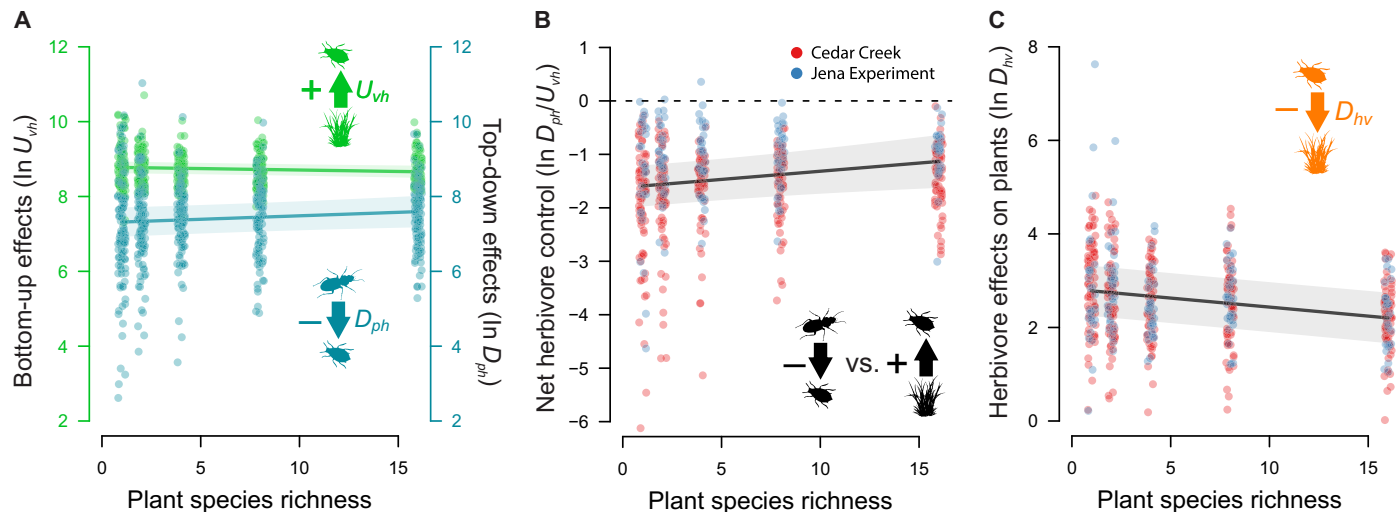


Fig. 3. Effects of plant diversity on bottom-up and top-down control of herbivores and their impacts on plants. We show empirical support for effects of plant diversity on (A) bottom-up pressure (log-transformed U_{vh}) applied by plants on arthropod herbivores (green symbols) and top-down pressure (log-transformed D_{ph}) applied by predators on arthropod herbivores (blue symbols; $P > 0.05$) and for (B) the log ratio of top-down versus bottom-up pressure simultaneously imposed on herbivores. As expected, this led to (C) declining top-down pressure (log-transformed D_{hv}) of herbivores on plants (per unit plant biomass) with increasing plant diversity. Trend lines show the partial effects of plant diversity from the linear mixed effects models (see table S4) after accounting for different years (\pm 95% CI).

increases in plant biomass at high plant diversity, our study demonstrates that naturally assembling arthropod food webs control mass-specific effects of herbivores on plants through a complex of trophic interactions, which are also crucial for maintaining ecological stability (33). Decades of research on integrated pest management have shown that pest control that relies heavily on insecticides can lead to detrimental rebounds of herbivore pests, due to destabilizing nontarget effects on natural enemies following pesticide application (34). Nonetheless, the exact mechanisms underlying the differences between these two studies remain hidden and require further experimental, targeted manipulations of predators and herbivores to understand the negative influence of the arthropod food web on the relationship between plant diversity and biomass production (31). Still, together, these results demonstrate that plant biodiversity is a strong driver of primary productivity and may be crucial for limiting herbivore pest outbreaks by simultaneously constraining energetic gains of herbivores and supporting effective communities of natural enemies.

By distinguishing among the different functions provided across trophic levels in grassland food webs, our study reveals how increasing plant diversity strengthens the multitrophic controls that can yield net benefits for plants. We show that simultaneous changes in energy gained from resources and predation pressure received by arthropod predators suppress herbivores and their impacts on plant communities. This brings to light the importance of biotic interactions for maintaining ecosystem services and points to the need for further research into the role of food web structure for controlling the relationship between biodiversity and ecosystem functioning. Our study reconciles long-standing competing hypotheses about the ability of plant diversity to reduce herbivore impacts, by demonstrating that both natural enemies and resource concentration act in concert to constrain the negative effects of herbivores on plant performance. Hence, conserving plant diversity could be vital for maintaining natural control of herbivores and thereby help to minimize inputs of agrochemicals and maximize plant performance.

MATERIALS AND METHODS

Experimental field sites

We used aboveground arthropod community data from two plant diversity experiments located on two different continents, namely, the “Jena Experiment” in Central Europe and the “Cedar Creek Biodiversity Experiment” in North America. The Jena Experiment, established in 2002 in the floodplain of the Saale River (Thuringia, Germany, 50°55'N, 11°35'E; 130 m above sea level), is an experimentally maintained plant diversity gradient using 60 plant species native to Central European mesophilic grasslands. Plant communities were sown in 400-m² plots with species richness levels of 1, 2, 4, 8, and 16, replicated across four spatial blocks (35). The diversity levels of 1 to 8 plant species were replicated 16 times, and the 16-species treatment was replicated 14 times, making a total of 78 replicate plots. In 2009, the plot size was reduced to 100 m² and the monocultures of *Bellis perennis* (L., 1753) and *Cynosurus cristatus* (L., 1753) were excluded due to poor cover of the target species, leaving a total of 76 plots considered in the present study. Twice per year, the plots are mown to mimic traditional management practices and also weeded to maintain the experimental species richness levels (35). A detailed description of species selection for each plot and for the management of the Jena Experiment can be found in (35).

Similarly, the Cedar Creek Biodiversity Experiment was established in 1994 at the Cedar Creek Ecosystem Science Reserve near East Bethel (Minnesota, USA) to create an experimental plant diversity gradient. Here, plots of 169 m² (reduced to 81 m² in 2000) were also sown with plant species richness levels of 1 ($n = 39$), 2 ($n = 35$), 4 ($n = 29$), 8 ($n = 30$), and 16 ($n = 35$), for which species were randomly drawn from a total species pool of 18 plant species. As in the Jena Experiment, experimental plant diversity levels were maintained by weeding plots two to four times during the growing season but were burned once per year in spring to mimic natural disturbance regimes typical of the region (1).

Arthropod sampling and data collection

To account for colonization time of arthropod communities since the establishment of both experiments, we used arthropod data collected

after 8 and 10 years from the initial experimental planting (i.e., years 2010 and 2012 from the Jena Experiment and years 2002 and 2004 from Cedar Creek). At the Jena Experiment, aboveground vegetation-dwelling arthropods were collected via suction sampling in June and July between 9:00 a.m. and 4:00 p.m., within two sampling periods of 4 days for the entire experiment. Two subplots of 0.75 m × 0.75 m were randomly placed within each plot, covered with a fine mesh cage, and exhaustively sampled using a modified commercial vacuum cleaner (Kärcher A2500, Kärcher GmbH, Winnenden, Germany) until no further arthropods were sighted. Arthropod samples were pooled from the two sampling times (June and July) to maximize coverage of species assemblages. At the Cedar Creek Biodiversity Experiment, vegetation-dwelling arthropods were collected via sweep net sampling at peak plant biomass (in August) over a single day. A total of 25 sweeps were conducted on each plot using a 38-cm-diameter net consisting of muslin mesh and by walking a 10-m line transect within 2 to 3 m of the plot's edge. The use of different collection methods at each experimental site potentially had an effect on sampled species and their abundances. Specifically, sweep net samples may exclude many ground-dwelling arthropods that suction sampling would be more likely to capture. In contrast, some highly mobile groups such as Orthoptera were undersampled with suction sampling at the Jena Experiment, so they were not included in the Jena Experiment food webs (table S1). Nevertheless, past research has found that these two methods do generally provide comparable data of arthropod species across trophic levels and even appear to capture similar responses of arthropods to variation in plant diversity (36). Although these different sampling methods could presumably lead to inconsistent results in our analyses, we found no significant differences between the experimental sites in any arthropod food web variables.

All specimens from both experiments (with the exception of Diptera and Lepidoptera from the Jena Experiment, due to lack of taxonomic expertise) were identified to at least family level, or to genus and species level where possible, and abundances of species at each plot were recorded. For taxa from the Jena Experiment, body lengths were obtained from (37), and for Cedar Creek, average species body lengths were measured for approximately 70% (313 of 450) of the taxa (7). For all remaining taxa, average body lengths were retrieved from the literature. Body length was converted to fresh body mass (in milligrams) using taxon-specific length-mass regressions of temperate arthropods (38). In addition, the average assimilation efficiency, e (that is, the proportion of energy assimilated into arthropod biomass from total consumed energy), was assigned for each trophic interaction based on resources consumed (39). This was set to 0.158 for arthropods consuming detritus, 0.545 for arthropods consuming live plant material, and 0.906 for arthropods consuming other live arthropods (39). These values are based on well-known difference among trophic levels in their ability to extract energy from ingested material, whereby herbivores and detritivores are faced with resources of a lower digestibility than predators. Specifically, the assimilation efficiencies used in our study are taken from model estimates for each trophic level that were quantified using the most comprehensive meta-analysis on assimilation efficiencies to date (39).

Estimation of arthropod metabolic rates

Mean metabolic rates were calculated for each taxon for each of the two sampling years using published metabolic rate regressions for arthropod taxa (24, 40). Estimation of arthropod metabolic rates

was made using regressions from fresh body mass, temperature (mean summer temperature of each experimental site from both sampling years), and phylogeny using the formula

$$\ln X = \ln x_0 + a \left(\ln M - \frac{E}{kT} \right)$$

where X is the metabolic rate, a is the allometric exponent, M is the fresh body mass, E is the activation energy, k is the Boltzmann's constant, T is the temperature, and x_0 is a normalization factor (40). Taxon-specific values were used for x_0 , a , and E to calculate metabolic rates for Arachnida, Coleoptera, and Hymenoptera, and parameters from a general insect metabolic rate regression were used for the remaining taxa. Metabolic rates were calculated as joules hour⁻¹ and then converted to joules month⁻¹ by multiplying by the average number of hours per month from when samples were collected.

Construction of aggregated food webs

All taxa were assigned to a functional feeding group (FFG) by first separating into taxonomic orders and then further identifying taxa within orders as either carnivores, herbivores, detritivores, or omnivores. Omnivores were further classified as carnivore-herbivores, carnivore-detritivores, herbivore-detritivores, or generalist omnivores (that consume other arthropods, plants, and detritus). We used this combined approach of taxonomic and functional distinctions because feeding associations have been shown to be highly phylogenetically conserved, particularly in our study system (41). Therefore, taxonomic groupings provide additional information on likely feeding behavior beyond general feeding traits alone. Furthermore, taxonomic groupings also provide information about the likely vulnerability of arthropods to predators, by indicating traits such as sclerotization or movement behavior. An adjacency matrix of possible trophic links among all FFGs (16 for the Jena Experiment and 23 for Cedar Creek) was created for each experimental site, yielding a so-called meta-web for the Jena Experiment and for Cedar Creek (fig. S1). Trophic links were assigned on the basis of all likely feeding interactions among FFGs, which were derived from a number of steps that combined expert knowledge and extensive literature searches. Specifically, general trophic links were first assigned at the functional group level based on expert knowledge. Then, we screened taxa that occurred within each functional group to ensure that feeding links were still meaningful for each given taxa. For example, predatory beetles (Coleoptera) were first assigned a feeding link with booklice (Psocoptera) based on co-occurrence and likely ability of beetles to overcome these prey. This link was then validated by finding literature support for some predatory beetles present in our food webs (e.g., Coccinellidae) that feed on booklice. These feeding links were additionally cross-referenced with matching taxonomic groups from recent species-level food webs constructed from the Jena Experiment, using feeding interactions reported in the literature, trophic levels, and a range of trait-based rules (22). For each plot and year in both experiments, we extracted local food webs (i.e., subsets of the meta-webs) based on the presence of FFGs at a given plot and year, yielding a total of 152 food webs from the Jena Experiment and 335 food webs from Cedar Creek.

Calculating food web energy fluxes

Energy fluxes (as joules per month) among all nodes in the local food webs were calculated, where links were assigned using the food web energetics approach (21, 23, 24). Although energy flux is expressed

in flow of energy (joules) per unit time, energy flux directly relates to material ingested by consumers in food webs as it describes the chemical energy that is taken up by heterotrophs and both converted to biomass and processed and lost as kinetic energy through metabolism (42). Furthermore, the material ingested by heterotrophs is composed of a suite of chemical elements (e.g., C, P, and N) that comprise organic compounds, which harbor chemical energy that is released and transformed through the process of metabolism (42). Therefore, energy fluxes are also closely correlated with elemental fluxes in food webs (21). To quantify energy fluxes in food webs across both grassland experiments, we assumed a steady-state system, whereby all energetic losses of nodes in the food webs (estimated by metabolism and predation by higher trophic levels) must be exactly balanced by energy intake, via consumption of resources, after accounting for efficiency of energy assimilation from ingested material. F_{ij} , the flux of energy from resource i to consumer j , was thus calculated as

$$\sum_i e_{ij} F_{ij} = X_j + \sum_k W_{jk} F_k$$

where e_{ij} is the efficiency that consumer j converts energy consumed from resource i into energy used for metabolism and biomass production, which varies with trophic level (39). Thus, the left side of the equation represents the energetic gains of consumer j via consumption of resources, and the right side of the equation defines energetic losses resulting from metabolism X_j (the sum of individual metabolic rates from arthropods in node j) and from predation on consumer j by higher trophic levels (21, 23). Energy flux to each consumer was defined as $F_{ij} = W_{ij} F_j$, where F_j is the sum of ingoing fluxes to species j and W_{ij} is the proportion of F_j that is obtained from species i , which was obtained by scaling consumer preferences w_{ij} to the biomasses of different available prey using

$$W_{ij} = \frac{w_{ij} B_i}{\sum_k w_{kj} B_k}$$

where B_i is the biomass of resource i . To ensure realistic calculations of the proportions of energy flux from multiple resources to omnivores that feed either on both plants and arthropods or on detritus and arthropods, we set equal preferences among arthropod prey, plants, and detritus but maintained biomass-dependent preferences among arthropod prey. This was done to avoid extreme preferences of omnivores toward plants and detritus, which typically have far higher biomass than arthropod prey but are likely to be less preferred by omnivorous consumers due to lower nutritional value (43).

However, we suspected that variation in the assignment of feeding preferences of omnivores for plants versus arthropods could affect calculations of predatory and herbivorous energy fluxes, which could lead to different overall conclusions for the effects of plant diversity on herbivore control depending on preferences set in the food webs. To assess whether this was the case here, we conducted a sensitivity analysis whereby we incrementally altered the proportional omnivore preferences for plants versus arthropods from 0.2 to 0.9 (in increments of 0.1) and reanalyzed each model used to produce (Fig. 3, D and E). Our sensitivity analysis revealed that our results are highly robust to changes in feeding preferences of omnivores, as we found no discernible changes in the outcome of all but one of our models testing the effects of plant diversity on net herbivore

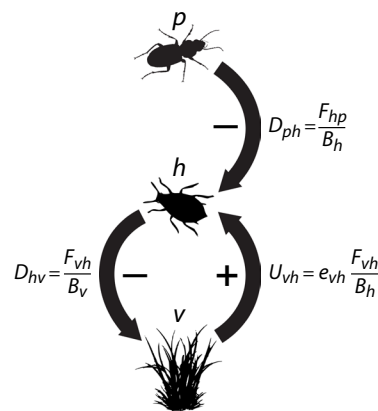


Fig. 4. Calculation of top-down and bottom-up effects in the arthropod food webs. F_{ij} is the total flux from resource i to consumer j , B is the community biomass of resource or consumer, and e_{ij} is the efficiency with which energy from a resource is assimilated (for allocation to, e.g., biomass production, movement, etc.).

control and on herbivore effects on plants (fig. S3 and table S6). Only in one scenario, testing the effect of plant diversity on herbivore control with omnivore preferences set to the most extreme preference for plants (90% preference for plants versus arthropods), we find only a marginally significant relationship ($P = 0.058$; fig. S3 and table S6). Therefore, we chose to assign a standardized equal preference for plants and arthropods (50% preference for each resource pool). In addition, cannibalistic links were allowed for several predator groups, but preference for cannibalism was set to 0.1 in the adjacency matrix to strongly down-weight the amount of energy a predator consumed from its own biomass pool. This was because biomass-dependent links yielded unrealistically high feeding preferences for cannibalism when the cannibalistic node was among the most abundant in a given food web. Energy flux calculations were performed using the “fluxweb” package (23) in R 3.4.2 (44).

To quantify whole-food web energy flux, we calculated the sum of energy flux along all trophic links within each entire food web, regardless of where in the food web the energy was flowing. Total herbivory was calculated as the sum of all outgoing energy flux from plants to account for the consumption of plant material by both strict herbivores and omnivores that partition their feeding between plant and other material (e.g., detritus and/or arthropod prey). Last, total predation was calculated as the sum of all outgoing energy flux from arthropod nodes to include predation by omnivores that feed on both arthropod prey and other energy sources (e.g., detritus and/or plants).

Quantifying bottom-up and top-down forces in plants and herbivores

To assess herbivory, we quantified the total consumption of plant energy by herbivores, per unit biomass of plants using $D_{hv} = \frac{F_{vh}}{B_v}$, where F_{vh} is the energy flux from plants to herbivores and B_v is the community biomass of plants in the food web (Fig. 4), yielding mass-specific energetic losses of plants to herbivores as joules month⁻¹ g⁻¹ of plant biomass. To further determine the forces regulating the herbivore effects on plant communities in the two diversity experiments, we additionally quantified both positive effects of plants on herbivores and negative effects of predators on herbivores in each food web across the experimental plant diversity gradients.

Effects of predators on herbivores were calculated as $D_{ph} = \frac{F_{hp}}{B_h}$, where F_{hp} is the total energy flux from herbivores to their predators and B_h is the community biomass of herbivores in a given food web, yielding mass-specific energetic losses of herbivores to predators as joules month⁻¹ g⁻¹ of herbivore biomass. Effects of plants on herbivores were calculated as $U_{vh} = e_{vh} \frac{F_{vh}}{B_h}$, where e_{vh} is the efficiency at which herbivores convert consumed plant material into herbivore biomass, F_{vh} is the total energy flux from plants to herbivores, and B_h is the community biomass of herbivores in the food web (Fig. 4), yielding mass-specific energetic gains of herbivores from plants as joules month⁻¹ g⁻¹ of herbivore biomass. Furthermore, we estimated the simultaneous top-down and bottom-up forces on herbivores at each grassland plot by calculating the log ratio, $\log(D_{ph}/U_{vh})$, to describe the negative top-down forces imposed by predators on herbivores relative to the positive bottom-up forces imposed by plants. Hence, a log ratio of 0 would indicate that top-down (per unit biomass energy loss) and bottom-up (per unit biomass energy gain) forces were equal at the community level with positive and negative values, indicating a net energetic loss or gain, respectively, per unit biomass of herbivores.

Statistical analyses

To analyze the effects of plant species richness on energy flux along all trophic links (whole-food web energy flux), energy flux to all herbivores, and energy flux to all predators in the 487 grassland food webs, we constructed linear mixed effects models using the “nlme” R package (45), with plant species richness as a fixed effect and experimental year as a random effect. In addition, our maximal models included experiment (whether data were from the Jena Experiment or the Cedar Creek Biodiversity Experiment) as a fixed effect and its interaction with plant species richness to account for variation in response variables arising from different experimental locations and collection methods as well as to test for consistency of findings across both grassland experiments. All models were checked for homoscedasticity of variance and normality of model residuals, following which each response variable (whole-community flux, flux to herbivores, and flux to predators) was log-transformed to meet the assumptions of normality and remove heteroscedasticity of variance. We finally conducted model simplification using Akaike information criterion (AIC) selection to identify a minimal adequate model for each response variable. We applied a minimum threshold of two AIC units to determine the best model, but where multiple models fell within this threshold, we selected the model with the fewest parameters as the minimum adequate model.

Similar to the models on summed energy fluxes, we constructed four linear mixed effects models [using the nlme package (45)] to test for a relationship between plant species richness and the bottom-up and top-down control of herbivore biomass (U_{vh} and D_{ph} , respectively) as well as on net herbivore control, $\log(D_{ph}/U_{vh})$, and herbivore effects on plants (D_{hv}). Again, plant diversity, experiment, and their interaction were specified as fixed effects and experimental year as a random effect. As we identified issues with heteroscedasticity of variance in all of these four models, we first log-transformed each response variable (excluding the log ratio D_{ph}/U_{vh} response). This sufficiently improved only one of the models (with top-down effects on herbivores as the response), with considerable issues in heteroscedasticity still remaining in the other three models. Therefore, we included a “varIdent” variance function (46) in each remaining model, allowing for different variances for each

experimental year and value of plant species richness across the two experiments. Model simplification was again carried out (as above) to identify a minimum adequate model in each case.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/45/eabb6603/DC1>

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