Plant diversity promotes aboveground arthropods and associated functions despite arthropod loss over time

A. Ebeling[†, *, 1], Maximilian Bröcher[†, 1], Lionel Hertzog[2], Holger Schielzeth[1], Wolfgang W. Weisser[3], Sebastian T. Meyer[3]

[1]Institute of Biodiversity, Ecology and Evolution, University of Jena, Jena, Germany

[2]Laboratoire d'Inventaire Forestier, Ecole Nationale des Sciences Géographiques-Géomatique, Institut National de l'Information Géographique et Forestière, Nancy, France

[3]Terrestrial Ecology Research Group, School of Life Sciences, Technical University of Munich, Freising, Germany

[*]corresponding author: anne.ebeling@uni-jena.de, Phone: 0049-3641-949437, Fax: 0049-3641-949402

[†]these authors contributed equally

Abstract

Arthropods make up the vast majority of terrestrial biodiversity and play essential roles in ecosystem functioning. Biodiverse grasslands support large numbers of arthropods, yet such ecosystems have faced significant declines due to land conversion and changes in management. While restoration efforts aim to conserve species-rich grasslands, the long-term effects of plant species richness on arthropod communities and associated functions (e.g. herbivory and pest-control) remain underexplored. We addressed this knowledge gap by quantifying grassland arthropods, herbivory, and predation over 13 years (2010-2022) across 80 plots with varying plant species richness. We explored (1) how arthropod communities and associated functions have changed over the study period and if any change is affected by plant species richness, (2) if effects of plant species richness on arthropods vary or even strengthen over time, and (3) if changes in arthropod communities affect associated functions. Our findings reveal that, at all levels of plant species richness, arthropod community metrics declined over time, with average losses being mainly more pronounced in species-poor plant mixtures. Plant species richness consistently had a positive effect on arthropod communities and their functions. This positive plant species richness effect strongly varied between years, but showed no consistent change over time. Predators experienced greater annual losses compared to herbivores, but herbivore declines were more influenced by changing plant species richness. Notably, temporal changes in arthropod community metrics did not predict functional changes, as the effect of plant species richness on predation strengthened over time, whereas its effect on predator richness remained stable. Overall, our study highlights the complex and dynamic interactions between plant species richness and arthropod communities over time. Maintaining high plant diversity in semi-natural grasslands might mitigate arthropod loss over time, but this stabilizing effect may take years to fully establish, emphasizing the long-term nature of conservation efforts.

Keywords: arthropod loss, plant-consumer interactions, herbivores, predators, grassland, biodiversity experiment

Introduction

Arthropods make up about 96% of known biodiversity in terrestrial ecosystems. As *"the little things that run the world"* [1], arthropods strongly contribute to the high social, cultural and economic value of species-rich, extensively managed grasslands [2,3]. Compared to grasslands with low plant diversity, arthropods appear in high richness and numbers in grasslands with high plant diversity [4–6]. Arthropods also provide a variety of important ecosystem functions [4,6–8], such as decomposing dead plant material and enriching the soil with plant-available nutrients [7,9]. As herbivores, they mediate the transport of energy from primary producers to higher trophic levels [10] and cause feedbacks to plant fitness and community composition [11]. In addition to their role as herbivores, many arthropods also serve as pollinators, facilitating the reproduction and survival of various plant species [12,13], or as predators, regulating populations of herbivorous insects [9,14]. Furthermore, arthropods build a fundamental food resource for other consumers, such as birds and many other vertebrates, thereby acting as an integral component of food webs in grasslands [15]. Given the crucial role of arthropods in ecosystems, reports of drastic declines in their abundance, biomass and diversity have sparked both scientific and societal concern [16,17]. Over the past decades, global arthropod declines have been well-documented, with biomass losses reaching up to 75% [18] and significant reductions in species richness [18–21].

Grasslands cover about 40% of the earth's terrestrial surface and are thus one of the most common ecosystems with important contributions to global ecosystem functioning and services [3,22]. Extensively-used grasslands, that host most of grassland diversity in Central Europe, have declined significantly over the past century, primarily as a result of land conversion into arable land or land use intensification characterized by more fertilization and more grazing or more frequent mowing [22–24]. On the other hand, also cessation of management

and abandonment have contributed to grassland decline [25]. As a consequence there has been a staggering loss of over 90% of semi-natural grasslands since the 1940s in northern Europe [3,24,26]. To counteract this trend and to meet targets of the Convention of Biological Diversity (CBD), conservation efforts should focus on the maintenance of existing semi-natural grasslands (conservation) and the restoration of currently species-poor meadows (diversification) [2,4,27].

There is increasing evidence that species-rich grasslands not only function better than low-diversity grasslands, with respect to a large number of ecosystem functions, but also, that the benefits gained by increasing plant species richness become stronger over time [28]. This applies in particular to increased plant species richness effects on plant productivity, but also to other ecosystem functions [8,29–31]. Hence, maintaining existing species-rich semi-natural grasslands as a conservation strategy is expected to have stronger positive effects than newly establishing such grasslands. So far, however, there are only few studies investigating temporal changes in the relationship between plant species richness and arthropod communities with their mediated functions [8,32]. In other words, our understanding of temporal dynamics in grasslands lacks a multitrophic perspective [28].

Arthropods generally show a higher species richness, diversity and abundance in grasslands with higher plant species richness and are also more diverse in their interactions and their functional traits compared to low-diversity grasslands [5,6,33–36]**.** However, plant species richness effects may vary or even become stronger over time either because arthropods perform better in species-rich plant communities, perform worse in species-poor plant communities, or a combination of both [8]. Alternatively, higher plant species richness might mitigate the ubiquitous declines in arthropod numbers, making the losses less severe. Hence while, arthropod communities in species-poor and in species-rich grasslands both tend to depauperate over time, the performance losses are expected to be less pronounced in species-rich grasslands.

Multiple mechanisms can cause variation in the relationship between plant species richness and arthropod communities, such as changes in the plant community composition [29,37] or abiotic

conditions. Specifically, due to community assembly processes and selection for specific plant phenotypes, the functional and genetic diversity and thus the complementarity among plants might increase over time in diverse plant communities [29,31,38,39]. In addition, species-rich plant communities fluctuate less in productivity, structure, or soil temperature [40–42]. Because arthropods in grasslands are strongly bottom-up controlled [4,43,44], plant species richness-induced temporal changes in plant attributes are expected to escalate to arthropod communities, their interactions and related processes [28,35,45–47]. A greater arthropod diversity (as found in species-rich plant communities) can lead to greater temporal stability in arthropod communities and contribute to changes in the relationship between plant species richness and arthropods over time via various mechanisms.

A high diversity of arthropods might increase the chance of communities to include species that perform well under changing or harsh environmental conditions (such as dry summers). Furthermore, diverse arthropod communities are more likely to include species that are either very robust (trait-dependent resistance), have a high reproduction rate (fast recovery), or have capacity to adapt (highly plastic in their traits). These effects are known as sampling or selection effect. Alternatively, or in addition, a high functional complementarity between arthropod species combined with asynchronous fluctuations (asynchrony) could lower fluctuations in arthropod community properties and arthropod-mediated functions (portfolio or insurance effect of biodiversity) [48–50].

Despite these insights, the enormous diversity, and the critical ecosystem functions provided by grassland arthropods, there has been no long-term study on arthropod communities in plant diversity experiments to explore the temporal trajectory of cascading biodiversity effects. To address this gap, we here test how experimentally manipulated plant species richness influences arthropod communities, plant consumption by herbivores, and predation over a time course of 13 years. Using standardized methods, we collected arthropods, measured leaf damage and quantified predation on 80 experimental plots differing in plant species richness.

We used these data to calculate complementary arthropod community metrics (species richness, diversity, abundance, biomass for all arthropods together and herbivores and predators separately) and their mediated functions (biomass ratios across trophic groups, percentage herbivory and predation rate). Whereas arthropod community metrics inform about the "attractiveness" of plant communities for arthropods, functional analysis allow us to quantify top-down effects on plant communities and herbivores [5,14]. With this approach, we asked the following questions:

(1) Do arthropod communities and associated functions change over time, and are these changes influenced by plant species richness? Based on the reported global loss in arthropods and the expected buffering effect of plant species richness, we predict that overall arthropod communities will decline, but that losses will be less pronounced in species-rich plant communities than in species-poor ones.

(2) Do effects of plant species richness on arthropod communities vary or even strengthen over time? Based on the finding that the relationship between plant species richness and productivity becomes stronger over time and the potentially buffering effect of species richness, we expect a strengthening plant species richness effect over time.

(3) Do temporal changes in the strength of the relationship between plant species richness and arthropod communities affect associated functions, such as arthropod loads, ratios of herbivore-plant and predator-herbivore biomass, herbivory or predation? We expect a strong coupling of stocks and flows, so that the performance of arthropod communities explains the temporal variation in predation and herbivory.

Results

In total, we collected about 44.900 individual arthropods assigned to 400 taxa. Coleoptera were the most dominant group, contributing 35% and 32% to overall abundance and

species richness, respectively, followed by Hemiptera (33%, 34%), Hymenoptera (24%, 20%) and Araneae (8%, 14%).

Temporal changes in arthropod community metrics and associated functions and its dependence on plant species richness

Over a period of 11 years, we observed a strong decrease in all arthropod community metrics (Figures 1, 2, S1, Tables S1, S2). Across seasons, at intermediate plant species richness, arthropod species richness, abundance and biomass decreased by -5.2%, -6.7%, and -7.4% per year, respectively, with stronger decreases in spring than in summer (Table S2). When comparing herbivorous and predatory arthropods, we found that the annual losses were more pronounced in predators (Figure 2, Table S2; richness: -6.1% versus -3.9%; biomass: -8.1% versus -7.0%, abundance: -6.8% versus -6.1%). However, the annual rate of change differed slightly between high and low diverse plant communities and between sampling seasons. For example, across sampling seasons, we found that the annual abundance loss of herbivores and predators was stronger in species-rich compared to species-poor plant communities (herbivore abundance high and low plant species richness: -6.5% versus -6.0%, predator abundance high and low plant species richness: -7.5% versus -6.3%), while we observed the opposite pattern for the annual loss in arthropod species richness (herbivore richness high and low plant species richness: -3.7% and -4.2%, predator richness high and low plant species richness: -6.0% versus -6.2%) (Figure 2, Table S2). Furthermore, in spring (May) the annual decrease in arthropod species richness, abundance and biomass was generally stronger in high species mixtures (60 plant species) compared to monocultures (except for predator richness). In contrast, during summer (July), herbivores (but not predators) in monocultures suffered more from the overall loss than those in high diverse plant communities (Figure 2, Table S2).

With respect to ecosystem functions, we observed a significant annual decline in herbivory (-4.8%) and predation (-9.1%), with comparably minor changes in arthropod load (-0.7%), and the predator-herbivore ratio (+0.4%) (Figures 1, S2, Tables S3, S4). In contrast, the herbivore-

plant ratio increased across season at intermediate level of plant species richness by +4.6% per year (Figure S2, Table S3). The annual rate of change varied between high- species richness plant communities (60 species) and monocultures. Predation loss was more pronounced in species-poor plant communities compared to species-rich ones (-11.9% versus -5.4%), whereas the opposite trend was observed for herbivory (-4.2% versus -5.5%) and the predator-herbivore biomass ratio (-0.7% versus -2.2%) (Figure 2, Table S3). Interestingly, arthropod load and the biomass ratio between herbivores and plants in high and low diverse plant communities showed completely opposing trends over time. Both biomass ratios showed strong annual increases in species-poor (arthropod load +6.5%, herbivore-plant ratio +11.9%), but annual decreases in species rich plant communities (arthropod load -7.8%, herbivore-plant ratio -7.3%) (Table S3).

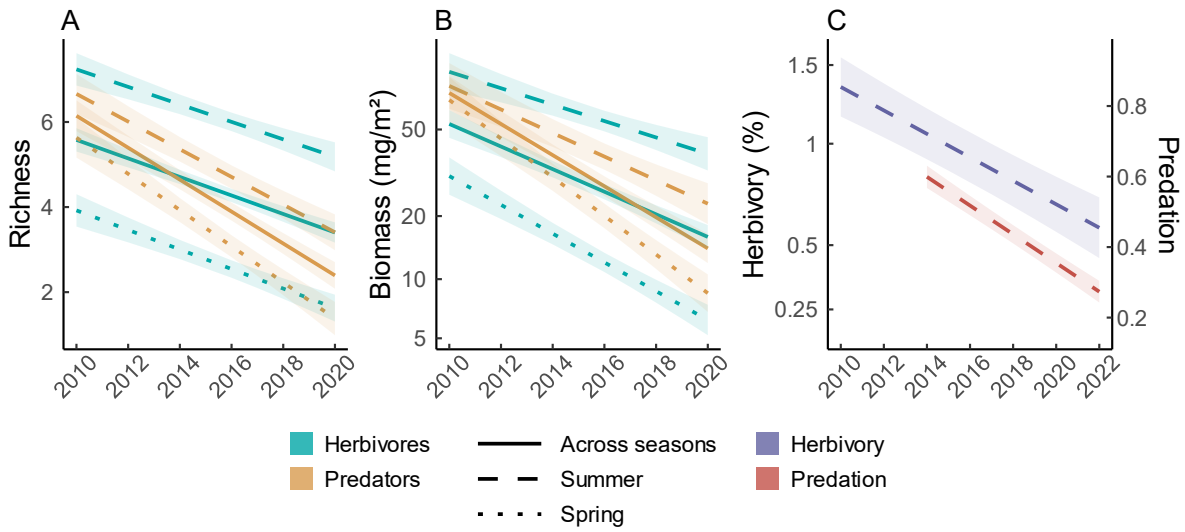

Figure 1: Temporal trends in arthropod richness, biomass and functions (herbivory and predation). Regression lines and 95% confidence intervals in panels A and B show average arthropod richness and biomass per plot from 2010 to 2020 separately for herbivores (blue) and predators (orange). For herbivory (violet) and predation (red) timeseries from 2010 to 2022 are shown. Line styles indicate changes in spring (dotted), in summer (dashed) and across seasons (solid). Biomass and herbivory were log-transformed prior to the analyses and regression lines were derived from model (1).

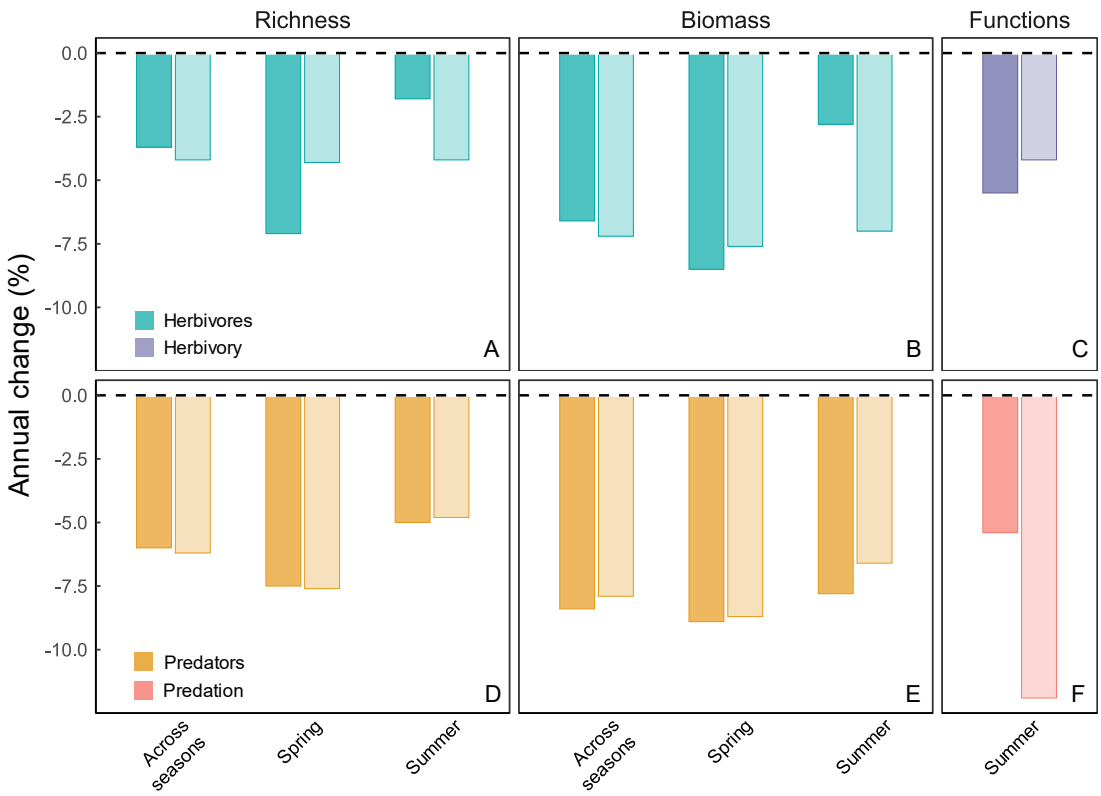

Figure 2: Annual (%) change in arthropod richness, biomass and functions (herbivory and predation). Values are predicted changes extracted from model (1) for 60-species plant mixtures (high plant species richness in dark) and monocultures (low plant species richness in bright) and are shown separately for herbivores (A and B, blue), predators (D and E, orange), herbivory (C, violet) and predation (F, red).

Effects of plant species richness on arthropod community metrics over time

Across all sampling years, we found a consistent positive effect of plant species richness on arthropod species richness, diversity, abundance, and biomass—for the entire arthropod community, and for herbivores and predators separately (Figures 3, S1-S4, Table S5). However, the effects of plant species richness varied significantly among years, particularly for the richness and abundance of arthropod communities (Figures 2, S3-S6, Table S5, significant interactions between PSR and CY). For example, the standardized PSR slope ranged from 0.10 to 0.19 (average PSR effects in 2014 and 2017, respectively) for herbivore richness, and from 0.04 (2014) to 0.11 (average PSR effects in 2014 and 2016, respectively) for herbivore abundance (Figure S3).

When testing for directional temporal changes we found that the positive plant species richness effects on overall arthropod communities, herbivores and predators did not significantly change over time (Figures 3, S3, Tables 1, S6).

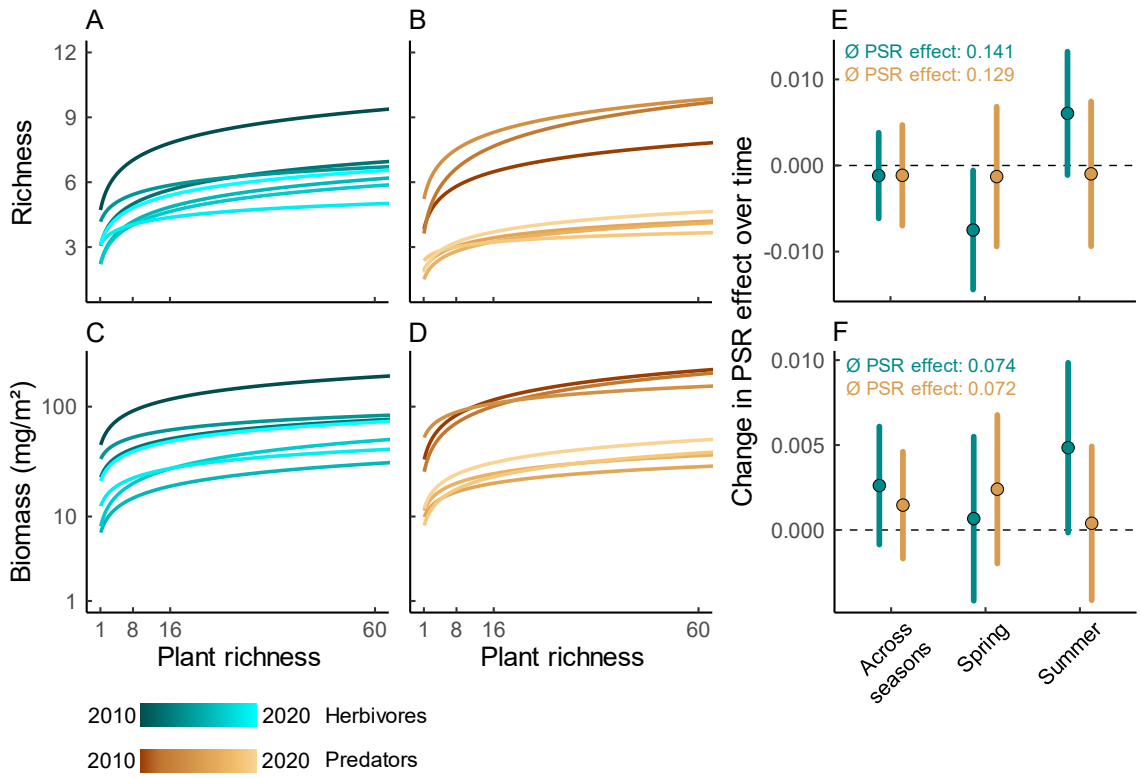

Figure 3: Plant species richness effects on arthropod richness and biomass and its change over time. Panels A-D show plant species richness effects on herbivores (blue) and predators (orange) from 2010 (dark colours) to 2020 (bright colours). Regression lines were extracted from model (2), with biomass (mg/m²) and plant species richness being log-transformed prior to the analyses. Panels E and F show the average effect of plant species richness across years (PSR) and its change over time, for each sampling season (spring/ May and summer/ July) and across seasons. Plant species richness effects for each year and both sampling seasons were average corrected (slope from model (2)/ average value in a given year) before testing for temporal changes (see description of model (3)).

Arthropod communities and their responsiveness to changing plant species richness were also influenced by the sampling season. We consistently observed a significant increase in arthropod community metrics from spring to summer, with herbivore richness and biomass, for example, being around 134% and 178% higher in summer than in spring, respectively (Figures 1, S1, S4-S6, Table S5). Moreover, plant species richness effects on summer arthropod communities tended to strengthen over time, whereas they either remained stable or weakened in spring arthropod communities (Figure 3, S3). Even though this is only significant for

herbivore estimated richness (interaction of time and season in Tables 1 and S6), it is a consistent pattern for most metrics describing the total arthropod community or herbivores only (Figures 3, S3).

Table 1: Changes in plant species richness effects over time. Results from linear models testing whether plant species richness effects on arthropod richness, biomass (mg/m²), herbivory and predation (PSR slope) change over **time** (calendar year as numerical variable), between sampling **seasons** (May/ spring and July/ summer) or for an interactive effect of both (**time x season**). For a detailed model description see model (3) in the section *Statistical analysis*. Significances are indicated by asterisks as followed: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

	Time		**Season**		**Time x Season**	
Richness						
Total	$F_{1,11}$	= 0.1	$F_{1,11}$	= 2.1	$F_{1,11}$	= 0.5
Herbivores	$F_{1,11}$	< 0.1	$F_{1,11}$	= 2.7	$F_{1,11}$	= 1.8
Predators	$F_{1,11}$	< 0.1	$F_{1,11}$	= 1.4	$F_{1,11}$	< 0.1
Biomass						
Total	$F_{1,11}$	= 0.5	$F_{1,11}$	= 0.6	$F_{1,11}$	= 0.2
Herbivores	$F_{1,11}$	= 0.6	$F_{1,11}$	= 0.4	$F_{1,11}$	= 0.4
Predators	$F_{1,11}$	= 0.2	$F_{1,11}$	= 0.3	$F_{1,11}$	= 0.1
Functions						
Herbivory	$F_{1,10}$	= 1.0				
Predation	$F_{1,7}$	= 6.4*				

Effects of plant species richness on arthropod-mediated functions over time

Across all sampling years, we found a negative relationship between plant species richness and the overall arthropod-plant biomass ratio, as well as the biomass ratio between herbivores and plants (Figures S7, S8, Table S7). In other words, the amount of arthropod biomass (mg) per unit plant biomass (g) was generally lower in species-rich compared to species-poor plant communities. Contrary to what we might expect based on these findings, functions mediated by herbivores and predators (herbivory and predation) generally increased with increasing plant species richness over a time-course of 13 and 9 years, respectively (Figures 4, S9, Table S7).

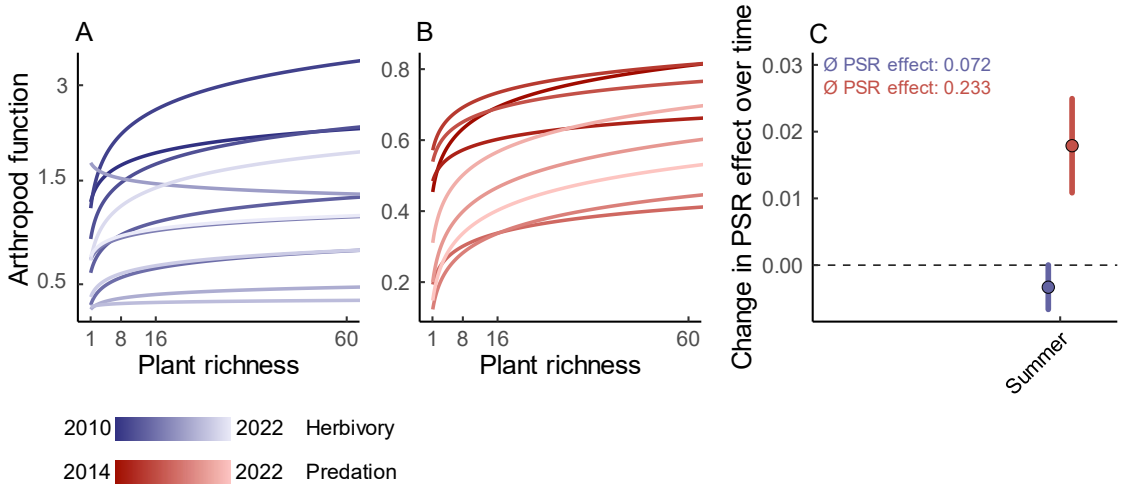

Figure 4: Plant species richness effects on herbivory and predation and its change over time. Panels A and B show plant species richness effects for herbivory (violet) and predation (red) from 2010 (dark colours) to 2022 (bright colours). Regression lines were extracted from model (2), with herbivory and plant diversity being log-transformed prior to the analyses. Panel C shows the average effect of plant species richness across years (PSR) and its change over time. Plant species richness effects for each year were average corrected (slopes from model (2)/ average value of each year) before testing for temporal changes (see description of model (3)).

The strength of the relationship between plant species richness and arthropod function varied significantly between years. For instance, the average plant species richness slopes for the arthropod-plant ratio ranged from -0.06 (2012) to -0.28 (2019) and the effect of plant species richness on herbivory ranged between slightly negative in a single year (-0.02 in 2017) to positive in all other years (maximum 0.12 in 2021) (Figures 4, S7). Over time, the negative relationship between plant species richness and arthropod load (arthropod-plant biomass and herbivore-plant biomass) became more pronounced, while the ratio between predator and herbivore biomass remained stable (Figures S7, S8, Table S6). Furthermore, we found a directional increase in the effect of plant species richness on predation, but not on herbivory (Figures 4, S9, Table 1).

Discussion

Previous studies have shown strong decreases in arthropods during the last decades [19,20,51,52] and supporting effects of plant species richness for arthropods and associated functions

[4,5,33,53]. However, it is largely unknown whether plant species richness helps buffer arthropod loss over time and, as a consequence, how plant species richness effects might change over time [28]. Based on our analysis of long-term arthropod, herbivory and predation data, we can draw conclusions about the interactive effect of plant species richness and time: (1) arthropod community properties strongly decrease over time, with declines across seasons and in summer being slightly more pronounced in species-poor compared to species-rich plant mixtures, (2) the effects of plant species richness on arthropods are consistently positive, vary in strength among years, but neither clearly strengthen nor weaken over time, (3) predators experience a higher annual loss than herbivores, but herbivore loss is more influenced by plant species richness than predator loss, (4) annual losses in arthropods, the effect of plant species richness, and their interaction all differ between spring and summer, (5) plant species richness effects on predation strengthened over time, indicating that (6) temporal changes in arthropod community properties (stocks) in differently diverse plant communities do not predict the observed variation in arthropod associated functions (flows).

Temporal changes in arthropod communities and its dependence on plant species richness

Over a period of 11 years, we could show a strong decline in arthropods, which aligns with previous studies documenting significant declines in arthropod richness, biomass and population size [18–21]. With 76% loss between 2010 and 2020, the average annual loss in arthropod biomass in our study is higher than reported in many other studies. For example, in a study from 2017, Hallmann et al. [18] showed the similar total decline over a time period of 27 years, and in a meta-analysis, van Klink et al. [20,21] showed a decline in insect abundance of 11% in a decade. Most previous studies on arthropod decline cover data spanning several decades, but since the dramatic declines have only begun more recently, calculations based on longer time frames may show lower rates of average loss compared to those focused on the past few years [20,21]. Annual loss in predatory arthropods was more pronounced than in herbivores, which can be explained by a higher sensitivity of higher trophic levels to abiotic changes [54].

Interestingly, especially in herbivores and in summer communities, we observed slightly lower average annual losses in species-rich compared to species-poor plant mixtures, suggesting that the plant species richness effects could be strengthened over time [8,28].

Inter-annual variation in the plant species richness- arthropod relationship

Previous research has consistently demonstrated that high local plant species richness promotes aboveground arthropods, in terms of their species richness, diversity, abundance, biomass, or functional diversity [6,33,34,34,35,55,56]. Many of these studies have focused on single time points (such as specific years or seasons) or focused only on particular aspects of the arthropod community. Our results confirm previous findings of a positive relationship between plant species richness and arthropod communities. Notably, this relationship applies to multiple facets of the arthropod community, is qualitatively consistent across different seasons (spring and summer), and persists over many years.

Mechanisms driving positive effects of plant species richness on arthropods include increased plant productivity, and structural complexity [30], which provide more and more diverse resources and microhabitats, supporting higher arthropod diversity and abundance [57,58]. Since the described mechanisms are driven by bottom-up processes, we expected the positive relationship between plant species richness and arthropods to strengthen over time, similar to patterns observed for aboveground primary productivity [29,31]. However, instead of a clear linear trend over time, we found significant year-to-year variation in the strength of this relationship, with only a weak linear trend for individual arthropod community metrics (such as biomass). Various extreme events that occurred during the study period [59] have likely contributed to these fluctuations, making it impossible to see a clear linear trend over the 11-year period [18]. Specifically, Müller et al. [59] showed that deviations from 'optimal' weather conditions significantly impact the population size of arthropods. Since the buffering effect of biodiversity (better performance of high- compared to low-species richness communities; [37,48–50,60–62]) only comes into play under unfavorable conditions, climate extremes could contribute to the

observed annual fluctuations in the plant species richness effect. In other words, to a certain extent, plant species richness effects on arthropod communities might be stronger under harsh conditions.

Overall, it appears that plant biomass alone does not drive the strength of the relationship between plant species richness and arthropod community metrics, and that other biotic (both extrinsic and intrinsic) and abiotic factors may play a crucial role. Potential candidates include interannual fluctuations in the effects of plant species richness on plant traits (such as defense traits and palatability) [47,63,64], plant species performance [47], or microclimatic conditions (such as soil moisture and temperature) [41]. Furthermore, the stability of the arthropod community when faced with unfavorable conditions might also be an important factor.

Intra-annual variation among arthropod communities

Our results indicate that arthropod communities in spring and summer strongly differ in their response to time, plant species richness and their interactive effect. Arthropod communities appearing in spring experienced a higher annual loss than summer communities, maybe due to their weaker response to increasingly frequent winter weather anomalies [59]. In contrast, due to their phenology, summer species may be better in coping with dry and hot conditions. Additionally, spring species might be more negatively affected by phenological shifts in plant communities or may experience a mismatch with their plant hosts due to earlier seasonal occurrences [65,66].

Our finding that loss in most arthropod community metrics is less pronounced in species-poor plant mixtures during spring and in species-rich plant mixtures during summer may be due to rising temperatures having a positive effect on arthropod communities in spring but a negative effect in summer. Specifically, as a consequence of spring temperatures rise, species-poor plant communities may heat up more than species-rich plant communities due to lower structural complexity. Consequently, since arthropod performance benefits from increasing temperature [67], the loss in monocultures could be lower than in high species mixtures.

In summer, when temperatures are high, the more productive, species-rich mixtures are likely favored because they provide protection against heat, drought, and temperature fluctuations [41].

Finally, we could show that the positive relationship between plant species richness and arthropod community metrics was more pronounced in summer than in spring. Amongst others, this could be explained by the gradual development of plant species richness over the growing season; i.e. diverse plant mixtures become richer as the season progresses, leading to a cumulative effect on arthropod communities. Further, the better survival and accumulation of arthropods in species-rich plant mixtures might be more pronounced in summer, when species-poor plant mixtures become less favorable due to heat, resource limitations, and lack of shelter. In contrast, even in species poor plant mixtures, resources in spring are less limited, so the advantages of species-rich mixtures are less apparent early in the season.

Overall, plant species richness effects over time warrant further investigation, not only regarding the buffering effects of plant species richness across years but also within years among seasons. Future research should aim to identify the most critical time points during the vegetation period when arthropod losses are most pronounced.

Links between temporal changes in arthropods (stocks) and associated functions (flows)

Our study reveals that temporal changes in arthropod community metrics differ from patterns observed for plant biomass in previous studies [31], both, in terms of the temporal trend and the dependency on plant species richness. Specifically, in plants, the decrease in biomass over time is stronger in monocultures than in species-rich plant communities [31], however, in arthropod communities the annual biomass loss across seasons is similar in high and low diverse mixtures (Figure 2B and D). As a consequence, the biomass ratio between arthropods and plants or herbivores and plants- increases over time in low and decreases in high plant species mixtures.

Further, responses in biomass to increasing plant species richness seem to differ in strength between arthropods and plants, i.e. plant biomass increases to a higher extent in species

-rich compared to species-poor plant communities than arthropods, leading to a dilution effect in arthropod-plant and herbivore-plant ratios with increasing plant species richness [5]. As the change in biomass ratios differs between high and low plant species richness, the negative effect of plant species richness becomes stronger over time (Figure S7).

Interestingly, as temporal changes and their response to changing plant species richness in herbivore and predator biomass follow similar patterns, the predator-herbivore ratio remains stable, both, over time and along the plant species richness gradient. This higher stability might indicate that predator biomass is even more bottom-up controlled (i.e. linked to its prey biomass) than herbivores are.

Surprisingly, neither temporal, nor plant species richness patterns for the directly assessed functions (herbivory and predation) can be explained by patterns in biomass ratios. Based on the biomass ratios, no loss and no plant species richness effect would be expected for predation. Similarly, for herbivory, patterns in biomass ratios suggest a negative relationship between plant species richness and herbivory and a decreasing plant species richness-herbivory relationship over time. However, in fact we found that (1) both functions decrease over time (2) with species-rich plant communities being less affected than species-poor plant communities (predation), (3) both functions are positively affected by increasing plant species richness [see also 68,69], and (4) the positive effect of plant species richness on predation, but not herbivory becomes stronger over time.

There are two possible explanations for this uncoupling of biomass ratios (stocks) and ecosystem functions (flows). First, methodological limitations might play a role. Our arthropod sampling does not fully capture all groups contributing to predation and herbivory. For example, we exposed the dummy caterpillars for 24 hours, whereas the arthropod sampling was conducted during the day only. That means, with the suction sampling we missed all night-active predatory arthropods, for example some carabids and staphylinids. Further, with the assessment of leaf damage during the time of maximal biomass production, we recorded

accumulated damage by various herbivores occurring over the entire growing season. That means we also recorded damage caused by arthropod groups, which are not present during the time of suction sampling or that are not caught at all by our regular sampling (e.g. slugs). Second, and probably most important, changes in ecosystem functions (herbivory and predation) may be driven less by the quantity of arthropods and more by their functional composition. As ecosystems become more diverse, shifts in traits such as food specialization, feeding mode and overall trait diversity [34] might increase the functioning of arthropod communities [70–72]. In addition, higher functional complementarity, both in space and time, could lead to more efficient resource use, even in environments with stable or declining arthropod biomass [34,53,73,74].

Overall, our results underline that the main and interactive effects of time and plant species richness on ecosystem functions like herbivory and predation are not simply a result of biomass ratios. Analysing compositional shifts in arthropod communities, but also applying a more complete arthropod sampling at a higher temporal resolution would be crucial to understand temporal variation in the plant species richness- ecosystem functioning relationship.

Conclusion

Our findings suggest that high plant species richness in semi-natural grasslands can mitigate arthropod loss over time- especially in summer communities- but this stabilizing effect may take years to become fully established, emphasizing the value of long-term conservation efforts. Since temporal variation in plant species richness effects cannot be fully explained by plant productivity alone, future research should explore the roles of changing abiotic factors. Likewise shifts in arthropod biomass and biomass ratios among trophic levels could not explain the temporal dynamics in arthropod community function over time underlining the need for more detailed studies of shifts in arthropod community and trait composition to better understand the mechanisms behind these patterns.

Methods

The Jena Experiment

The Jena Experiment was established in 2002 in the floodplain of the river Saale (Thuringia, Germany, 50°550 N, 11°350 E) and uses 60 plant species native to Central European mesophilic grasslands. Plant communities were sown in 82 plots of 20 x 20 m with a gradient of species richness (1, 2, 4, 8, 16 and 60) arranged in four spatial blocks [75]. This setup includes 16 replicates each for monocultures, 2-species, 4-species, and 8-species mixtures, along with 14 replicates for 16-species and 4 replicates for 60-species mixtures (totaling 82 plots). In 2009, plot sizes were reduced to 100 square meters, and monocultures of *Bellis perennis* (L., 1753) and *Cynosurus cristatus* (L., 1753) were abandoned due to insufficient cover of the target species, leaving 80 plots for the current study [30]. The specific species mixtures were randomly chosen under certain constraints [75]. Regular maintenance involves mowing and weeding twice per year, which sustains the plant species richness gradient and maintains a strong correlation between the sown and realized numbers of target species [30].

Measuring plant biomass

We measured aboveground plant biomass in every year between 2010 and 2022 [31]. Always at the time of peak biomass in late May and August, we harvested plant material in two frames of 0.1 m² each on every single plot. Finally, we sorted the samples by species, dried them for 72 hours at 70°C and weighed them. To quantify community productivity, we summed up dried biomass of all target species per sample, averaged values of both samples and extrapolated to 1 m². Similarly, for each target species we averaged the dry weight of both samples, and extrapolated the resulting mass to 1 m² to obtain species-specific productivity.

Estimation of herbivory

Between 2010 and 2022, we measured leaf damage on all species sown on the respective plot once per year in late August (second biomass harvest, see above) [47,69]. Data collection

resulted in leaf damage data for 3,020 plant species x plot x year combinations. For each species, we assessed damage on 20 randomly selected leaves per plant species (or all leaves if fewer than 20 leaves were available) from the biomass sample (see section: Measuring plant biomass). First, we visually estimated the absolute area damaged by (1) chewing, (2) rasping, and (3) leaf-mining herbivores (in mm^2) using a template card containing various circles and squares of known sizes for reference. Second, we used a leaf area meter (LI-3000C Area Meter, LI-COR Biosciences, Lincoln, Nebraska, USA) to measure the leaf area of all leaves per species. As the area meter solely calculates the remaining area, encompassing rasping and mining damage but excluding chewing damage, we estimated the initial leaf area by adding the area lost due to chewing damage. For our analysis, we calculated the percentage herbivory of each species in a plot by dividing the damaged leaf area by the initial leaf area and multiplying by 100. Plot-level herbivory was calculated as the abundance-weighted mean of species-specific herbivory percentages (weighted by leaf biomass for each plot).

Estimation of predation

Between 2014 and 2022, we measured predation rates by invertebrates (mainly arthropods and snails), small mammals, and birds once per year and plot by using artificial dummies [68]. The cylinder-shaped dummies (0.6 x 2.5 cm in size) were made from green plasticine (Staedtler Noris Club, Nuremberg, Germany) and mimic lepidopteran larvae [68,76]. Always at peak biomass in late August, we placed 10 dummies per plot on the ground with a distance of 20 cm from each other. After 24 hours, we inspected the dummies for (1) mandibular marks, (2) stylet (predatory bugs) or ovipositor marks (e.g., from parasitic Hymenoptera), (3) beak marks (birds), and (4) tooth marks (rodents). We recorded binary data for the presence or absence of any of these bite marks. The percentage of attacked dummies served as a measure of predation rate per plot and year.

Sampling of arthropods and their functional traits

Between 2010 and 2016, we sampled aboveground arthropods every two years, and from 2017 onwards (until 2020) every year. We collected arthropods by suction sampling on all 80 plots twice per year, in May (spring) and July (summer; in 2018 only May sampling. Using a modified commercial vacuum cleaner (Kärcher A2500; Kärcher GmbH, Winnenden, Germany), we randomly selected two subplots of 0.75 m x 0.75 m within each plot, covered them with a gauze-coated cage of the same size, and sampled until no more arthropods were visible in the cage. We sampled between 9 am and 4 pm on sunny days without wind. In May 2019 we only sampled one replicate per plot, due to unfavorable weather conditions. All species groups that can be representatively sampled with our method (Araneae, Coleoptera, Hemiptera, Hymenoptera) were sent to specialized taxonomists for identification. Due to difficulties in identification caused by larval stages, small sizes (e.g., hymenopterans), or damaged individuals, we could not identify all individuals to the species level. For our analyses, we used the highest taxonomic resolution that was reliably identifiable (81% species or genus level, 19% subfamily or family level). For all taxa that were sampled more than once in suction campaigns (non-singletons), we compiled information about feeding guild and wet body mass [77]. For each year, sampling campaign and plot, we first calculated species richness, extrapolated species richness (Chao estimate [78]), abundance, Shannon diversity, biomass (mg/m²) and the biomass ratio (arthropod biomass in mg/m² divided by plant biomass in g/m²) for each sample within a plot and then averaged the two values per plot. We repeated the calculation for the subset of herbivores (biomass ratio here: herbivore biomass/ plant biomass) and predators (biomass ratio here: predator biomass/ herbivore biomass), which resulted in a total of eighteen metrics describing arthropod communities, for each combination of plot x sampling x year x season.

Statistical analyses

All data processing and analyses were conducted using the statistical program R, version 4.3.3 [79].

Models testing for directional temporal changes and its dependence on plant species richness

With a first mixed-effects model (Type I Sums of Squares; 'lmer'- function, 'lme4' package [80]; 'lmerTest' package [81]) we tested for overall changes in the response variable over **time** (calendar year fitted as a centered numerical variable), in both sampling **seasons** (categorical variable with two levels) across a gradient in plant species richness (**PSR**; log transformed and centered). For herbivory and predation, season was not fitted in the model, as only one sampling campaign is available.

(1) response ~ PSR*time*season + (1|plot) + (1|plot:calendar_year) + (1|plot:season)

All models contained plot identity as a random term to account for spatial non-independence of the data. Moreover, if the response variable was measured multiple times in the same year the combination of plot and calendar year (nine levels) and the interaction of plot and season (two levels) were fitted as random effects to account for spatio-temporal non-independence of the data. Further, we use the model to estimate the relative annual changes in the response (fitted values for year i / fitted values for year i+1) in high (60 plant species) and low (monoculture) species mixtures.

Models testing for variability in plant species richness effects across multiple years

In a second mixed-effects model, we tested if **PSR** affects the response variable in different **calendar years** (fitted as a factor) and, if available, sampling **season** (fitted as a two-level factor).

(2) response ~ PSR*calendar_year*season + (1|plot) + (1|plot:calendar_year) + (1|plot:season)

Models contained the same random terms as above. We use this model to extract the PSR effect on the response variable for every year (slope of the interaction of PSR and calendar year, or the interaction of PSR, calendar year and season). Each slope was divided by the average (across all plots) of the respective year or season within a year to make slopes independent of

absolute differences between years and seasons (**corrected PSR effect** on the response variable).

Models testing for directed temporal changes in the effects of plant species richness

Lastly, in a linear model we tested for directional changes in plant species richness (PSR) effects (slopes) over **time** (calendar year fitted as centered, numerical variable) for both **seasons**.

(3) corrected PSR effect on the response ~ time*season

Acknowledgements

We thank the technical staff of the Jena Experiment for their work in maintaining the experimental field site and also many student helpers for weeding of the experimental plots and support during measurements. Further, we thank Roland Achtziger, Eric Anton, Theo Blick, Frank Creutzburg, Ralf Heckmann, Christoph Muster, and Oliver Wiche for their tremendous work with identifying arthropod individuals and Alex Strauss for helpful comments on the manuscript. This work was supported by the German Science Foundation (DFG FOR 1451 EB 555/3-1, WE 3081/15-2, FOR 5000 EB 555/6-1, EB 555/6-2, ME 5474/1-1, ME 5474/1-2).

Author contributions

A.E., and S.T.E. developed and framed the research question. A.E. and M.B. analysed the data. H.S. and S.T.M. contributed to the data analysis. A.E. wrote the manuscript with contributions from all other authors. A.E., L.H. and M.B. contributed to data collection.

Data accessibility statement

We confirm that, should the manuscript be accepted, the data supporting the results will be archived in the repository Jexis2.0. The data DOI will be included at the end of the article.

References

1. Wilson, E. O. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* **1**, 344–346 (1987).
2. Soliveres, S. *et al.* Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* **536**, 456–459 (2016).
3. Bengtsson, J. *et al.* Grasslands—more important for ecosystem services than you might think. *Ecosphere* **10**, e02582 (2019).
4. Scherber, C. *et al.* Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**, 553–556 (2010).
5. Ebeling, A. *et al.* Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. *Basic and Applied Ecology* **26**, 50–63 (2018).
6. Wan, N. F. *et al.* Global synthesis of effects of plant species diversity on trophic groups and interactions. *Nature Plants* **6**, 503–510 (2020).
7. Ebeling, A. *et al.* Plant diversity impacts decomposition and herbivory via changes in aboveground arthropods. *PLoS ONE* **9**, e106529 (2014).
8. Meyer, S. T. *et al.* Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity. *Ecosphere* **7**, e01619 (2016).
9. Yang, L. H. & Gratton, C. Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* **2**, 26–32 (2014).
10. Buzhdygan, O. Y. *et al.* Biodiversity increases multitrophic energy use efficiency, flow and storage in grasslands. *Nature Ecology and Evolution* **4**, 393–405 (2020).
11. Hulme, P. E. Herbivory, plant regeneration, and species coexistence. *Journal of Ecology* **84**, 609 (1996).
12. Klein, A.-M. *et al.* Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B* **274**, 303–313 (2007).

13. Rodger, J. G. *et al.* Widespread vulnerability of flowering plant seed production to pollinator declines. *Science Advances* **7**, eabd3524 (2021).
14. Barnes, A. D. *et al.* Biodiversity enhances the multitrophic control of arthropod herbivory. *Science Advances* **6**, eabb6603 (2020).
15. Vickery, J. a. *et al.* The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* **38**, 647–664 (2001).
16. Cardoso, P. *et al.* Scientists' warning to humanity on insect extinctions. *Biological Conservation* **242**, 108426 (2020).
17. Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R. & Stopak, D. Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences* **118**, 1–10 (2021).
18. Hallmann, C. A. *et al.* More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* **12**, e0185809 (2017).
19. Sánchez-Bayo, F. & Wyckhuys, K. A. G. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* **232**, 8–27 (2019).
20. van Klink, R. *et al.* Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**, 417–420 (2020).
21. van Klink, R. *et al.* Erratum for the Report "Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances" by R. Van Klink, D. E. Bowler, K. B. Gongalsky, A. B. Swengel, A. Gentile, J. M. Chase. *Science* **370**, eabf1915 (2020).
22. Gibson, D. J. *Grasses and Grassland Ecology*. (Oxford University Press, 2009).
23. Gibbs, H. K. & Salmon, J. M. Mapping the world's degraded lands. *Applied Geography* **57**, 12–21 (2015).
24. Bardgett, R. D. *et al.* Combatting global grassland degradation. *Nat Rev Earth Environ* **2**, 720–735 (2021).

25. Queiroz, C., Beilin, R., Folke, C. & Lindborg, R. Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. *Frontiers in Ecology and the Environment* **12**, 288–296 (2014).
26. UNEP-WCMC. *UK National Ecosystem Assessment: Synthesis of the Key Findings*. (2011).
27. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **489**, 326–326 (2012).
28. Eisenhauer, N. *et al.* Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity–ecosystem functioning relationships. *Research Ideas and Outcomes* **5**, e47042 (2019).
29. Reich, P. B. *et al.* Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336**, 589–592 (2012).
30. Weisser, W. W. *et al.* Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: patterns, mechanisms, and open questions. *Basic and Applied Ecology* **23**, 1–73 (2017).
31. Wagg, C. *et al.* Biodiversity–stability relationships strengthen over time in a long-term grassland experiment. *Nature Communications* **13**, 7752 (2022).
32. Lange, M., Ebeling, A., Voigt, W. & Weisser, W. Restoration of insect communities after land use change is shaped by plant diversity: a case study on carabid beetles (Carabidae). *Scientific Reports* **13**, 2140 (2023).
33. Haddad, N. M. *et al.* Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* **12**, 1029–1039 (2009).
34. Ebeling, A. *et al.* Plant diversity induces shifts in the functional structure and diversity across trophic levels. *Oikos* **127**, 208–219 (2018).
35. Schuldt, A. *et al.* Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications* **10**, 1460 (2019).

36. Giling, D. P. *et al.* Plant diversity alters the representation of motifs in food webs. *Nature Communications* **10**, 1226 (2019).

37. Eisenhauer, N. *et al.* The multiple-mechanisms hypothesis of biodiversity–stability relationships. *Basic and Applied Ecology* **79**, 153–166 (2024).

38. Roscher, C. *et al.* Using plant functional traits to explain diversity-productivity relationships. *PLoS ONE* **7**, e36760 (2012).

39. Vellend, M. *et al.* Drawing ecological inferences from coincident patterns of population- and community-level biodiversity. *Molecular Ecology* **23**, 2890–2901 (2014).

40. Guimarães-Steinicke, C. *et al.* Biodiversity facets affect community surface temperature via 3D canopy structure in grassland communities. *Journal of Ecology* **109**, 1969–1985 (2021).

41. Huang, Y. *et al.* Enhanced stability of grassland soil temperature by plant diversity. *Nature Geoscience* **17**, 44–50 (2024).

42. Schnabel, F. *et al.* Tree diversity increases forest temperature buffering. *bioRxiv* 2023.09.11.556807 (2024) doi:10.1101/2023.09.11.556807.

43. Rzanny, M., Kuu, A. & Voigt, W. Bottom-up and top-down forces structuring consumer communities in an experimental grassland. *Oikos* **122**, 967–976 (2013).

44. Hertzog, L. R., Meyer, S. T., Weisser, W. W. & Ebeling, A. Experimental manipulation of grassland plant diversity induces complex shifts in aboveground arthropod diversity. *PLoS ONE* **11**, e0148768 (2016).

45. Loranger, J. *et al.* Predicting invertebrate herbivory from plant traits: evidence from 51 grassland species in experimental monocultures. *Ecology* **93**, 2674–2682 (2012).

46. Koricheva, J. & Hayes, D. The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. *Functional Ecology* **32**, 1704–1717 (2018).

47. Bröcher, M. *et al.* Effects of plant diversity on species-specific herbivory: patterns and mechanisms. *Oecologia* **201**, 1053–1066 (2023).

48. Bartomeus, I. *et al.* Biodiversity ensures plant–pollinator phenological synchrony against climate change. *Ecology Letters* **16**, 1331–1338 (2013).

49. Blüthgen, N. *et al.* Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nature Communications* **7**, 10697 (2016).

50. Senapathi, D. *et al.* Wild insect diversity increases inter-annual stability in global crop pollinator communities. *Proceedings of the Royal Society B* **288**, 20210212 (2021).

51. Seibold, S. *et al.* Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674 (2019).

52. Hallmann, C. A., Ssymank, A., Sorg, M., de Kroon, H. & Jongejans, E. Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. *Proceedings of the National Academy of Sciences* **118**, e2002554117 (2021).

53. Schuldt, A. *et al.* Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. *Oecologia* **174**, 533–543 (2014).

54. Voigt, W. *et al.* Trophic levels are differentially sensitive to climate. *Ecology* **84**, 2444–2453 (2003).

55. Haddad, N. M., Tilman, D., Haarstad, J., Ritchie, M. & Knops, J. M. H. Contrasting effects of plant richness and composition on insect communities: A field experiment. *American Naturalist* **158**, 17–35 (2001).

56. Borer, E. T., Seabloom, E. W., Tilman, D. & Novotny, V. Plant diversity controls arthropod biomass and temporal stability. *Ecology Letters* **15**, 1457–1464 (2012).

57. Hutchinson, G. E. Homage to Santa-Rosalia or why are there so many kinds of animals. *American Naturalist* **93**, 145–159 (1959).

58. Srivastava, D. S. & Lawton, J. H. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist* **152**, 510–529 (1998).

59. Müller, J. *et al.* Weather explains the decline and rise of insect biomass over 34 years. *Nature* **628**, 349–354 (2024).

60. Bello, F. de *et al.* Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends in Ecology & Evolution* **36**, 822–836 (2021).

61. Wang, S. *et al.* Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology* **102**, e03332 (2021).

62. Lázaro, A., Gómez-Martínez, C., González-Estévez, M. A. & Hidalgo, M. Portfolio effect and asynchrony as drivers of stability in plant–pollinator communities along a gradient of landscape heterogeneity. *Ecography* **2022**, e06112 (2022).

63. Mraja, A., Unsicker, S. B., Reichelt, M., Gershenzon, J. & Roscher, C. Plant community diversity influences allocation to direct chemical defence in Plantago lanceolata. *PLoS ONE* **6**, e28055 (2011).

64. Ruiz-Guerra, B., Velázquez-Rosas, N., Díaz-Castelazo, C. & Guevara, R. Functional plant traits and plant-herbivore interactions. in *Evolutionary ecology of plant-herbivore interaction* (eds. Núñez-Farfán, J. & Valverde, P. L.) 191–207 (Springer, Cham, 2020). doi:10.1007/978-3-030-46012-9_10.

65. Gutiérrez, D. & Wilson, R. J. Intra- and interspecific variation in the responses of insect phenology to climate. *Journal of Animal Ecology* **90**, 248–259 (2021).

66. Abarca, M. & Spahn, R. Direct and indirect effects of altered temperature regimes and phenological mismatches on insect populations. *Current Opinion in Insect Science* **47**, 67–74 (2021).

67. Welti, E. A. R. *et al.* Temperature drives variation in flying insect biomass across a German malaise trap network. *Insect Conservation and Diversity* **15**, 168–180 (2021).

68. Hertzog, L. R., Ebeling, A., Weisser, W. W. & Meyer, S. T. Plant diversity increases predation by ground-dwelling invertebrate predators. *Ecosphere* **8**, e01990 (2017).

69. Meyer, S. T. *et al.* Consistent increase of herbivory along two experimental plant diversity gradients over multiple years. *Ecosphere* **8**, e01876 (2017).

70. Gagic, V. *et al.* Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B* **282**, 20142620 (2015).

71. Greenop, A., Woodcock, B. A., Wilby, A., Cook, S. M. & Pywell, R. F. Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology* **99**, 1771–1782 (2018).

72. Woodcock, B. A. *et al.* Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nature Communications* **10**, 1481 (2019).

73. Hoehn, P., Tscharntke, T., Tylianakis, J. M. & Steffan-Dewenter, I. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B* **275**, 2283–2291 (2008).

74. Fründ, J., Dormann, C. F., Holzschuh, A. & Tscharntke, T. Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology* **94**, 2042–2054 (2013).

75. Roscher, C. *et al.* The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology* **5**, 107–121 (2004).

76. Meyer, S. T., Koch, C. & Weisser, W. W. Towards a standardized Rapid Ecosystem Function Assessment (REFA). *Trends in Ecology & Evolution* **30**, 390–397 (2015).

77. Bröcher, M., Meyer, S. T., Leher, Ana Garcia & Ebeling, A. Ecological traits for 1,374 arthropod species collected in a German grassland. *Ecology* **in press**, (2025).

78. Chao, A. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* **11**, 265–270 (1984).

79. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing https://doi.org/10.1890/0012-9658 (2024).

80. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48 (2015).

81. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* **82**, 1–26 (2017).