Enemy impact on plant communities in a changing world

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Highlights

- Predicting how global change affects our ecosystems remains a current challenge. Global change can directly affect plant communities, but it can also indirectly affect plant communities by altering species interactions.
- Plant enemies, such as herbivores or pathogens, can strongly affect plant productivity, diversity and composition. Their impact on plant communities is notoriously context-dependent and may be strongly altered by global change drivers.
- We synthesize current knowledge on the context-dependency of plant-enemy interactions and illustrate how nitrogen enrichment, climate change, and elevated CO_2 as well as a loss of plant diversity and insects, may alter enemy communities and their impact on plant communities.
- Understanding the indirect effects of global change on our ecosystems can fundamentally improve our ability to predict the consequences of global change.

Abstract

Indirect effects of global change via changing species interactions have been largely ignored in studies predicting global change impacts on ecosystems. Antagonistic biotic interactions, however, can strongly affect ecosystems and are likely to be affected by global change drivers themselves. We synthesize current knowledge on the impact of invertebrate herbivores and pathogens on plant productivity, diversity and community composition, and outline theory and expectations on how important global change drivers – nitrogen enrichment, climate change and elevated CO^2, and plant and insect diversity loss, may affect enemy impact on plant communities. We illustrate that our ability to predict global change impact requires a holistic perspective, taking into account direct as well as indirect effects via the biotic component of ecosystems.

Global change can indirectly affect plant communities by changing species interactions

A major challenge is to predict how biodiversity and ecosystem functioning will respond to environmental global change. Global change can directly affect the productivity, functional composition and diversity of plant communities by changing environmental conditions [1–3], however, it can also affect communities indirectly by altering species interactions [4, Fig. 1]. Indirect effects have just recently started to be explored in studies on global change, mainly mediated through changing competitive interactions [4,5] or plant mutualist interactions [6,7]. However, we lack a general understanding of indirect effects mediated through altered antagonistic trophic interactions, such as between plants and their herbivores or pathogens [8]. Altered plant-enemy interactions following global change may profoundly affect, and even reverse, ecosystem responses [9,10]. To predict ecosystem responses to environmental change, we need to also enhance our understanding of how global change drivers alter the interactions of plant communities with their enemies.

Herbivores and pathogens can have strong impacts on plant communities, with large effects on primary production, species composition, plant diversity and ecosystem functioning [11–14]. The intensity of these interactions vary substantially in space [12,15,16], and enemy impact on ecosystems is likely to be altered by global change drivers. We still have a limited understanding of the key abiotic and biotic factors driving variation in enemy impact on plant communities [12,17], however developing general predictions is essential to understand how global change will affect our ecosystems.

In this review we summarize recent advances in our understanding of the impact of less well studied plant enemies, invertebrate herbivores and fungal pathogens, on three key aspects of plant communities: plant diversity, community composition and productivity, and highlight open questions and knowledge gaps. Then, we outline relevant ecological theory and empirical studies on how variation in environmental conditions will affect plant-enemy interactions, and use this to develop predictions for how key global change drivers, nitrogen enrichment, climate change, and increased CO_2, could indirectly affect plant communities via changing enemy impact. We unpack these overall indirect effects and consider how global change might affect enemy communities alone or how it might alter feedbacks between plant and enemy community structure. Finally, we consider how the current losses of plant and insect diversity might alter enemy impact on plant communities. We do not discuss effects of global change on the geographical distribution of plant species and their natural enemies (including biological invasions), and effects on phenology.

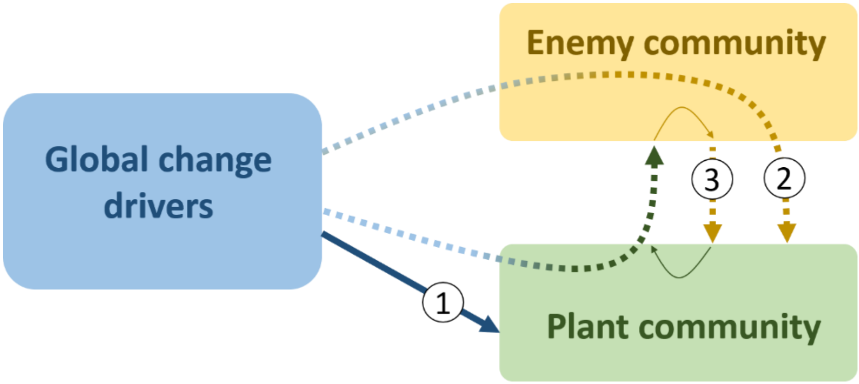

Fig. 1: Global change drivers can *directly* affect plant communities (solid line, ①) but can also *indirectly* (dashed lines) affect plant communities through changing interactions of plant communities with their enemy communities. This can happen because global change drivers directly affect the enemy community (②) and hence their impact on plants, or because global change drivers directly affect the plant community which has consequences for the enemy community and hence their impact on plant communities (③).

General impact of plant enemies on plant communities

Plant enemies can alter several aspects of plant communities, including productivity, diversity and composition [12,13,18,19]. Enemies alter primary productivity by consuming or preventing the accumulation of plant biomass. For herbivores, the strength of such top-down control depends on whether they are limited by predation [20,21]. Herbivores and plant pathogens can further be important drivers of plant coexistence and affect plant diversity [13,22,23]. Even if enemies do not alter diversity, they frequently change competitive interactions between plant species and alter the composition of plant communities [18]. We discuss the impact of plant enemies on these three aspects of plant communities - productivity, diversity, and composition.

Impact of enemies on plant productivity

Plants are consumed by numerous organisms that feed in different ways and on different types of plant tissue, above- or belowground. These enemies can be very restricted in their diet or can be highly generalist. Despite the high diversity of plant enemies, studies aiming to understand their role in determining plant community dynamics have mainly focused on vertebrate herbivores [24,25]. While highly debated in the past [26], today there is ample evidence for their widespread, top-down effects on plant communities [11,12]. In contrast to vertebrates, it has often been assumed that invertebrate herbivores and pathogens are too small, specialised or strongly regulated by predators to have large effects on plant productivity [24]. Several individual studies, however, have shown that invertebrate herbivores and fungal pathogens *can* affect plant productivity [e.g. 13,27–29], but effects are often variable between studies. While one meta-analysis on insecticide experiments in grassland found an increase in primary production when insects where removed [30], a recent meta-analysis showed no consistent top-down effect of aboveground invertebrate herbivores on plant biomass [12]. For other groups, such as belowground invertebrates, molluscs or fungal pathogens, the impact on plant communities is even less clear, although strong effects have been shown in some studies, under certain conditions [28,29,31–33].

Impact of enemies on plant diversity

Enemies frequently alter competitive interactions between plants and can therefore alter the *diversity* of plant species in a community [22,23,34]. Enemies can promote coexistence if they more strongly attack the most abundant species within a community [34–37]. This can arise if attack rate declines with decreasing host frequency (negative-frequency dependence). Enemies then drive niche differences between plant species, stabilizing coexistence (e.g. [23]). Particularly the attack rate of specialist enemies has been suggested to decline non-linearly with host abundance as rare hosts are difficult to locate and escape attack (Janzen-Connell effect, e.g. [36,38]). Enemies can also promote coexistence and more strongly attack dominant plant species through a correlation between palatability and dominance or a correlation between sensitivity of plants to attack and dominance. This could be driven by, for instance, a trade-off between the growth of plants in a resource rich environment and their defense against enemies [39–42], or a trade-off between the competitive ability for belowground nutrients and defense [43]. In this case, enemies promote coexistence by reducing the competitive ability (fitness) of more vigorously growing plant species, equalizing fitness between dominant and less dominant species.

Empirical studies excluding plant enemies have found highly variable effects on plant diversity [24,25,28,29,44,45]. While large vertebrate herbivores were found to slightly promote grassland diversity (evenness) in a recent meta-analysis, effects of invertebrates were variable [12,32]. Evidence from the tropics [38,46] and also from plant-soil feedback experiments in temperate grasslands [36] suggest that soil-borne pathogens are able to maintain high levels of diversity through Janzen-Connell effects. However, pathogens or invertebrate herbivores may also destabilize coexistence by creating positive feedbacks or by increasing fitness differences among plant species [13]. Apparent competition through shared enemies could enhance fitness differences, for instance through spillover of pathogens from a tolerant to a less tolerant host [13,47].

Effects of plant enemies on plant species composition

Plant enemies may also alter plant species *composition* without changing diversity. Compositional changes are driven by the same basic mechanisms that also affect diversity. Plant enemies can reduce the competitive ability of certain species, leading to competitive release for others [18]. Plant enemies might generally change *plant functional composition* by preferentially attacking faster growing, less defended plant species rather than slower growing, and more defended ones [19,41,42]. Recent work on fungal pathogens in grasslands has shown that fast-growing plant species were more likely to be infested than slow-growing species [42]. Communities consisting of fast-growing species were thus more strongly impacted by pathogens (they lost more biomass) than communities consisting of slower growing species, leading to a shift towards more slow- growing species [42]. Similarly, invertebrates have been shown to affect plant community composition [e.g. 19,29], however the effects depended on the group of enemies excluded, or herbivore preference, and were not linked to plant growth strategy [16,45]. Pathogens and invertebrate herbivores might also change composition by favouring later successional species [48]: Studies have shown that early successional plant species experience stronger and more negative feedbacks with root-feeding invertebrates than mid- or late-successional ones [49], and that species replacement during primary or secondary succession can be driven by soil pathogens [50] and insect herbivores [51].

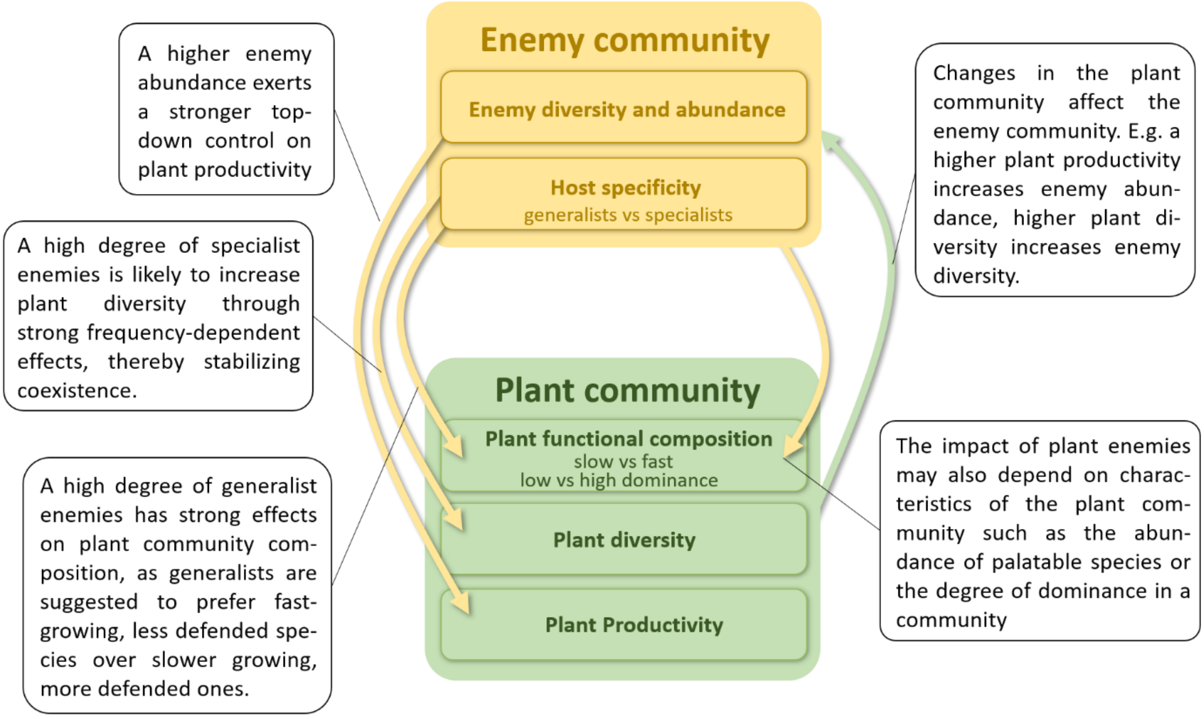

Fig. 2: Illustration of the general effects of the enemy community on different aspects of the plant community (plant productivity, diversity, and functional composition).

Context dependency in plant enemy impact: predicting indirect effects of global change

The outcome of biotic interactions are notoriously context-dependent, with enemy impact depending on many abiotic and biotic factors [16,52,53]. In general, variation in impact can be driven by changes in the enemy or the plant community. Changes in the abundance and per capita feeding rate of enemies will alter their impact on plant productivity [54], while changes in enemy diversity and in their degree of specialisation will alter impact on plant diversity and species composition (Fig. 2). At the same time, characteristics of the plant community may determine the impact that enemies can have, e.g. enemies may have a larger impact in communities dominated by a few plant species [55,56] or in communities dominated by palatable, fast growing species [42, Fig.2]. Indirect effects of global change on plant communities through altered biotic interactions can thus arise because global change alters the enemy community alone (Fig. 1, ②) or because it alters feedbacks between plant and enemy community structure (Fig. 1, ③). For example, increased temperature might directly alter enemy per capita feeding rates (Fig. 1, pathway ②). In addition, global change drivers might alter enemy communities by changing the plant community: increases in plant productivity might increase enemy abundance [57], increases in plant diversity are expected to increase enemy diversity [58] and perhaps the proportion of specialists [59], while a shift to fast growing plant species might increase the abundance of generalists (Fig. 1, pathway ③). Understanding how global change drivers alter the feedback between enemies and plants would fundamentally enhance our ability to improve global change forecasts. Here, we provide a framework for how important global change drivers, namely nitrogen enrichment, climate change, and an increase in atmospheric carbon dioxide might modify the impact of plant enemies on plant productivity, diversity and plant functional composition (Box 1). In addition, we discuss the consequences of plant diversity loss and declines in insect abundance arising from other global changes.

Effects of nitrogen enrichment

Nitrogen enrichment is a key global change driver. It typically causes a loss of plant diversity [60], increases plant biomass production [61] and tissue nitrogen concentrations [62] and leads to a shift towards faster-growing plant species [63]. Nitrogen may alter enemy impact through several of these mechanisms. Theory predicts that low-resource environments select for slow-growing, highly defended species whereas high-resource environments select for fast-growing, less defended species [39]. Similarly, the nitrogen disease hypotheses predicts that plants growing in fertile environments are more attractive to enemies due to higher tissue nitrogen concentrations [64]. Consequently, fast-growing, acquisitive species, and species growing in nitrogen rich conditions, should suffer higher levels of herbivory or pathogen infection than species with a conservative strategy [40,65,66]. However, fast-growing species or species with access to more soil resources might be more tolerant of enemy attack, meaning that the actual impact of enemies on them, in terms of plant biomass loss, could be lower despite higher infestation [67]. In addition, the exploitation ecosystem hypothesis [20,21] predicts that in resource rich environments with high primary production, natural enemies of herbivores (predators) should control herbivore populations and herbivores should only have large impacts at lower productivity. In this case nitrogen enrichment would not change enemy impact on plant productivity, if all the additional plant biomass is transferred to predators, however so far the pattern has been only shown for vertebrates and not for invertebrate herbivores [68].

The evidence for changes in herbivore and pathogen impact with productivity and fertility is mixed. Herbivore biomass has been shown to increase with plant productivity [69,70], however, herbivore *impact* (see Box 2) has sometimes been shown to be unaffected or even to decrease with increasing productivity [30,69]. Results from a recent meta-analysis were surprisingly uninformative for understanding patterns in the strength of herbivore impact among systems differing in net primary production (indicator of soil fertility, [12]). For pathogens, enhanced disease and impact with nitrogen enrichment has been shown in agricultural studies, but findings from grasslands are contradictory, with some studies finding support [71] and others not [42]. Whether the *impact* of plant enemies increases with increasing soil fertility is therefore not fully resolved.

Effects of temperature and precipitation

Increases in temperature and changes in precipitation following climate change will not only affect plant growth directly but are likely to change plant communities indirectly by modifying their pathogen and herbivore communities. Warming is expected to increase the impact of herbivores and pathogens because higher temperatures lead to higher metabolic rates [72,73], accelerated development and reproduction [74,75]. However, this will only occur if precipitation remains high - warming in arid environments would be expected to reduce enemy attack. Theory on how plant-enemy interactions change with temperature largely come from latitudinal and altitudinal gradients. Biotic interactions have long been predicted to be strongest in the warm, low latitudes [15,59]. The mechanisms driving this latitudinal gradient are likely to emerge over long time scales and involve increased coevolution and speciation in more predictable and benign climates [59,76]. Similarly, herbivore pressure is expected to be higher at lower elevations, which are warmer and less variable climatically [77,78]. This should result in decreased plant defense at high elevations and a higher proportion of generalist consumers. Plant-fungal interactions are also likely to vary with elevation, as fungal communities are sensitive to changes climatic conditions [79,80]. Altitudinal gradients occur over much smaller scales and are less confounded by historical or macro-evolutionary processes [81]. They may therefore be more promising than latitudinal gradients for predicting changes in enemy impact with climate change [5,80].

Results from existing elevational gradients and warming experiments indicate that herbivore pressure is indeed higher at lower elevations [77,78], however, recent studies questioned the generality of previous findings [78,81]. Similarly, results from a global field survey suggests that the relative abundance of soil-borne fungal pathogens increase with warming [82]. Most warming experiments have shown an increase in pathogen and herbivore attack at higher temperatures in the field [75,83–85] or in the lab [86,87]. However, other warming experiments found no change [88] or even a decrease [89] in herbivory. Results from agriculture indicate that temperature effects on pathogen impact are species-specific. While several cold-sensitive pathogens would benefit from mild winters [90], others are impeded in their infection potential by higher temperatures [91]. This suggests that species-specific changes in plant quality (leaf nutrients, defensive compounds), herbivore and pathogen thermal limits [89] or changes in herbivore natural enemy activity or abundance [92,93] also determine enemy attack and hence their impact on plants. Rarely, studies assess *impact* of enemies on plant communities or functioning along altitudinal gradients, i.e. by using exclusions [80], or combine warming experiments with the exclusion of pathogens and herbivores (but see [94]. More studies are needed to reliable predict the impact of plant enemies on plant communities in a warmer world. The effects of changes in precipitation or extreme whether events on enemy impact are more difficult to predict, as water on the one hand affects habitat characteristics for enemies (soil and air humidity), but also acts as a resource, affecting plants and enemies via changes in productivity. Effects on habitat characteristics are likely to be species or group-specific. While many pathogens, e.g. rusts, may depend on humidity during infection and may decrease during drought, others may benefit [95,96]**.** Changes in soil moisture may affect habitat conditions differently for herbivores or predators, with consequences for predator-prey interactions [97,98]. Extreme weather events such as storms may facilitate natural dispersal for pathogens, whereas other enemy groups may decrease [99,100]. When water acts as a resource, changes in precipitation affect enemies indirectly via changes in plant quality and community composition. E.g. periodic drought stress in plants may impede the ability of plants to compensate for enemy attack, making plants more susceptible to disease. Continuing drought may shift plant community composition towards more stress tolerant, well-defended species, at the expense of fast-growing more competitive ones. A reduction in precipitation may further increase mutualistic interactions, which can play an important role in plant resistance [101]. This may decrease plant quality and the impact of enemies on plant communities, similar to the opposite effects of increases in temperature and nitrogen. Because changes in precipitation may result in complex responses of plants and enemies, drawing predictions on how such changes affect the impact of enemies on plant communities is challenging.

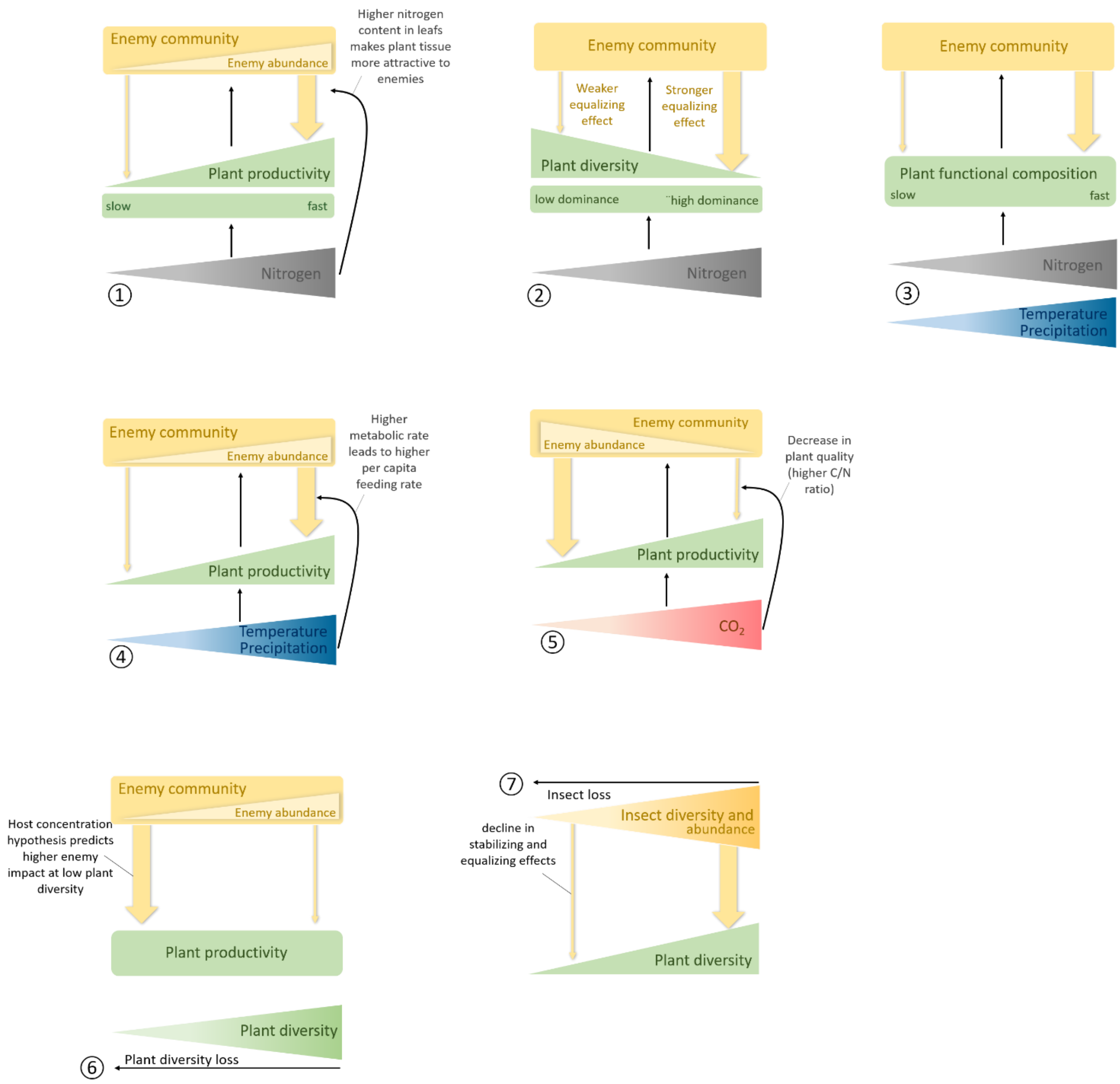

Fig. 3. ①-⑤ Illustrations indicate how the global change drivers nitrogen, temperature and elevated CO2 may affect the impact of plant enemies (*yellow arrows*) on plant productivity. Moreover, we depict how nitrogen enrichment may affect the impact of plant enemies on plant diversity and functional composition. ⑥ depicts the consequences of plant diversity loss on the impact of enemies on plant productivity, and ⑦ the effect of insect decline on plant diversity. Explanations see Box 1.

Box 1: Expectations of how global change drivers affect enemy impact

① **Nitrogen enrichment affects impact of enemies on plant productivity**. The nitrogen disease and resource availability hypotheses would both suggest that the impact of herbivores and pathogens on plant productivity should be higher following N enrichment, due to changes in plant nutrient contents or functional composition. Moreover, a high soil fertility may reduce the presence of beneficial soil microbes, which have been shown to provide plants with resistance against enemies [128–130], further increasing enemy impact. While both plant and herbivore biomass have been shown to increase with soil fertility, herbivore impact has not [69]. This might suggest that fast-growing plant species are more tolerant and compensate for leaf loss, or that top-down control of herbivores by predators is stronger at high soil fertility. Predicting how the impact of enemies on plant productivity will change with nitrogen enrichment will therefore require more information on variation in plant tolerance and predator communities with nitrogen addition.

② **Nitrogen enrichment increases impact of enemies on plant diversity.** Nitrogen enrichment usually reduces plant diversity and evenness, through an increase in light competition, which is expected to alter enemy impact. We expect that the impact of enemies on plant diversity is stronger at high soil fertility because there is more opportunity for plant enemies to equalise fitness differences and promote diversity by reducing the dominance of the good light competitors [25]. Enemies might also be particularly likely to reduce the dominants in resource rich environments because they are less defended (growth-defense trade-off), or because they are tall and are therefore more likely to be removed by vertebrate grazers. Changes in the feedbacks between enemies and plants may therefore offset some of the negative effects of nitrogen enrichment on plant diversity.

③ **Nitrogen enrichment increases the impact of enemies on plant functional composition.** Nitrogen enrichment tends to shift plant functional composition towards dominance by fast growing species. We expect that this will increase enemy impact on plant functional composition because fast-growing plants are preferentially attacked by generalist enemies, allowing slower growing but more defended species to persist. Excluding enemies from fertile communities would result in a loss of slower growing species, shifting functional composition towards even faster growing species. However, excluding enemies from resource poor environments would have minor effects on plant functional composition, as fast-growing species will still be outcompeted by the slow growing ones and are therefore unlikely to be able to increase.

④ **Temperature affects impact of enemies on plant productivity.** A higher plant productivity as well as an accelerated development and reproduction of plant enemies with warmer temperatures and higher precipitations are both likely to increase enemy abundance and consumption, and therefore enemy impact on *plant productivity*. However, this might be offset by changes in plant nutrients and defences, or – for herbivores - by altered top-down control of predators. For example, it has been shown that spiders produce a second clutch in arctic environments with climate warming [93]. Thus, whether the impact of invertebrate herbivores and fungal pathogens on productivity increases with climate warming is not fully resolved.

Predictions for how enemy impact on *plant diversity* and *composition* will change with alterations in the climate are even less clear, as only few studies have interactively manipulated temperature and enemy abundance [94].

⑤ **Elevated CO_2 reduces impact of enemies on plant productivity.** An increase in atmospheric carbon dioxide is expected to decrease plant quality via an increase in the C:N ratio and carbon-based secondary compounds. We therefore expect that, at least for herbivores, enemy abundance and hence impact will decrease. For pathogens, we need more studies to draw general conclusions on how increases in CO_2 affect pathogen impact on plants, particularly in natural systems [108]. We also expect that the effect of CO_2 on plant functional composition will remain stable as herbivores will prevent an increase in N-fixing species with elevated CO_2.

⑥ **Plant diversity loss affects impact of enemies on plant productivity.** We would expect that the impact of natural enemies on plant productivity increases with plant diversity loss (host concentration hypothesis, diversity-disease hypothesis). However, the effect of plant diversity loss on enemies will also depend on the species that are lost first from the community [131]: if susceptible or palatable species are lost last, for instance if fast growing species remain following nutrient enrichment, then diversity loss will enhance disease transmission. However, the opposite will occur if resistant species are lost last.

⑦ **Insect decline alters effects on plant diversity.** A loss of insect biomass, abundance and diversity is likely to weaken the stabilizing and equalizing effects of herbivores on plant coexistence. This might have far reaching consequences for plant diversity.

Effects of elevated atmospheric carbon dioxide

Another key element of anthropogenic climate change is an increase in atmospheric CO_2 levels. The drastic rise in CO_2 is likely to not only affect plant growth but also plant interactions with their enemies either by changing plant nutritional quality or functional composition and hence the feedbacks between plant and enemy communities [102,103]. Experiments have shown that elevated CO_2 generally enhances plant growth and increases tissue C:N ratios [104,105]. Moreover, it is likely that an increased C supply to plants leads to an increase in C-based secondary and structural compounds, and a dilution of nutrients [103], decreasing plant quality [104,106]. As invertebrate herbivores and pathogens are N-limited, an increase in C:N ratios is likely to lead to lower food quality.

Results from meta-analyses suggest that while chewing herbivores respond with increased food consumption in the short term to compensate for the lower nutritional quality, they also grow more slowly and have a longer development time, which increases exposure to enemies, all of which reduce herbivore abundance under elevated CO_2 [104,106]. Phloem feeding insects instead tend to increase with elevated CO_2 [104]. For pathogens, studies suggest that elevated CO_2 can have positive, negative or neutral effects on infection intensity, as different pathogens might respond differently [71,74,107,108].

In addition to changes in plant quality, changes in plant functional composition with elevated CO_2 might alter enemy impact. While C_4-plants are relatively unresponsive to elevated CO_2, C_3-plants often increase their growth [109]. Even more positively affected are legumes thanks to their close mutualistic interaction with nitrogen fixing bacteria in root nodules. Legumes shunt excess carbon to their mutualists which stimulates their growth and subsequently the growth of legumes [110]. However, the positive effect on legumes is likely to be offset by a shift in preference of generalist plant enemies to the more nutritive N-fixing species, preventing them from increasing.

Declines in plant and insect diversity – consequences for plant-enemy interactions

Other global change factors such as invasive species or pesticides may cause declines in plant and insect diversity [1,111]. A decline in plant diversity is likely to alter the impact that invertebrate herbivores and pathogens have on plant communities. The idea that plant communities with higher densities of a few species should be more vulnerable to negative effects of specialized enemiew, and that communities with high plant diversity harbour a larger community of natural enemies, has a long history in ecology ([55], host concentration hypothesis, [112]). Indeed, studies manipulating plant diversity of grasslands have shown that pathogen attack is generally higher in species poor compared to species rich communities

[56,113–117]. For herbivores, previous results have been ambiguous, and abundance, diversity and impact of herbivores have also been shown to increase be highest at high plant diversity [32,33,118–121]. However, results for specialist insect pests are more consistent and resource concentration effects are commonly observed [122]. Most of the evidence for resource concentration effects comes from experiments in which diversity is manipulated and species compositions are random [117]. Responses of herbivores and pathogens to real world gradients of diversity are less well known [123] and will depend on how plant functional composition changes at the same time.

Recent studies have also suggested that insect populations are declining in abundance [111,124] and this loss of insect abundance and diversity is likely to have consequences for plant communities. A loss of herbivore abundance and diversity is likely to result in a decline in their impacts on plant communities. This might have far reaching consequences for plant diversity by disrupting coexistence mechanisms and allowing competitive species to dominate.

Concluding remarks and future avenues

Our review highlights the multiple indirect effects that global change can have through altering enemy impact. Global change is expected to profoundly alter feedbacks between plants and enemies and to have strong indirect effects on biodiversity and ecosystem functioning. This review also points out the gaps in our understanding of the context-dependency of plant-enemy interactions [16]. The reason why we know so little about how enemy impact varies along abiotic or biotic gradients is that large-scale patterns are usually pieced together from data obtained by a variety of methods and protocols [125]. Moreover, while effects on enemy communities are rather well studied, we often know little of whether such changes translate into changes in *impact* of plant enemies, as studies often rely on comparing herbivore or pathogen *attack* along gradients and rarely measure *impact* experimentally (see Box 2), i.e. by using exclusions [80,126,127]. To predict the consequences of global change on ecosystems we need to develop a predictive understanding of why and how antagonistic biotic interactions vary in space. Exclusion of different plant enemies along environmental gradients is one way to find general predictors of context-dependency. Moreover, experiments simultaneously manipulating various global change drivers while excluding enemy groups can inform us about potential changes in plant-enemy impacts on plant communities under global change. Enhancing our knowledge on how antagonistic biotic interactions alter the diversity and functioning of plant communities, and how their impact depend on abiotic and biotic factors is a pressing priority given accelerating global change.

Box 2: Assessing plant-enemy impact: impact does not equal damage!

The interactions of plants with their enemies are notoriously context dependent and the impact of plant enemies therefore differs strongly in space. For example, ecological theory suggests that enemy impact on plant communities is strongest at low latitudes, low elevation or in very fertile habitats [15,39,77]. Most studies that test for such patterns collect data on herbivore or pathogen attack [78,132]. However, damage by herbivores or pathogens is not necessarily related to their impact, i.e. their effect on plant biomass, demography or other community components. Some plant species might be more tolerant to enemy attack than others (particularly species with an acquisitive, fast-growing strategy) and the actual *impact* of enemies on them might be lower than one would expect based on enemy infestation. Similarly, some plant species might be highly susceptible to already low levels of enemy damage and decline in abundance, and these strong effects of enemies on plant community structure cannot be assessed with damage assessments alone [133].

To best predict the impact of plant enemies on plant productivity, diversity or community composition a comparison of plant communities in the presence and absence (low densities) of enemies would be necessary, e.g. with addition/infection or exclusion experiments. Addition or infection experiments are only meaningful for determining the role of enemies in natural communities if the added enemy community composition and density mirrors the naturally occurring one, which is challenging and has so far not been done in terrestrial systems. Exclusion experiments have the advantage that they reduce natural levels of enemies, allowing to draw realistic inferences about the role of enemies in plant communities. However, reducing invertebrate herbivores and pathogens from plant communities often requires the use of chemical biocide application. While this approach has sometimes been criticized as not being effective and having non-target effects [133], as long as ecologists are careful about the inferences and mindful of the limitation of this approach the chemical exclusion of plant enemies offers a valuable opportunity to study the importance of enemy-plant interactions in terrestrial ecosystems. Combined with investigations along environmental gradients [32] or global change experiments (e.g. warming, [94]), the exclusion of enemies might reveal important insights into how enemy impact in plant communities may change in the future.

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