doi:10.20944/preprints202002.0005.v1

Context-dependency of enemy impact on plant communities in a changing world

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Abstract

Global environmental change is strongly altering biodiversity and ecosystem functioning. Antagonistic biotic interactions affect the diversity and functioning of plant communities but are notoriously context dependent and are therefore likely to be altered by global change drivers. Global change can directly affect biotic interactions and can also indirectly alter the abundance, diversity and composition of plant enemy communities, via changes to plant productivity, diversity and functional composition. Changes in the enemy community feedback to alter the plant community. However, we lack predictions for how different global change drivers may alter enemy communities and their impact on plant communities. In this review we summarize current knowledge on the impact of invertebrate herbivores and fungal pathogens on plant productivity, diversity and community composition, and outline theory and expectations on how important global change drivers – nitrogen enrichment, warming and elevated CO^2, as well as the loss of plant and insect diversity, may affect the impact of plant-enemies on plant communities.

Keywords: Global change, plant-herbivore interactions, plant-pathogen interactions, coexistence, antagonistic biotic interactions

Introduction

A major current challenge is to predict how biodiversity and ecosystem functioning will respond to ongoing environmental change. One key knowledge gap limiting our predictive ability, is how changes in antagonistic biotic interactions will alter the diversity, composition and functioning of plant communities. The few studies on effects of global change that explicitly considered antagonistic interactions among species indicate, however, that such interactions may profoundly affect, and even reverse, ecosystem responses (Suttle *et al.* 2007; Post & Pedersen 2008). Today, it is widely appreciated that vertebrate herbivores can have strong impacts on plant communities with large effects on plant primary production, species composition, plant diversity, or ecosystem processes (e.g. Duffy et al. 2003, Borer et al. 2014b, Jia et al. 2018). However, for the vast majority of consumer groups, such as invertebrate herbivores and plant pathogens, we still lack a general understanding of their contribution to biodiversity and ecosystem functioning (Mordecai 2011; Myers & Sarfraz 2017; Jia *et al.* 2018), as only a few studies have compared the impacts of the different enemy groups or tested for interactions between them. Moreover, a large body of theoretical and empirical work suggests that biotic interactions vary substantially in space and time. Hence, the impact of plant enemies on plant communities might differ depending on many abiotic and biotic factors (e.g. Dobzhansky 1950, Ford et al. 2014). However, there is no consensus on the key factors driving variation in impact (Maron *et al.* 2014a; Jia *et al.* 2018), which is essential to predict effects of global change on our ecosystems.

In this review we summarize recent advances in our understanding of the impact of invertebrate herbivores and fungal pathogens on different aspects of plant communities: plant diversity, plant community composition and plant productivity, and highlight open questions and knowledge gaps. Moreover, we outline the ecological theory on how variation in environmental conditions will affect plant-enemy interactions, and use this to develop predictions for how important direct global change drivers - nitrogen enrichment, warming, and increased CO_2, and indirect global change drivers such as plant and insect diversity loss, may affect the impact of plant-enemies on plant communities.

General impact of plant enemies on plant communities

Plant enemies can alter several aspects of plant community structure (Crawley 1997; Mordecai 2011; Kempel *et al.* 2015; Jia *et al.* 2018). Enemies alter primary productivity by consuming or preventing the accumulation of plant biomass. However, they will only do this if they are not limited by predation (Fretwell 1987; Oksanen & Oksanen 2000). Herbivores and plant pathogens can also be important drivers of coexistence between plant species and can therefore affect plant diversity (Holt 1977; Chesson 2000). Even if enemies do not alter diversity, they frequently change competitive interactions between plant species or sometimes even directly exclude plant species from communities, and can therefore alter the composition of plant communities even if they do not alter diversity (Crawley 1997). We discuss the impact of plant enemies on these three aspects of plant communities.

Impact of enemies in plant productivity

Plants are consumed by a variety of 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 very generalist. Despite the high diversity and foraging strategies of plant enemies, studies aiming to understand their role in determining plant community dynamics have mainly focused on vertebrate herbivores (Olff & Ritchie 1998; Hillebrand *et al.* 2007). Their effect on *plant productivity* has intrigued ecologists for many decades and early theory suggested that herbivores were typically top-down regulated and therefore unable to affect plant biomass (Hairston *et al.* 1960). However, today there is ample evidence for widespread, top-down effects of vertebrate herbivores on plant communities (e.g. Borer et al. 2014b, Terborgh 2015, Jia et al. 2018). It has often been assumed that invertebrate herbivores and pathogens are too small or specialised to have large effects (Olff & Ritchie 1998). Invertebrate herbivores are also frequently assumed to be regulated by predators and therefore unable to exert strong top down control on plant production. However, several individual studies have now shown that invertebrate herbivores and fungal pathogens can affect plant productivity (e.g.

Buschmann *et al.* 2005; Van Der Heijden *et al.* 2008; Allan *et al.* 2010; Allan & Crawley 2011; Mordecai 2011; Seabloom *et al.* 2018). Nevertheless, effects are often highly variable between studies. While one meta-analysis on insecticide experiments in grassland found an increase in primary production when insects where removed (Coupe & Cahill Jr 2003), a recent meta-analysis showed no consistent top-down effect of aboveground invertebrate herbivores on plant biomass (Jia *et al.* 2018). For other groups, such as belowground invertebrates, molluscs or fungal pathogens, the impact on plant communities is even less well known, although strong effects have been shown in some studies (e.g. Stein *et al.* 2010; Allan & Crawley 2011). It is therefore important to develop predictions about when invertebrate herbivores and pathogens could affect plant productivity.

Impact of enemies on plant diversity

Plant enemies frequently alter competitive interactions between plants and can therefore alter the *diversity* of plant species in a community (Holt 1977; Chesson 2000; Bever *et al.* 2015). Enemies can promote coexistence if they preferentially attack the more abundant plant species within a community (Carson and Root 2000, Petermann et al. 2008, Bever et al. 2015, Pacala & Crawley 1992). This can arise either through a correlation between palatability and dominance or a correlation between sensitivity of plants to attack and dominance (Pacala and Crawley 1992). If enemy attack rate declines with decreasing frequency of the host plant (negative-frequency dependence), enemies can drive niche differences between plant species and therefore stabilise plant coexistence (e.g. Chesson 2000). If the attack rate by specialist enemies declines non-linearly with host abundance, e.g. if rare hosts are difficult to locate and therefore escape attack, then specialists will stabilise coexistence. However, generalist enemies can theoretically also have stabilizing effects on plant communities if they switch host or food plant species to disproportionally consume whichever species is most abundant (Murdoch 1969; Chase *et al.* 2002; Ishii & Crawley 2011). Plant enemies can also promote diversity by reducing average fitness differences between plant species. This also requires a trade-off between dominance and palatability, e.g. if there is a trade-off between the growth of plants in a resource rich environment and their defense against enemies, assuming that defense is costly and constrains investment in other important traits (Coley *et al.* 1985; Herms & Mattson 1992; Kempel *et al.* 2011). In this case enemies promote coexistence by reducing the competitive ability (fitness) of more vigorously growing plant species, which can equalize fitness between dominant and less dominant plant species, even if enemy attack is not frequency dependent. Such equalizing effects have mainly been attributed to generalist enemies, however specialist enemies can theoretically also equalize fitness differences between plant species if they specialize predominantly on fast growing but poorly defended plant species (Chesson 2000; Chase *et al.* 2002).

Empirical studies excluding plant enemies have found highly variable effects on plant diversity (Olff & Ritchie 1998; Proulx & Mazumder 1998; Hillebrand *et al.* 2007; Allan *et al.* 2010; Allan & Crawley 2011; Korell *et al.* 2017). While large vertebrate herbivores were found to slightly promote grassland diversity in a recent meta-analysis (evenness, Jia *et al.* 2018), effects of invertebrates were more variable (Stein *et al.* 2010; Jia *et al.* 2018). Evidence from the tropics (Mangan *et al.* 2010; Bagchi *et al.* 2014) and also from plant-soil feedback experiments in temperate grasslands (Petermann *et al.* 2008) suggest that soil-borne plant pathogens are able to maintain high levels of diversity through Janzen-Connell effects.

Effects of plant enemies on plant species composition

Plant enemies may also alter plant species composition without changing diversity. Plant enemies can reduce the competitive ability of certain species, leading to competitive release for other plants and in some cases the exclusion of the preferred species and its replacement by other less preferred species (Crawley 1997). For instance, insects strongly changed species composition by increasing seedling mortality for certain species, without altering diversity in tropical rainforest (Bagchi *et al.* 2014). In general, plant enemies might change *plant functional composition* by preferentially attacking faster growing, less defended plant species rather than slower growing, and more defended ones (e.g. Lind *et al.* 2013; Kempel *et al.* 2015; Cappelli *et al.* 2019). Recent work on fungal pathogens in grassland has shown that plant species with a fast growth strategy are more likely to be infested by pathogens than species with a slow growth strategy (Cappelli *et al.* 2019). Communities consisting of fast growing species were also shown to be more strongly impacted by fungal pathogens (they lost more biomass) than communities consisting of slower growing species (Cappelli *et al.* 2019), indicating that fungal pathogens consistently shift plant communities towards more slow growing, better defended species. Similarly, invertebrates have been shown to drive plant community composition (e.g. Allan & Crawley 2011; Kempel *et al.* 2015), however effects depended on the group of enemies excluded, or the preference of herbivores, and were not necessarily linked to a fast or slow growth strategy of plants (Maron *et al.* 2014a; Korell *et al.* 2017).

Context-dependency of enemy impact on plant communities

The outcome of biotic interactions are notoriously context-dependent (Chamberlain *et al.* 2014; Maron *et al.* 2014a; Kempel *et al.* 2019) and the impact of enemies on plant communities might differ depending on many abiotic and biotic factors. In general, enemy impact can be driven by changes in the enemy and plant community. Changes in enemy abundance, diversity and per capita feeding rate will alter the impact of enemies on plant productivity, while changes in enemy diversity and degree of specialisation are likely to determine the impact of enemies on plant diversity and species composition (Fig. 1). Global change can alter all of these characteristics of the enemy community. Global change drivers might directly alter per capita feeding rate and/or they might indirectly alter enemy communities by changing the plant community. For instance, increases in plant productivity might increase enemy abundance (Haddad *et al.* 2000), increases in plant diversity are expected to increase enemy diversity (Scherber *et al.* 2010) and perhaps the proportion of specialists (Schemske *et al.* 2009), while a shift to fast growing plant species might increase the abundance of generalists. Characteristics of the plant community may also determine the impact that enemies can have on the community, for instance enemies may have a larger impact in communities dominated by a few plant species (resource concentration hypothesis) or in communities dominated by more palatable fast growing species. Global change drivers can therefore alter the feedbacks between enemy and plant communities and thereby drive changes in biotic interactions. Understanding how they do so is one of the greatest current ecological challenges and would provide essential information for a range of pressing problems, from improving global change forecasts to predicting the efficacy of weed biocontrol (HilleRisLambers *et al.* 2012; Louthan *et al.* 2015). In the following, we provide a framework for how important global change drivers, namely nitrogen enrichment, climate warming and an increase in atmospheric carbon dioxide might modify the impact of plant enemies on plant productivity, diversity and plant functional composition. In addition, we discuss the consequences of the ongoing plant diversity loss and the massive insect die off for plant-enemy interactions.

Effects of nitrogen enrichment on plant-enemy impact on plant communities

Nitrogen enrichment is a key global change driver altering biodiversity and ecosystem functioning. It typically causes a loss of plant diversity (Stevens *et al.* 2004) and increases plant biomass production (Crawley *et al.* 2005) and tissue nitrogen concentrations (Wardle *et al.* 2012) and leads to a shift towards faster growing plant species (Lavorel & Grigulis 2012). It is likely to alter enemy impact on plant communities through several of these direct and indirect effects. Theory predicts that low resource environments select for slow growing species with high levels of defence whereas high resource environments select for fast growing, less defended species (Coley *et al.* 1985). Similarly, the nitrogen disease hypotheses states that plants growing in nitrogen rich environments are more attractive to enemies due to a higher nitrogen concentration in their tissue (Dordas 2008). Consequently, fast growing, more acquisitive species, and species growing in nitrogen rich conditions, should suffer higher levels of herbivory or pathogen infection than species with a conservative strategy (Fine *et al.* 2004; Kempel *et al.* 2011; Seabloom *et al.* 2018). However, species with acquisitive traits or with access to more soil resources might be more tolerant of enemy attack, meaning that the actual impact of enemies could be lower, despite higher infestation (Cronin *et al.* 2010). In addition, for herbivores, the exploitation ecosystem hypothesis (Fretwell 1987; Oksanen & Oksanen 2000) predicts that in resource rich environments with a high primary production, natural enemies of herbivores (predators) should control herbivore populations. This might lead to no change in enemy impact on plant productivity, if all the additional plant productivity is transferred to predators, however so far the pattern has been only shown for vertebrates and not for invertebrate herbivores (Schädler *et al.* 2003).

The evidence for changes in herbivore and pathogen impact with productivity and fertility is mixed. Herbivore biomass has been shown to increase with increases in plant productivity (Chase *et al.* 2000; Lind *et al.* 2017, Kempel et al. in prep), however, herbivore *impact* has sometimes been shown to be unaffected or even to decrease with increasing productivity (Chase *et al.* 2000; Coupe & Cahill Jr 2003). 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, Jia et al. 2018). Yet, whether the impact of plant enemies increases with increasing soil fertility is not fully resolved.

Expectations. ① **Nitrogen enrichment affects impact of enemies on plant productivity**.

The nitrogen disease hypothesis suggests that the impact of enemies on plant productivity is higher in resource rich environments, because a higher nitrogen content in leaves makes plants more attractive. The resource availability hypothesis further predicts that fast-growing plant species, which are favoured by nitrogen enrichment, are less defended and should therefore suffer more from enemy attack. Moreover, a high soil fertility may reduce the presence of beneficial soil microbes, which have been shown to provide resistance against herbivores to plants (Pozo & Azcón-Aguilar 2007; Koricheva *et al.* 2009; Kempel *et al.* 2010), further increasing enemy impact. While plant and also herbivore biomass have been shown to increase with soil fertility, impact has not. This might suggest that fast-growing plant species are more tolerant and compensate leaf loss, or that top-down control of herbivores by predators might be stronger at high soil fertility. It is therefore not clear how the impact of enemies on plant productivity will change with nitrogen enrichment.

② **Nitrogen enrichment affects impact of enemies on plant diversity.** At high soil fertility plant communities are *dominated* by fast growing plant species, which usually reduces plant diversity. We therefore expect that the impact of enemies on plant diversity is stronger at high soil fertility, as plant enemies reduce plant dominance of good light competitors, equalizing fitness. (Hillebrand *et al.* 2007). The mechanisms behind this might be that in resource rich environments dominant species are less defended (growth-defense trade-off), or that good light competitors are tall and are therefore more likely to be removed by grazers. The latter would mainly apply to vertebrates.

③ **Nitrogen enrichment affects impact of enemies on plant functional composition.** We expect that the impact of enemies on plant functional composition is stronger at high soil fertility, because fast-growing but less defended plant species from fertile environments are held in check 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. In resource poor conditions however, slower growing species with high levels of defences are favoured as they are usually better at competing for soil resources than fast growing, poorly defended plant species (Lind *et al.* 2013). Excluding enemies in resource poor environments would therefore have minor effects on plant functional composition, as fast growing species will still be outcompeted by the slow growing species and are therefore unlikely to be able to increase.

Effects of temperature on plant-enemy impact on plant communities

Increases in temperature following global climate change will not only affect plant growth directly but are also likely to change plant communities indirectly by modifying their pathogen and herbivore communities. The current prediction for herbivores and pathogens is that their impact on plants will increase because warmer temperatures tend to increase insect and pathogen metabolic rates (Brown *et al.* 2004), accelerating their development and reproduction (Coakley *et al.* 1999; Malmström & Raffa 2000; Roy *et al.* 2004). However, this will only occur if precipitation remains high and increases in temperature in arid environments would be expected to reduce herbivore and pathogen attack. Existing environmental gradients in climate can be used to predict changes in plant enemy impact with changes in temperature and precipitation. For example, it has long been predicted that the importance of biotic interactions is strongest at low latitudes and declines towards the poles (Dobzhansky 1950, Schemske et al. 2009), which would suggest a potential increase in biotic interactions with increased temperature. However, the mechanisms driving this emerge over long time scales and are typically thought to be that a more predictable and benign climate in the tropics leads to stronger and more specialized biotic interactions, promoting coevolution and speciation (Coley and Kursar 2014), and further diversification of species (Vermeij 2005, Schemske et al. 2009). Particularly, a stronger impact of plant herbivores and soil fungal pathogens is suggested to be a major mechanism for the maintenance of high tropical diversity (Janzen 1970, Connell 1971, Mangan et al. 2010, Bagchi et al. 2014). It is therefore unlikely that current changes in temperature and precipitation will lead to an increase in the strength of biotic interactions. Further, evidence for the so-called biotic interaction hypothesis from studies comparing herbivory rates across latitudes is mixed (Schemske et al. 2009, Moles et al. 2011, Anstett et al. 2016, Jia et al. 2018). Similarly, evidence for a higher degree of specialist herbivores (Dyer et al. 2007, Novotny et al. 2007, Slove and Janz 2010), and plant defense (Moles et al. 2011) in the tropics is conflicting, so that the generality of the biotic interaction hypothesis has been questioned (Anstett et al. 2016, Moles and Ollerton 2016, Jia et al. 2018).

Latitudinal gradients in the intensity of biotic interactions may not predict changes with climate change but altitudinal gradients are frequently used as proxies of future climate change (Sundqvist *et al.* 2013; Alexander *et al.* 2015). They are ideal to address the question how abiotic factors drive variation in species interactions, as they occur over much smaller scales and are less confounded by historical or macro-evolutionary processes, such as dispersal limitation, or regional variation in day length or inter-annual climatic variations (Moreira et al. 2018). Accordingly, several studies have shown that herbivore pressure is higher at lower elevations, which are warmer and less variable climatically with reduced wind and sun exposure, (Rasmann *et al.* 2014; Galmán *et al.* 2018). This should result in decreased plant defense at high elevations and a higher proportion of generalist consumers, however, recent studies reported inconsistent patterns between elevation and herbivory, questioning the generality of previews findings (Galmán et al. 2018, Moreira et al. 2018). Interactions between plants and fungi are also likely to vary with elevation as fungal communities are sensitive to changes in temperature and precipitation (Bryant et al. 2008, Vacher et al. 2008, McGuire et al. 2012, Sundqvist et al. 2013). Previous studies have shown that soil microbial diversity (Fierer et al. 2011, Singh et al. 2012), community structure (Margesin et al. 2009, Pellissier et al. 2014) and abundance (Djukic et al. 2010) vary along several elevational gradients. However, studies rarely assess *impact* of enemies on plant communities or functioning along altitudinal gradients, i.e. by using exclusions (Sundqvist *et al.* 2013). Thus, whether the impact of invertebrate herbivores and fungal pathogens on ecosystems increases with climate warming is not fully resolved.

Expectations. ④ **Temperature affects impact of enemies on plant productivity.** Plant productivity increases with warmer temperatures and higher precipitation, and this would be predicted to increase enemy abundance and therefore enemy impact on plant productivity. Evidence for this comes from increased rates of herbivory in the tropics and at low elevations, and an increase in pathogen and herbivore attack also in warming experiments (Roy *et al.* 2004; Liu *et al.* 2011; Gillespie *et al.* 2013; Birkemoe *et al.* 2016). However, other warming experiments found no change (Richardson *et al.* 2002) or even a decrease (Barrio *et al.* 2016) in herbivory, suggesting that species-specific changes in plant quality (leaf nutrients, defensive compounds) also determine enemy attack.

Predictions for how enemy impact on plant diversity and composition will change with alterations in the climate are not so clear, as only few studies have interactively manipulated temperature and enemy abundance (but see Suttle *et al.* 2007; Lemoine *et al.* 2017).

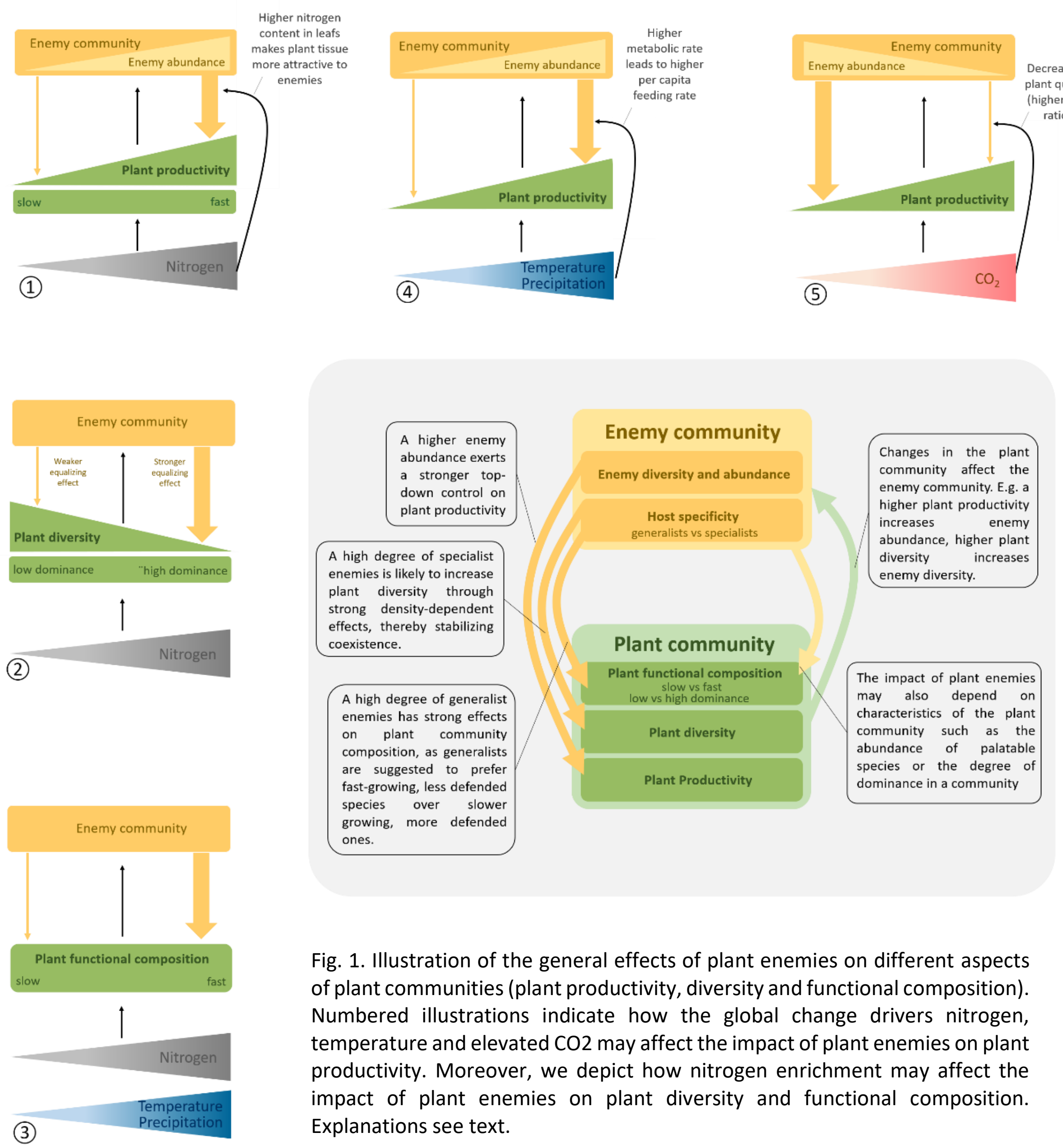
Effects of elevated atmospheric carbon dioxide on enemy impact on plant communities

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 their interactions with their enemies.

Experiments have shown that elevated CO_2 has large impacts on plant physiology, generally enhancing plant growth and increasing the C:N ratio in plants (Robinson *et al.* 2012; Sardans *et al.* 2012). Moreover, it is likely that an increased C supply to plants leads to an increase in C-based secondary and structural compounds, further decreasing plant quality (Stiling & Cornelissen 2007; Robinson *et al.* 2012). As invertebrate herbivores and also pathogens are largely N-limited an increase in C:N ratios is likely to lead to lower food quality. Results from meta-analysis suggest that while chewing herbivores respond in the short term with increased food consumption 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 (Stiling & Cornelissen 2007; Robinson *et al.* 2012). Phloem feeding insects instead tend to respond positively to elevated CO_2 (Robinson *et al.* 2012). In addition, the effect of elevated CO_2 on plant pathogen disease might be different for plants with a C_4 metabolism. C_4 plants are suggested to be less water stressed under elevated CO_2, which will increase pathogen disease severity (Thompson & Drake 1994; Mitchell *et al.* 2003). Concordantly, pathogen load has also been shown to increase under elevated CO_2 for certain species (Coakley *et al.* 1999; Mitchell *et al.* 2003; Lake & Wade 2009).

Results from global change experiments further suggests that plant community composition might change in response to CO2 enrichment. Legumes have been shown to increase in response to elevated CO2, whereas C3 and C4 grasses are less responsive (Jablonski *et al.* 2002). As C_3 and C_4 plants respond to elevated CO_2 with an increase in the C:N ratio, it is likely that enemy preference may shifts towards N-fixing plant species, counteracting enhanced growth in these functional groups. Thus, plant community shifts that are predicted to occur under elevated CO2 might be modified by variation in enemy impact driven by changes in host preference. However, current knowledge on how plant enemy affect plant functional composition under elevated CO_2 is limited.

Expectations. ⑤ **Elevated CO_2 affects 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 enemy abundance and hence impact will decrease. However, for pathogens effects might be different, depending on a plants photosynthetic pathway: for C_4 plants pathogen load might increase under elevated CO_2, as their water stress decreases which can increase fungal sporulation (Thompson & Drake 1994).



Higher nitrogen content in leafs makes plant tissue more attractive to enemies

Higher metabolic rate leads to higher per capita feeding rate

Decrease in plant quality (higher C/N ratio)

A higher enemy abundance exerts a stronger top-down control on plant productivity

A high degree of specialist enemies is likely to increase plant diversity through strong density-dependent effects, thereby stabilizing coexistence.

A high degree of generalist enemies has strong effects on plant community composition, as generalists are suggested to prefer fast-growing, less defended species over slower growing, more defended ones.

Changes in the plant community affect the enemy community. E.g. a higher plant productivity increases enemy abundance, higher plant diversity increases enemy diversity.

The impact of plant enemies may also depend on characteristics of the plant community such as the abundance of palatable species or the degree of dominance in a community

Fig. 1. Illustration of the general effects of plant enemies on different aspects of plant communities (plant productivity, diversity and functional composition). Numbered illustrations indicate how the global change drivers nitrogen, temperature and elevated CO2 may affect the impact of plant enemies on plant productivity. Moreover, we depict how nitrogen enrichment may affect the impact of plant enemies on plant diversity and functional composition. Explanations see text.

Consequences of decline in plant and insect diversity for plant-enemy interactions

In addition, to the impacts of nitrogen and climate change, other global change factors such as invasive species or pesticide use may cause declines in plant and insect diversity (Sala *et al.* 2000; Seibold *et al.*

2019). A decline in plant diversity is likely to alter the impact that invertebrate herbivores and pathogenic fungi 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 pathogens and herbivores, and that communities of high plant diversity harbour a larger community of natural enemies has a long history in ecology (Root 1973, host concentration hypothesis, Pimentel 1961). Indeed, studies manipulating plant species diversity of grassland communities have shown that pathogen attack is generally higher in species poor compared to species rich communities (Mitchell *et al.* 2002; Maron *et al.* 2011; Schnitzer *et al.* 2011; Schnitzer & Klironomos 2011; Johnson *et al.* 2013; Rottstock *et al.* 2014). For herbivores, results from previous studies have been ambiguous, and abundance, diversity and impact of herbivores have also been shown to be highest at high plant diversity (Haddad *et al.* 2001; Stein *et al.* 2010; Borer *et al.* 2012; Loranger *et al.* 2014; Seabloom *et al.* 2017, but see Koricheva *et al.* 2000). However, results for specialist insect pests are more consistent and resource concentration effects are commonly observed (Jactel & Brockerhoff 2007). However, most of the evidence for resource concentration effects comes from experiments in which diversity is manipulated and species compositions are random (e.g. Rottstock et al. 2014) and responses of herbivores and pathogens to real world gradients of diversity are less well known (Halliday & Rohr 2019).

Several recent studies have also suggested that insect populations are declining in abundance (Hallmann *et al.* 2017) and this loss of insect abundance and diversity is likely to have consequences for plant communities. In German grasslands it has been shown that all trophic guilds of insects, including herbivores, have declined in their biomass, abundance and diversity (by 67%, 78 and 34% respectively) since 2008 (Seibold *et al.* 2019). The decline has been associated with land-use intensification at the landscape level. Because herbivores are suggested to promote plant coexistence by preferentially attacking fast-growing dominant plant species (equalizing fitness differences), or by exerting frequency dependent effects on their specific host plants (increasing niche differences which are necessary for stable coexistence, Chesson 2000; Bartomeus & Godoy 2018), a decline in herbivore abundance and diversity is likely to result in a decline in their diversity-promoting effects. This might have far reaching consequences for plant diversity.

Expectations. 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 (Keesing *et al.* 2010): 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.

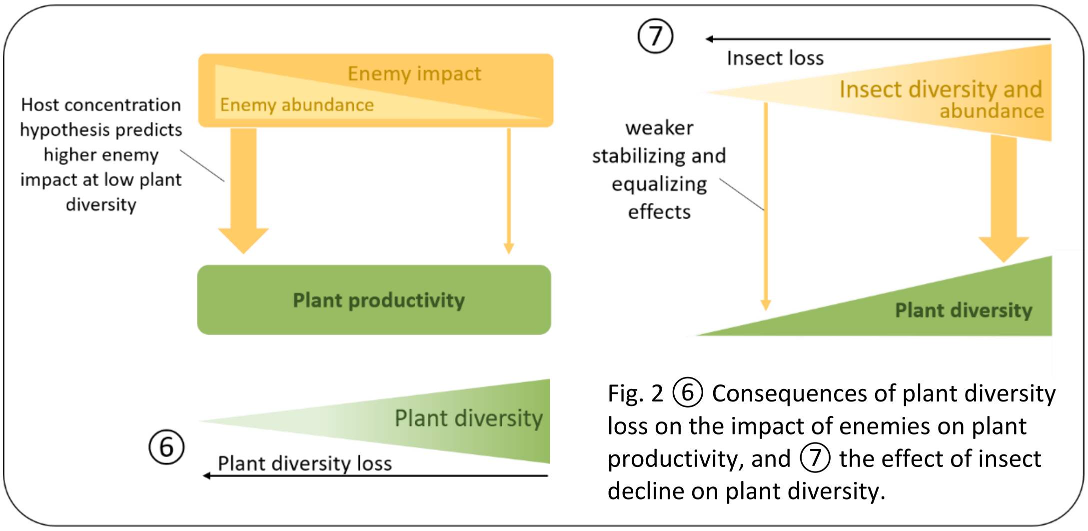


Fig. 2 ⑥ Consequences of plant diversity loss on the impact of enemies on plant productivity, and ⑦ the effect of insect decline on plant diversity.

Global change effects on plant-enemy interactions at a population level

In addition to the indirect effects taking place at the community level, global change drivers may also strongly affect host plants and their enemies at the individual and population level. For instance, global change may affect host plant populations and enemy populations in parallel, leading to a temporal mismatch due to changing phenology or spatial mismatch (due to changing geographic ranges, e.g. (Schweiger *et al.* 2012) of interacting species, which in turn may alter enemy impact. For example range expanding plant species have been shown to move faster than their belowground enemies, leading to enemy release in their new range (e.g van Grunsven *et al.* 2010; Zuppinger-Dingley *et al.* 2011), similarly to the hypothesized release of enemies of exotic plant species in their new range (Keane & Crawley 2002; Maron *et al.* 2014b). Moreover, interactions of plants with belowground mutualists such as mycorrhizal fungi might be affected by global change drivers such as warming or nitrogen enrichment (Egerton-Warburton *et al.* 2007), which might also indirectly affect plant-enemy interactions. Thus, global change drivers will not only affect resident plant communities (and their interactions with insects and pathogens), but will also lead to novel species assemblages with different interactions (Tylianakis *et al.* 2008; Alexander *et al.* 2015).

Concluding remarks and future avenues

Global environmental change may strongly alter the impact of plant enemies on several aspects of plant communities, and our review revealed several patterns. Results from studies comparing enemy impact along natural environmental gradients suggests that an increase in nitrogen as well as temperature may both lead to an increase in enemy abundance. Whether this will feedback on plant productivity and will increase the *impact* (loss of biomass due to enemies) of enemies, however, is less clear. Contrarily, elevated CO_2 might reduce certain enemy groups via a reduction in plant quality, potentially counteracting nitrogen and temperature effects. However, studies mainly focussed on enemy groups such as lepidopteran caterpillars and the few studies on other enemy groups (e.g. sucking herbivores or fungal pathogens) suggest that responses depend on enemy guild. Nitrogen enrichment and warming might both lead to a shift in the plant functional composition towards more fast growing plant species with a high competitive ability in nutrient rich environments, elevated CO_2 might specifically favour N-fixing plant species. In these fast-growing communities plant enemies may be particularly important for the maintenance of plant diversity, as they equalize fitness differences between plant species by preferentially attacking the dominant, less defended species. Thus, the importance of plant-enemies as diversity-promoting agents might increase with global change. The ongoing decline in insect species, biomass and abundance, including herbivores, might therefore have far-reaching consequences for plant diversity, particularly in a warmer and nutrient richer world as a lower top-down control by enemies might lead to a greater dominance by certain species, potentially leading to competitive exclusion and a loss of plant diversity.

In sum, our review revealed several general patterns in how global change affects enemy communities directly and indirectly via changes in the plant community, however it also revealed gaps in our understanding of the context-dependency of plant-enemy interactions (Maron *et al.* 2014a). The reason for this is that experiments are typically not designed to identify drivers of context-dependence and that large-scale patterns are usually pieced together from data obtained by a variety of methods and protocols (Gurevitch & Mengersen 2010). Moreover, while effects on enemy communities are well studies, we often have a limited idea of whether such changes also translates into changes in the *impact* of plant enemies on plant communities, as studies often rely on comparing herbivore or pathogen *attack* along environmental gradients and rarely measure *impact* experimentally, i.e. by using exclusion to look at the consequences of herbivory or fungal infection for plant diversity, composition or functioning (Anstett et al. 2016, Burdon et al. 2006, Sundqvist et al. 2013, Louthan et al. 2015). Thus, to predict the consequences of global change on the diversity and functioning of our 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 might be one way forward to obtain generality in the impact and context-dependency of plant enemies on the diversity, composition and functioning of plant communities. Moreover, experiments simultaneously manipulating various global change drivers while also 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 current global change scenarios, and the recently observed insect die-off.

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