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Current Opinion in Insect Science

Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent findings, and future directions

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A rich body of theory has been developed to predict the effects of plant diversity on communities at higher trophic levels and the mechanisms underpinning such effects. However, there are currently a number of key gaps in knowledge that have hindered the development of a predictive framework of plant diversity effects on consumers. For instance, we still know very little about how the magnitude of plant trait variation (e.g. intra-specific vs. inter-specific), as well as the identity and combined effects of plant, herbivore and natural enemy traits, mediate plant diversity effects on consumers. Moreover, the fine-scale mechanisms (e.g. changes in consumer behaviour or recruitment responses) underlying such diversity effects in many cases remain elusive or have been overlooked. In addition, most studies of plant diversity effects on associated consumers have been developed under a static, unidirectional (bottom-up) framework of effects on herbivores and predators without taking into account the potential for dynamic feedbacks across trophic levels. Here we seek to address these key gaps in knowledge as well as to capitalize on recent advances and emerging frameworks in plant biodiversity research. In doing so, we provide new insights as well as recommendations which will stimulate new research and advance this field of study.

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Current Opinion in Insect Science 2016, **14**:1–7

This review comes from a themed issue on **Ecology/parasites/parasitoids/biological control**

Edited by **Sergio Rasmann** and **Kailen Mooney**

http://dx.doi.org/10.1016/j.cois.2015.10.003

Introduction

The consequences of plant intra-specific and inter-specific diversity on associated faunas have been the focus of much research over the last decade (e.g. [1••,2–8,9••]). Studies have found that plant diversity positively influences arthropod diversity and abundance [3,4,8,10], and alters plant–arthropod and arthropod–arthropod interactions [3,7,11,12]. These findings emphasize that conserving and manipulating plant diversity in natural and managed systems, respectively, is crucial for maintaining ecosystem function [13–15].

A rich body of theory has been developed to predict the effects of plant diversity on communities at higher trophic levels ([16–22], see Box 1). Despite this vast collection of theory behind plant diversity effects on associated faunas and the large number of empirical studies conducted thus far, formal evaluations of the mechanisms behind the observed patterns have been developed in natural communities (but see [20] for e.g. in agricultural systems). In addition, there are also a number of key gaps in knowledge that have hindered the development of a predictive framework of plant diversity effects on higher trophic levels (Figure 1). For example, we generally ignore how the magnitude of variation in plant traits (e.g. inter-specific vs. intra-specific diversity) or the identity (including independent and interactive effects of multiple traits) of plant traits determines such effects. Similarly, many studies have lacked an explicit evaluation of the influence of herbivore traits such as diet breadth, mobility and feeding behaviour, and the underlying mechanisms for diversity effects on consumer abundance or behaviour remain elusive (e.g. effects of diversity on consumers via increased plant growth vs. increased habitat heterogeneity). Finally, most empirical studies of plant diversity effects on associated faunas have been developed under a static, unidirectional (bottom-up) framework of effects on herbivores and predators, ignoring the intrinsic dynamism in the form of feedbacks between the bottom-up effects of plant diversity and top-down effects by consumers.

Based on the above, our aim here is to address what we consider are some of the key gaps in knowledge of plant diversity research conducted thus far and capitalize on recent advances in plant biodiversity research that

Box 1 Ecological theories for the effects of plant diversity on communities at higher trophic levels and the mechanisms underpinning such effects.

'Resource Specialization Hypothesis' argues that increased plant diversity provides a greater diversity of resources which favours an increase in consumer species richness due to an accumulation of consumers specializing on different resources [16,17].

'More Individuals Hypothesis' postulates that high plant diversity increases plant productivity, such that an increase in the resource base positively influences consumer abundance, and that this in turn leads to an abundance-driven accumulation of consumer species [18].

'Resource Concentration Hypothesis' poses that herbivores frequently forage in a density-dependent manner, and therefore increasing plant species or genotype number while keeping plant density constant reduces the probability of finding a preferred host plant species (or genotype), ultimately leading to lower herbivore abundance and damage on individual plants [21].

'Resource Dilution Hypothesis' posits exactly the opposite: as the density of plant items (species or genotypes) decreases (i.e. dilution), herbivores concentrate on the few available items and thus cause more damage in species-rich than in species-poor communities [22].

'Enemies Hypothesis' [19,20] invokes an indirect mechanism for plant diversity effects on herbivores as it holds that increasing plant diversity results in a greater availability of refuges and alternative resources, that this favours a greater abundance and diversity of predators and parasitoids, and that increased enemy recruitment ultimately leads to stronger enemy top-down effects on herbivore populations [19].

attempts to fill these gaps (Figure 1). In doing so, we provide novel ideas and recommendations which hopefully stimulate this field of research and contribute to build a predictive framework for work to come (Figure 1).

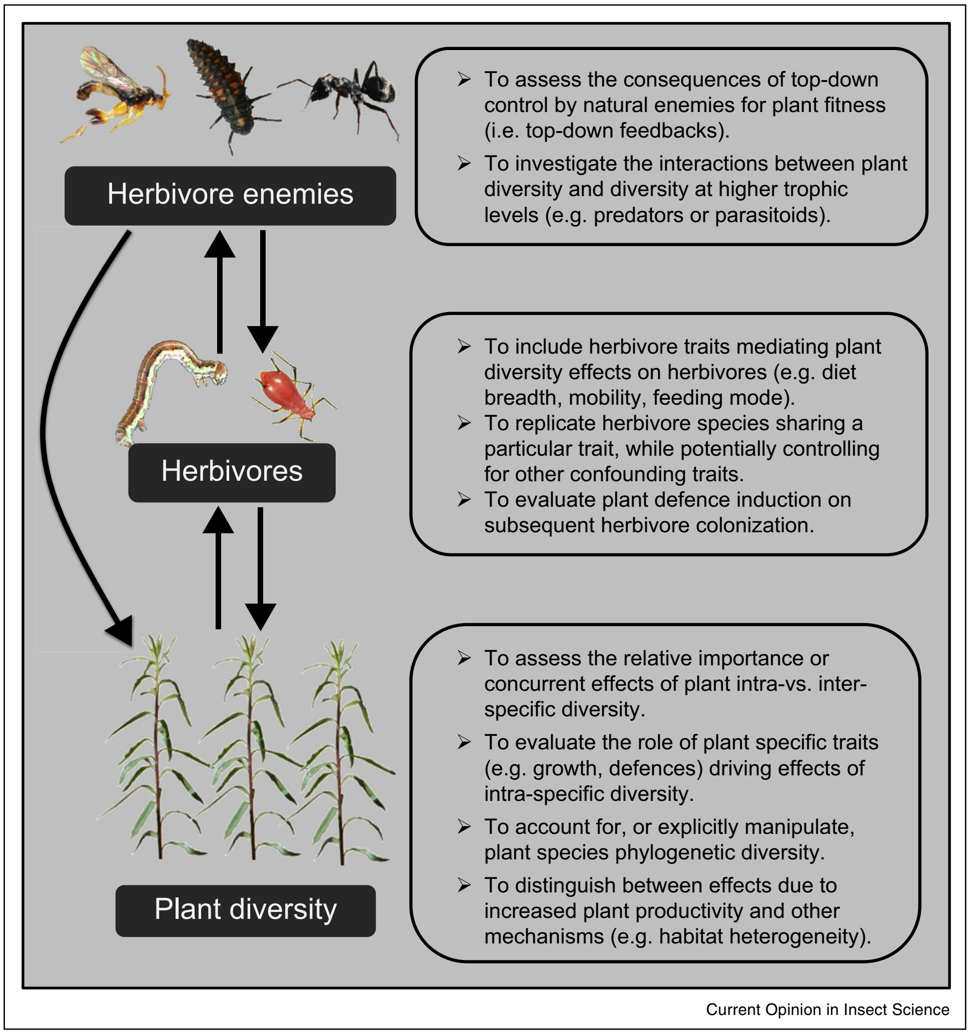
The predictive role of producer and consumer traits

Plant traits

Plant diversity effects on associated faunas are driven by multiple plant traits, which may act independently or in concert. Unfortunately, most empirical studies have failed to identify key plant traits or separated the effects of different sources of plant trait variation influencing insects. For example, most work has tested for plant intra-specific and inter-specific diversity effects on consumers separately (but see [6,9••,23]), restricting a direct test of these predictions and an assessment of the relative importance or concurrent effects of these sources of plant variation on herbivores. Because the magnitude of variation in plant traits is greater among plant species, the expectation is that species diversity effects will be stronger due to greater trait variation and increased habitat heterogeneity influencing herbivore and predator foraging behaviours [6,24]. Accordingly, the range of trait variation among genotypes within a species may not be large enough in some cases for plant intra-specific diversity to influence herbivores ([6,9••,24], but see [23]). For instance, Abdala-Roberts *et al.* [9••] recently reported that tree species diversity notably reduced leaf miner attack on mahogany (*Swietenia macrophylla*) trees, but found no evidence of mahogany genotypic diversity effects on these herbivores. Similarly, Cook-Patton *et al.* [6] found that plant genotypic and species diversity had effects of similar magnitude on insect herbivores, but that species diversity had stronger effects on predators. These studies call for further work determining how the magnitude of variation in plant traits, the relative importance of different sources of variation in plant traits (e.g. intra-specific vs. inter-specific), as well as the extent to which such traits or sources act independently or interactively. Interestingly, recent work has shown that, when intraspecific variability in plant traits is taken into account in the calculation of functional diversity indices and then correlated with ecosystem functions, models predict ecosystem functioning much better [25]. It is therefore likely that the effect of plant genetic and specific diversity on higher trophic levels results from interactive effects between these two sources of diversity [26].

Another important point is that considerable effort has been aimed at understanding and manipulating the effects of plant functional diversity in species diversity studies (e.g. [27]), and such body of research has shed light into some of the traits driving diversity effects. However, very little attention has been given to identify and explicitly evaluate the role of specific traits driving effects of intra-specific diversity (but see [28]). To date, most intra-specific diversity studies have used a posteriori correlations between plant traits and effects on higher trophic levels (e.g. [5,10]), which are useful, but are frequently burdened by low statistical power and the potential for spurious associations if many traits are evaluated simultaneously. One exception is a recent study by some of the co-authors of this paper where monocultures of male and female genotypes of *Baccharis salicifolia* (Asteraceae) were compared to mixtures of male and female genotypes, and monocultures of fast-growing and slow-growing genotypes to mixtures of fast-growing and slow-growing genotypes (Abdala-Roberts *et al.*, unpublished data). We found that sexual diversity increased plant growth and reduced the density of a generalist aphid and its associated aphid-tending ants. By contrast, growth rate diversity did not influence plant growth, but increased the density of a specialist aphid. Similarly, Hughes [28] found that intra-specific trait (plant stem height) diversity in a salt marsh plant (*Spartina alterniflora*) markedly affected plant performance and consumer community attributes. Based on these findings, we argue that a push towards studies that explicitly manipulate diversity in ecologically relevant traits, particularly in the case of intra-specific diversity, is needed in order to gain a predictive understanding of plant diversity effects on plant-centred arthropod communities. Moreover, we recommend manipulating plant diversity on the basis of functional traits with particularly strong effects on consumers and for which we know the

Figure 1



Summary of recommendations for addressing key gaps in knowledge for research on plant diversity effects on higher trophic levels.

factors that shape their variation. Knowing which factors and processes drive variation in such traits (e.g. habitat filtering, phenotypic plasticity) [25] might allow us to predict concomitant patterns of variation in arthropod communities.

In addition to manipulating specific traits, another potentially useful approach would be to account for or explicitly manipulate sources of plant trait variation that act as proxies of trait similarity or differences across species. For example, recent studies have manipulated plant species phylogenetic diversity [29,30], and a meta-analysis by Castagneyrol *et al.* [31•] reported that mixing closely related tree species increased the susceptibility of focal species to damage by generalist insect herbivores (see also [32] for phylogenetic diversity effects on plant performance). However, it is important to note that effects of phylogenetic diversity would be expected only when there is a strong phylogenetic signal in plant traits, and this is not always the case. Moreover, phylogenetic distance may in some cases lack the necessary resolution to predict effects on insects since consumers may interact with specific plant traits or groups of traits independently of the effects of plant trait variation associated with evolutionary history. A major task would be to identify traits that are relevant to herbivores, and manipulate phylogenetic diversity having accounted previously for such information. In addition, insight could be gained by using experimental designs that tease apart the relative effects of phylogenetic diversity and trait diversity. For example, one option might be to test for diversity effects using pairs of species that are phylogenetically close, but functionally dissimilar and vice versa.

Herbivore traits

The study of plant diversity effects on herbivores (damage, community structure) has received increasing attention in recent years, but findings are inconsistent to some extent. One plausible explanation for these inconsistencies might be that most studies have failed to consider herbivore traits that may largely determine plant diversity effects on herbivores. Traditionally, one of the traits that has received the most attention is herbivore diet breadth [9••,31•,33]. Accordingly, a fundamental premise of the Resource Concentration Hypothesis is that resource density or apparency effects of plant diversity on herbivores will take place to the extent that herbivores are more specialized in their feeding preferences [21]. Highly specialized herbivores should exhibit a strong response whereas generalist herbivores should exhibit weak responses because they are less limited to feeding on a specific host plant [21]. For example, in a meta-analysis, Jactel and Brockerhoff [33] found that increased tree diversity reduced herbivory by specialist species, whereas the response of generalist herbivores was variable. These predictions are supported by recent studies in both tropical [9••] and temperate [31•] forest systems.

Other traits such as herbivore mobility [13,34,35] and feeding mode [36] are also thought to be important predictors of plant diversity effects on herbivores but have received comparatively less attention. In an insightful review, Bommarco and Banks [35] reported that highly mobile herbivores responded more strongly to plant diversity than sedentary herbivores because they can disperse more readily and choose among plant patches of varying diversity. In addition, a recent study by Castagneyrol *et al.* [36] emphasizes the importance of feeding mode as they found that plant intra-specific diversity in oak sapling populations increased the abundance of ectophagous herbivores, but was a poor predictor of the abundance of endophagous herbivores.

To the extent that it is feasible based upon the study system's features and natural history, we recommend that future studies make an effort to replicate herbivore species or groups that share a particular trait, while potentially controlling for other confounding traits. Only in this way we will be able to unequivocally assess how consumer traits mediate plant diversity effects on herbivores. To the extent that we move in this direction, we will be able to nurture long-standing theoretical frameworks such as the Resource Concentration Hypothesis and the Enemies Hypothesis, and better predict the magnitude and direction of plant diversity effects on insect herbivores.

Emerging frameworks: considering the combined influence of traits across trophic levels

Clearly, an explicit consideration of plant and consumer traits will move this field of research in exciting and productive directions. At the same time, it will be important to integrate these new ideas and approaches with existing theory to develop new paradigms. In this sense, Underwood *et al.* [37] recently proposed a framework that distinguishes between the effects of plant conspecific density from effects of heterospecific neighbor frequency. As such, this model represents an important step forward from classic theory (Resource Concentration Hypothesis). Relatedly, Hambäck *et al.* [38] propose a mechanistic model that considers herbivore foraging behaviour and predicts effects of plant diversity on herbivore movement. They show that herbivore recruitment to plant patches is largely contingent upon the relative density of target versus non-target plant species. These studies point in a promising direction by stimulating novel experimental designs and frameworks for predicting the individual and combined influence of plant and consumer traits guiding plant diversity effects.

Effects of plant diversity on plant–insect herbivore and herbivore–enemy interactions

Whereas identifying specific plant traits or axes of plant trait variation underlying diversity effects is essential, of parallel importance is to determine the mechanisms by which such changes in plant traits or trait variation influence consumptive interactions or other attributes of consumer communities. For example, diversity may cause changes in plant traits which arise from aboveground and belowground interactions among neighbouring plants [4–6], or due to increased habitat heterogeneity affecting consumer foraging behaviour ([38,39], i.e. effects of trait diversity). The former group of effects can be further divided into effects on plant growth (biomass) or effects on plant traits associated to quality for herbivores (e.g. defences, nutrients). Surprisingly, most studies have not explicitly tested for these mechanisms, or controlled for one while testing for the other. For example, a commonly reported pattern is that increased plant growth in mixtures is associated with greater herbivore abundance and diversity [2,4,6,13]. However, these studies have not formally tested whether such effects are due to increased resource availability (higher plant biomass) and/or through increased resource heterogeneity influencing herbivore recruitment. One exception is a recent study which controlled for effects of plant intra-specific diversity on growth by eliminating belowground plant–plant interactions [12]. In doing so, they tested for effects of diversity on herbivore foraging behaviour arising due to increased habitat heterogeneity in genotype mixtures. In this sense, we call for future studies conducting experimental manipulations to test for the individual contribution of different mechanisms underlying diversity effects on associated faunas. Alternatively, effects of plant diversity arising via increased plant growth could be controlled statistically by testing for diversity effects on herbivores with and without plant biomass as a covariate [12,40] or analysing effects on insect abundance versus density (number of insects per unit of plant biomass). If diversity effects are mediated by plant biomass then significant effects on herbivores should disappear once biomass is accounted for [41•]. Greater plant growth rates at high diversity may also lead to reduced investment in plant defences via growth-defence trade-offs or, alternatively, to increased levels of plant defences via increased herbivore loads and damage (i.e. induced defences). In this sense, Moreira *et al.* [41•] found that plant species and genotypic diversity had positive effects on mahogany chemical defences, but these positive diversity effects on defences were not mediated by either growth-defence trade-offs or changes in herbivore damage. Further studies should thus investigate plant diversity effects on anti-herbivore defences at a finer/more mechanistic level. In particular, a push towards plant diversity work addressing the role of plant volatiles and defense induction in mediating herbivore movement will surely contribute to a better understanding of herbivore recruitment patterns.

Another mechanism which has been largely ignored is the potential for diversity to mediate interactions among herbivore species or guilds. There is a well-established literature on plant-mediated indirect interactions among herbivores via plant induced responses to herbivory (reviewed by Ohgushi [42]). For instance, damage caused by one herbivore species may induce plant chemical defences which in turn influence attack by another herbivore guild [43] as well as arthropod community structure [44]. Such effects are particularly common in systems where early-season herbivores triggers plant induced responses that affect late-season herbivores [45,46]. Surprisingly, however, this area of research has developed independently of plant diversity studies, despite the fact that diversity effects on herbivory would be expected to influence plant induced responses and thus potentially lead to plant-mediated interactions among herbivores. For example, Muiruri *et al.* [47••] recently found that moose browsing on birch altered responses to tree species diversity by insect herbivores feeding on birch. Similarly, unpublished work by some of the co-authors of this paper indicates that genotypic diversity in Lima bean (*Phaseolus lunatus*) influenced damage by early-season herbivores (leaf chewers and aphids) and such effects in turn determined responses to diversity by late-season seed predators (Abdala-Roberts *et al.*, unpublished data). We argue that these types of diversity-mediated indirect interactions are probably common and deserve more attention. In particular, systems where herbivore species exhibit contrasting phenologies offer a good opportunity to address these indirect interactions and the potential for priority effects.

Dynamic effects of plant diversity across trophic levels: bottom-up and top-down feedbacks

Although it has long been recognized that the effects of plant diversity on insect herbivores are likely frequently mediated by increased predator or parasitoid recruitment (the Enemies Hypothesis [19]), very few studies have actually measured the consequences of enhanced top-down control by natural enemies for herbivore population growth, plant–herbivore interactions, and ultimately plant growth (and/or reproduction). Most studies have been restricted to measuring plant diversity-mediated effects on predator or parasitoid abundance and diversity [2,6,13,20,48,49] as well as predation or parasitism rates [20], but almost no studies have documented the consequences of such effects on herbivory and plant growth. One exception is a recent study by Moreira *et al.* [7] showing that higher recruitment of predatory ants with increasing plant species diversity resulted in positive direct and indirect effects of ants on aphids and plant growth, respectively. Similarly, Haddad *et al.* [2] reported for a temperate grassland that higher primary production with increasing plant diversity was associated with a substantial increase in the ratio of natural enemy (predators, parasitoids) to herbivore abundance in diverse plant patches. Insectivorous birds are also shown to be sensitive to declines in plant biodiversity (e.g. [50]). For instance, Poch and Simonetti [50] found that complex forest plantations with more developed and diverse understorey markedly increase insect herbivore predation by birds. Further work should document the linkages between plant diversity and top-down feedbacks mediated by insectivorous birds. Finally, it is also necessary to investigate the interactions between plant diversity and diversity or complexity at higher trophic levels, for example, incorporating effects of intra-guild predation, simultaneous effects by multiple predators, indirect effects across four-trophic levels.

Collectively, the above studies point at a widespread potential for diversity-mediated ecological and evolutionary feedbacks on plant performance and plant community structure [2,39]. The outcome of such feedbacks will likely dependent strongly upon key plant traits igniting such dynamics and how plant and insect traits interact in shaping such effects (see section *Plant traits*). Interestingly, some of the previously described studies addressing feedbacks (e.g. [7]) looked at effects of ants, a particularly important group of predatory omnivores which may in some cases act as herbivore mutualists. In this sense, we note that although there are a vast number of studies on the effects of diversity on enemies of herbivores, almost no attention has been given to herbivore mutualists. The nature of herbivore interactions with species located at higher trophic levels is likely a key a determinant of the outcome of these bottom-up/top-down feedbacks that deserves future attention.

Acknowledgements

This research was financially supported by the Ramon y Cajal Research Programme (RYC-2013-13230) to XM and by the CONACyT Repatriation Programme (#250934) to LAR.

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