

## Review

# Effects of phytochemical diversity on multitrophic interactions

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The ecological effects of plant diversity have been well studied, but the extent to which they are driven by variation in specialized metabolites is not well understood. Here, we provide theoretical background on phytochemical diversity effects on herbivory and its expanded consequences for higher trophic levels. We then review empirical evidence for effects on predation and parasitism by focusing on a handful of studies that have undertaken manipulative approaches and link back their results to theory on mechanisms. We close by summarizing key aspects for future research, building on knowledge gained thus far.

## Addresses

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## Introduction

Plant diversity is a major driver of ecosystem function and community structure [1–3], and there is mounting evidence that such effects operate through changes in species interactions [4–6]. For instance, recent studies have shown that plant intra- and inter-specific diversity (i.e. the number of genotypes or species in a patch or stand) often lead to reductions in insect herbivory, which in turn contributes to higher productivity in plant mixtures [4,7,8]. Such effects on herbivory emerge from various, nonexclusive bottom-up or top-down processes

resulting from interactions among plant genotypes or species affecting consumer abundance or behavior (reviewed by Ref. [2]).

Within this body of research, there has been a strong emphasis to identify and tease apart different sources of plant trait variation underlying plant diversity controls over trophic interactions. One of such sources is variation associated with plant secondary or specialized metabolism (i.e. compounds not directly related to cell function and growth; [9]), a phenotypic component that has been shown to strongly influence ecosystem function [10,11] and species interactions [9,12,13•]. Accordingly, plant diversity effects on ecosystems are likely driven by patch-level variation in specialized metabolism, which is the focus of this paper (phytochemical diversity hereafter). This variation occurs among individual plants of the same (i.e. intraspecific phytochemical diversity) or different species (i.e. interspecific phytochemical diversity), both representing different forms of beta diversity in plant chemistry (sensu [13•]; see **Box 1**), but only until recently has robust and unequivocal evidence been gathered for such effects. Indeed, owing to technological breakthroughs (e.g. knockouts of genes coding for defensive metabolites, metabolome screening, marker-assisted breeding [12,14,15]) allowing to screen for or generate plant types varying in focal chemical traits, recent studies have shown that phytochemical diversity exerts strong controls over species interactions [13•,16].

Work on phytochemical diversity effects on species interactions involving higher trophic levels, that is, carnivores such as parasitoids and predators (natural enemies hereafter), is far less common compared with that focusing on herbivory. Recent syntheses reveal that plant diversity effects on natural enemies are highly variable [17], particularly in forests (reviewed by Ref. [18]), whereas agricultural systems show more consistent positive effects [19]. The contributions of phytochemical diversity to such effects are, however, yet to be unraveled. Outcomes presumably operate via different mechanisms and are conditioned by natural enemy traits [2], but mechanistic frameworks are lacking, and empirical studies are very limited. An expanded consideration of these bottom-up effects on natural enemies and their consequences for top-down trophic control holds the key for achieving a more robust understanding of how plant diversity effects, as dictated by variation in secondary chemistry, propagate up food webs and in

**Box 1 Glossary.**

*Associational resistance*: an indirect interaction, which in the case of plants takes place when neighboring heterospecific plants decrease herbivore or pathogen effects on focal plants and can also drive an overall reduction in attack in plant mixtures (associational susceptibility refers to the inverse outcome, e.g. due to attraction and spillover of herbivores among plants). Can be driven by different mechanisms (visual or chemical masking, repellence, etc.) and can also take place among genotypes (e.g. chemotypes) of the same plant species.

*Chemical masking*: associational resistance mechanism that occurs when neighboring conspecific or heterospecific plants produce chemical compounds that conceal or alter the sensory perception of focal host plants to herbivores (e.g. by suppressing or altering the smell of host plants).

*Chemotype*: polymorphism within a plant species responding to differences in the amounts and/or composition of specialized metabolites, which generally has a genetic basis that can be discrete (often studied) or complex (polygenic).

*Density-mediated indirect effect*: Occurs when one species (e.g. plant) causes a change in the abundance or density of a second species (e.g. herbivore), which in turn influences a third species (e.g. natural enemy). For example, a susceptible plant chemotype would be expected to have higher herbivore loads, and this would result in greater natural enemy recruitment (albeit with no change in the ratio of herbivore-to-natural enemy abundance, i.e. no shift in per capita effects). Effects on natural enemies due to phytochemical diversity can arise due to the presence of specific plant chemotypes or interactions between chemotypes in mixtures driving changes in herbivore abundance.

*Phytochemical diversity (also termed chemodiversity)*: variability in plant chemistry, including compound richness, evenness, or variety of structural types within, among, or across (i.e. aggregating) samples as defined by a given study, for example, leaves or other organs within a plant, individual conspecific plants, or individual heterospecific plants. Variation among plants (of the same or different species, i.e. beta diversity as calculated across plants, see Ref. [13•]) in specialized metabolism, for example in total compound abundance or composition, is the focus of this paper. Distinguishing phytochemical variation across different spatiotemporal scales and levels of biological organization provides the basis for hypothesis testing and study design.

*Plant volatile organic compound*: low molecular weight organic (carbon-based) compounds emitted by plants through processes, such as photosynthesis, respiration, and metabolic activities, which easily evaporate into the air. They are highly inducible in response to herbivore attack, and also vary in their expression levels in response to changes in abiotic conditions. They play various roles in plant physiology and act as semiochemicals mediating interactions with other organisms (e.g., as cues that attract or repel herbivores and natural enemies).

*Resource concentration effect*: phenomenon by which herbivore or pathogen loads (and resulting attack rates) increase with host plant density (i.e. positive density-dependent attack). Resource dilution refers to the inverse, that is, reductions in enemy attack with increasing host plant density (i.e. negative density-dependent attack). Because plant diversity (e.g. chemical) results in reductions in the density of suitable or preferred plant types (chemotypes or species), this is expected to lower herbivory in mixtures relative to monoculture. This phenomenon may act concurrently and interact with associational effects arising from interactions between plant types (see above), though these mechanisms are challenging to tease a part and often confounded.

*Selection and complementarity effects*: Terms derived from the Biodiversity Ecosystem Functioning (BEF) literature, which can be applied to phytochemical diversity effects on consumers. Selection effects refer to cases where dominant species or genotypes (e.g. with chemistries that have strong effects on consumers) occur, on average, more frequently in mixtures than in monoculture, and are responsible for driving overall effects of phytochemical diversity on herbivory and/or predation or parasitism (increases or decreases). In contrast, complementarity arises from interactions between plant chemical types (in space or time), leading to changes in trophic interactions in mixtures relative to monoculture. Either type of process can operate through density- or trait-mediated effects on natural enemies.

*Semiochemicals*: individual compounds or mixtures released by an organism that provide information and influence another species' abundance or behavior. In the case of plants, the influence of volatile organic compounds (e.g. terpenes) as cues influencing herbivore and natural enemy behavior has been extensively investigated.

*Trait-mediated indirect effect*: when one species (e.g. plant) causes a change in the traits of a second species (e.g. herbivore), which in turn influences a third species (e.g. natural enemy). For example, phytochemical mixtures can alter herbivore growth, either slowing it down or leading to lower mass due to different mechanisms (e.g. reduced chemical acclimation) or by affecting herbivore behavior (e.g. increased movement within or among plant patches), any of which can increase risk of herbivore predation or parasitism. These scenarios lead to changes in herbivore-to-natural enemy abundance ratios and consequently influence interaction strength (e.g. via shifts in natural enemy per capita effects) and thus top-down pressure.

*Trap plant*: species used to attract pests and in so doing drive them away from a focal plant (e.g. main crop), thereby reducing herbivory on the latter (could also apply to a chemotype at the intraspecific level).

turn affect ecosystem functions (e.g. insect herbivore control, primary productivity, nutrient cycling, etc.).

In this review, we examine research on the effects of phytochemical diversity on plant–insect multitrophic interactions. We start by providing a brief theoretical background on phytochemical diversity effects on herbivores and expand on effects on natural enemies to

shed light into mechanisms by which these effects might play out across consumer trophic levels. We then review empirical evidence for effects on natural enemies by focusing on a handful of studies that have used manipulative approaches and link back their results to the mechanistic background. We end by pointing key aspects for guiding future research, building on incipient knowledge gained thus far.

## Mechanisms overview

### Herbivory

Research on phytochemical diversity effects (as defined above) on trophic interactions has largely focused on herbivory (reviewed by Ref. [13•]; see Ref. [9] for mutualisms). Mirroring the broader plant diversity literature, observational and manipulative studies have overwhelmingly found a positive effect of phytochemical diversity on arthropod diversity (reviewed by Ref. [12]) and often negative effects on insect herbivory (e.g. [20–25••], but see Refs. [26,27•]); this includes several studies on plant volatile organic compounds (VOCs, e.g. [21,28,29••]). Importantly, this research has shown that phytochemical diversity can reduce herbivore performance and herbivory via different mechanisms, but that outcomes are also often context dependent and strongly contingent on herbivore traits.

Herbivore diet breadth emerges as a key predictor, with specialist herbivores being negatively affected by phytochemical diversity due to several mechanisms, including reductions in the abundance of focal plant chemotypes (i.e. a resource concentration effect; [30]) or a greater difficulty to locate their host plants due to chemical interference or masking among plant chemical types ([31]; i.e. associational resistance; [32,33]) or by hindering herbivore acclimation to plant chemistry ([34]; see Box 1). In contrast, positive effects (or no effects) have been reported for generalist herbivores via different mechanisms, among which diet mixing has received some attention [35,36]. That said, in some cases, studies have found phytochemical diversity to positively affect specialist herbivores via balance or dilution of nutrient or toxin uptake (e.g. [37]), and it is also possible that it negatively affects generalists via hindering of chemical acclimation [34]. Taken together, these findings indicate that the effects of phytochemical diversity on herbivores with contrasting diet breadths are not set in stone and require more nuanced assessments considering other insect (and plant) traits. Unfortunately, these mechanisms are often not examined under a specific or explicit consideration of herbivore diet breadth, and other relevant herbivore traits, such as foraging mode, mobility, and size, remain largely untested. This gap in knowledge hinders our understanding of how herbivore traits and their relationships with plant chemical traits shape interaction outcomes.

### Predation and parasitism

Phytochemical diversity effects on natural enemies can take place through multiple mechanisms involving direct effects of plants traits (or plant abundance), as well as indirect effects implicating the transmission of effects via trophically intermediate species (i.e. herbivores or other predators and parasitoids). For example, natural enemies respond directly to changes in the diversity or composition of plant VOCs, which are used as foraging

cues [38,39] but are also indirectly affected by phytochemical diversity via its influence on herbivore abundance or traits [20,40], that is, density- and trait-mediated indirect effects, respectively ([41]; see Box 1). Trait-mediated effects include, for example, anti-predator defenses [34], such as those associated with apparency or toxicity signaling (crypsis, plant toxin sequestration; [42,43]), as well as changes in herbivore behavior influencing the risk of predation [44]. In addition, trait-mediated indirect effects on natural enemies also include herbivore-induced changes in the amount or composition of plant VOC emissions [38]. This case mainly involves changes in plant traits rather than herbivore traits, although the quantity and composition (e.g. diversity, richness, evenness) of these induced VOCs can also be influenced by herbivore traits or identity. Moreover, interaction outcomes might also depend on natural enemy traits, such as mobility and diet breadth [45,46], though such contingencies remain poorly understood. Finally, the relative importance of direct and indirect (density mediated or trait mediated) effects of phytochemical diversity on natural enemies is largely unknown [47], reflecting our limited knowledge on multitrophic interaction mechanisms [48].

Often cited mechanisms for phytochemical diversity effects on herbivory such as resource concentration or chemical masking can presumably also be applied to effects on natural enemies, though these may operate directly or indirectly (i.e. via effects on herbivores) as effects ripple across trophic levels. Again, however, these phenomena have rarely been studied within a multitrophic context. For example, effects of plant chemical masking on herbivores may also directly hamper information transfer with predators and parasitoids, potentially leading to conflicting outcomes (see discussion ahead). Here, information theory applied to understand the effects of habitat complexity on consumers can shed light into phytochemical diversity effects on higher trophic levels [9]. For example, Aartsma et al. [49•] propose that prey become less apparent, and a larger number of foraging decision steps are needed by organisms at higher trophic levels, implying different systems for assessing cues (e.g. search templates) and information integration by natural enemies compared with herbivores. This is compounded by the fact that organisms at higher trophic levels are affected by induced changes in plant traits (e.g. VOCs, indirect defenses) due to herbivore feeding and by plant-mediated effects on herbivore traits or abundance (see above).

There is some evidence that plant-based habitat complexity (including chemistry) reduces natural enemy foraging efficiency (e.g. [50,51]), but at the same time, other studies have shown that higher trophic levels are attracted to combinations of plant and herbivore cues [52] and exhibit noise-correction mechanisms (e.g. for volatile

landscapes; [51]). Furthermore, there is evidence that natural enemies are attracted to volatile mixtures from different plant genotypes (e.g. ladybirds; [53]), but these responses appear to be overruled by herbivore-related cues once the latter become more common in the environment [54]. Thus, it appears that natural enemies can be resilient to phytochemical ‘noise’ and even leverage this complexity, but that its relative importance may decrease up food chains with intervening chemical cues of other trophic levels, including potential changes in the relative importance of density- and trait-mediated indirect effects.

Broadly speaking, a conceptual integration of information theory and community ecology would help advance our understanding of phytochemical diversity effects on natural enemies and guide empirical work. For now, the bulk of examples consist of case studies focused on a few species, making it difficult to generalize patterns.

## Recent empirical studies

### General considerations

We next examine a handful of manipulative studies testing for phytochemical diversity effects on multitrophic interactions, all at the intraspecific level (see Box 2 for a synthesis on related work at the interspecific level, namely, intercropping systems, which have yielded knowledge on plant chemically mediated effects but have usually not involved manipulations of phytochemical diversity).

The examined studies are largely exploratory in nature, that is, not based on a priori knowledge on chemically

mediated mechanisms (and their explicit manipulation), such as the use of targeted plant genotypes with specific chemical properties, for example, in push–pull or reward-attraction systems (see Box 2). In addition, they involve experimental designs *sensu* Biodiversity and Ecosystem Functioning (BEF) studies, that is, monocultures of all plant chemical types and mixtures, including different combinations of those types (at a constant or varying plant density), which allow to test ‘broad sense’ diversity mechanisms, namely, whether effects are additive (e.g. dominant species effects) versus nonadditive (e.g. overyielding via species complementarity effects; see Box 1). Plant genotypes in these studies exhibit contrasting chemical defense status, that is, in either compound amount or composition, and are originated via different approaches, ranging from focal gene knockouts to genotypes originated through breeding (e.g. inbred lines) or the use of clones or populations sourced *in situ*. The former approach has been used to manipulate focal compounds or chemotypes with a simple genetic basis and provides a higher control over and precision in testing the genetic basis of diversity effects, whereas the latter fits a quantitative genetics approach and is suitable for systems with more complex polygenic chemotypes [12,29••]. It is noted that the specific chemical traits underlying resistance in this latter type of studies are not always known or well characterized.

### Summary of main findings

Two pioneering studies set the stage for more recent work, all within the last decade. The first by Schuman et al. [55] manipulated phytochemical diversity (with

#### Box 2 Multitrophic interactions in intercropping systems.

Push–pull dynamics have been especially well studied and are explicit in their use of knowledge on chemically mediated interactions to inform cropping system design and management. Insect pests are repelled or deterred from the focal crop (push component) using different combinations of visual or chemical stimuli (e.g. gustatory or olfactory) known as semiochemicals (see Box 1). These combinations either mask host apparency or act as repellents to the pest. Simultaneously, the strategy employs attractive stimuli (pull component), such as trap plants (see Box 1), to draw pest aggregation to sites away from the focal crop (for a detailed discussion of cue types, refer to Ref. [65]). This method has been especially effective at reducing stem borer damage in sub-Saharan intercropping systems (reviewed by Refs. [60,65]; for pioneering studies, also see Ref. [65]), where attractive Napier grass (*Pennisetum purpureum*) or Sudan grass *Sorghum vulgare sudanense* are planted in crop borders as stemborer traps, while repellent plants such as molasses grass (*Melinis minutiflora*) and silverleaf desmodium (*Desmodium uncinatum*) are intercropped to drive these pests away from cereals crops such as maize and sorghum (for examples in other systems, see Ref. [60]). Crucially, most work has focused on pest behavioral responses, whereas effects on predators and parasitoids have received much less attention [65]. The few exceptions show positive effects of these intercropping systems on parasitism and predation, which presumably contribute to increased yield [60,66]. For instance, early work by Khan et al. [67] found that parasitism rates on maize stemborers increase when this plant is intercropped with molasses grass, which produces combinations of volatiles that attract female parasitoids (*Cotesia sesamiae*). A similar case was found with Sudan grass [68]. Since then, several pest-repellent compounds emitted by these companion plants have been shown to act as foraging cues for predators and parasitoids [66]. Likewise, combinations of volatiles produced by trap plants to attract pests have also been shown to increase predator and parasitoid attraction [66]. That said, different outcomes have been reported in other systems making use of push and/or pull components or other related mechanisms for which other types of traits (e.g. attract and reward) intervene. For example, recent work found that onion (*Allium cepa*) and garlic (*A. sativa*) volatiles repel aphids but not predators on cotton [25••], whereas rosemary volatiles used to repel thrips also repel predators on *Chrysanthemum* [69], findings which together highlight system-specific contingencies and responses across trophic levels. Finally, recent work has shown that plant–plant volatile signaling can contribute to pest control in intercropping systems, including work in maize push–pull systems whereby stemborers are repelled and their parasitoids attracted to maize plants previously exposed to molasses grass [70••]. Aside from volatile-mediated interactions, intercropping effects on natural enemies can also take place via spatial dynamics (pest concentration on trap plants favoring its detection by predators and parasitoids) or plant-based resource provisioning (e.g. nectar for adult parasitoids [65]). These mechanisms have received far less attention and their relative importance or synergistic effects including plant volatiles have not been investigated.

monocultures and polycultures of genotypes with contrasting relative concentrations of volatile compounds) in wild tobacco (*Nicotiana attenuata*) and found that it boosted plant performance but did not influence insect leaf herbivory or predation (by generalist *Geocoris* sp. bugs) and favored stemborer damage (the weevil *Trichobaris mucorea*). Notably, effects on trophic interactions appeared seemingly unrelated to effects on plant performance, suggesting links between multitrophic interactions and primary productivity were weak or, alternatively, went undetected. Following this study, Bustos-Segura et al. [20] manipulated phytochemical diversity (via monocultures and polycultures varying in the relative concentration of glucosinolates) in wild cabbage (*Brassica oleracea*). They found a positive effect on plant growth, and while herbivore abundance (dominated by the cabbage aphid, *Brevicoryne brassicae*) increased in mixtures, there was a negative effect on leaf herbivory and a positive effect on natural enemy abundance, including generalist predators and a specialist parasitoid (*Diaeretiella rapae*). The latter responded to an indirect effect via higher herbivore loads in mixtures (seemingly a density-mediated indirect effect), though a direct effect (via plant traits) likely also occurred but was stronger early in the season. These findings shed mechanistic insight into multitrophic effects and further highlighted the importance of temporal variability.

Research that followed involved additional manipulations (besides phytochemical diversity) to achieve more nuanced understanding on mechanisms. Wetzel et al. [56] found that phytochemical diversity (combinations of monocultures or mixtures of susceptible and resistant potato, *Solanum tuberosum*, genotypes) had a negative effect on the performance of a specialist beetle (*Leptinotarsa decemlineata*) but did not influence herbivory rates or plant growth. They also manipulated the risk of predation by establishing plots with and without predatory bugs (*Podisus maculiventris*, with tips of rostrum previously removed) and found that phytochemical diversity reduced beetle performance in the absence but not presence of predators, that is, diversity effects on herbivores were offset by predators, particularly early in the season, also highlighting marked temporal dynamics. Subsequently, two other studies by the same group tested for phytochemical diversity in tomato (*S. lycopersicum*). First, Hauri et al. [29••] manipulated two axes of phytochemical diversity (via changes in the relative concentration of terpenes and acyl sugars) in tomato plants together with predator presence (*P. maculiventris*). Consistent with previous studies, they found that phytochemical diversity reduced the performance (mainly growth) of the generalist herbivore *Trichoplusia ni*. Interestingly, this effect interacted with predation in a manner contingent on the type of compounds: plant volatile diversity but not surface chemistry (acyl sugars)

interfered with predator foraging and top-down control. Then, in the second study, Hauri et al. [57••] found that *T. ni* damage on tomato plants was lower in mixtures than in monoculture, but only when genotypes were spatially grouped, that is, phytochemical diversity effects interacted with genotype spatial distribution, possibly via chemical interference. Interactive effects extended to higher trophic levels, as predator abundance tended to be higher in mixtures than in monoculture but only when genotypes were grouped, thus highlighting spatial processes shaping multitrophic outcomes.

See Table 1 for summary of study features, namely, experimental design and approaches used to manipulate phytochemical diversity and traits. In addition, Box 3 provides a comparison of main findings from these studies highlighting demonstrated or likely mechanisms.

### Knowledge frontiers

Expanding from the above studies, we next point to what in our view are key interrelated research frontiers and future directions toward closing knowledge gaps.

#### i) Different types of plant traits

Plant specialized metabolites with defensive roles are often correlated or act concurrently with other types of chemical traits such as plant foods (e.g. nectar, food bodies) and physical traits such as domatia and trichomes to influence insects. Teasing apart their effects on natural enemies (e.g. by jointly manipulating diversity in chemical and other traits) can shed mechanistic insight into the relative effects of phytochemical diversity and its interactions with other sources of plant trait variation. The same rationale applies to teasing apart the effects of different types of plant chemical traits [29••]. In doing so, we can understand how focal chemical traits or their interaction with other traits shape interactions across trophic levels (e.g. differential effects on herbivores versus natural enemies; Aartsma et al. [49•]). These remain largely open questions even in well-studied systems (e.g. VOCs versus other plant traits in push-pull systems) and can help identify trait ecological conflicts versus synergisms within and across trophic levels shaping interaction outcomes. Knowledge gained can help to design systems, which, for example, reduce chemical noise for predator foraging or preclude ecological conflicts across trophic levels by informing the selection of plant types with traits that repel herbivores but do not negatively affect predators [25••,57] or even actively promote them (e.g. manipulations of diversity in plant chemical and reward traits in attract-reward systems; for example of latter case, see Ref. [58]). The intersection with predator-pollinator interactions is also particularly relevant within this context (see Ref. [59]).

Table 1

**Summary of main experimental and sampling features of studies reporting on intraspecific phytochemical diversity effects on multitrophic interactions.**

Study	Main features
Schuman et al. [55]	Tested for phytochemical diversity effects using wild tobacco ( <i>N. attenuata</i> ) by developing transgenic lines with contrasting levels of different types of volatile or nonvolatile defenses. They then established patches with monocultures of each line and polycultures in which a poorly or highly defended line was mixed with another line with the same level of defense but for the other type of compounds. They measured plant growth, herbivory (leaf chewers and stemborers), and predation rates (generalist <i>Geocoris</i> sp. bugs).
Bustos-Segura et al. [20]	Manipulated phytochemical diversity in wild cabbage ( <i>B. oleracea</i> ) by establishing plots with plants sourced from one, two, or three populations with contrasting levels of glucosinolates. They measured plant growth, herbivore abundance (generalist species and a specialist aphid [ <i>B. brassicae</i> ]), insect leaf herbivory, and natural enemy abundance (generalist predators and a specialist parasitoid, <i>Diaeretiella rapae</i> ).
Wetzel et al. [56]	Established monocultures and dicultures of two potato ( <i>S. tuberosum</i> ) genotypes, one with high resistance (underlying chemical traits not known), and the other was susceptible to insect herbivores, including the Colorado potato beetle ( <i>L. decemlineata</i> ), a specialist. They also inoculated half of the plots of each diversity level with generalist stink bugs ( <i>P. maculiventris</i> ), previously removing their rostrums to test for nonconsumptive predator effects (i.e. risk of predation). They measured plant growth, insect herbivore performance, and herbivory (by <i>L. decemlineata</i> ), as well as predation rates (by a generalist bug, <i>Podisus maculiventris</i> ).
Hauri et al. [29••]	Manipulated phytochemical diversity in tomato ( <i>S. lycopersicum</i> ) by establishing monocultures, dicultures, and tricultures of varieties differing in volatile or nonvolatile compound chemistry, combined with a manipulation of presence (inoculated) versus absence (excluded) of the predatory bug <i>P. maculiventris</i> . They recorded herbivore performance ( <i>T. ni</i> ) and predation rates by the bug.
Hauri et al. [57••]	Manipulated phytochemical diversity in tomato ( <i>S. lycopersicum</i> ) volatile emissions together with genotype within-plot spatial distribution (plants of each genotype alternated or grouped). The authors measured herbivory by <i>T. ni</i> and predator abundance ( <i>P. maculiventris</i> ).

## ii) Consumer traits

Dietary specialization is a key driver of herbivore responses to phytochemical diversity but has rarely been studied for natural enemies (likewise for other important traits, such as mobility or foraging behavior). A consideration of these predator and parasitoid traits (see Ref. [49•]) is key for achieving mechanistic insight into phytochemical diversity effects on multitrophic interactions. This will require understanding the chemical ecology underlying documented interactions under real life settings [39], complemented by controlled tests (e.g. laboratory or greenhouse experiments), which then inform subsequent, more nuanced field studies to identify relevant cues and test interaction

mechanisms. Experiments with multiple consumer species at each trophic level involving insect species-level replication (e.g. by feeding mode, specialization, and/or sensory system) would be highly valuable, albeit challenging. In addition, considering links between predator traits and phytochemical diversity in the context of predator–predator interactions (e.g. intraguild predation; [41]) can also help to understand how top-down control is regulated within complex (but tractable) food webs.

## iii) Spatial dynamics

Some consumer traits, including dispersal ability [46], have long been shown to predict insect scale-dependent responses to plant diversity, and this is highlighted by recent phytochemical diversity

**Box 3 Comparison of main findings from experimental studies testing for effects of intraspecific phytochemical diversity on multitrophic interactions.**

Studies in all but one case [55] report negative effects of phytochemical diversity on herbivore performance and/or plant damage. That said, herbivore population dynamics and herbivory rates do not always correlate, possibly reflecting methodological choices that do not fully capture herbivory patterns or a real uncoupling between behavioral and performance-related traits and resulting herbivory. Studies included specialist and generalist insect herbivores. In some cases [55], damage by generalist and specialists was pooled (possibly obscuring effects on latter), and some studies involved generalist caterpillars and also found negative effects [29••, 57••]. For natural enemies, effects of phytochemical diversity, namely, on generalist predators (e.g. bugs) and a specialist parasitoid, were positive, and there was evidence for both direct (via plant traits) and indirect (via herbivore abundance) pathways (e.g. [20]). In addition, effects on natural enemies were contingent on the types of plant compounds (e.g. volatile vs nonvolatile) varying among plant genotypes (e.g. [29••]), and several studies (e.g. [20, 56]) reported that effects on natural enemies were short lived or stronger early in the season, combined with uncoupled herbivore–natural enemy abundance dynamics. In particular, studies by Hauri et al. [29••, 57••] show that phytochemical diversity interfered with natural enemy recruitment or top-down control, but this depends on the type of plant compounds or plant genotype spatial arrangement (respectively), and in one case [56], effects on herbivores were offset by predators (i.e. bottom-up/top-down antagonism). Finally, there was evidence that phytochemical diversity positively influenced plant performance in some cases but in a manner not consistently related to effects on herbivores and predators. This suggests other intervening mechanisms that weakened links between plant growth or reproduction and multitrophic interactions, and in some cases it is possible that unmeasured effects on plant mutualists (e.g. soil microbes or pollinators) contributed to explain outcomes.

research [29••]. Still, our understanding of how plant-based spatial features and consumer traits interact to shape responses to phytochemical diversity is limited, even in well-studied intercropping systems and despite previous calls [60]. Population- and community-level variables that can be manipulated in a spatially explicit manner are, for example, plant chemotype density, relative frequency, and spatial distribution (e.g. dispersed vs aggregated). The choice of factor or design features should match the plant chemical traits (e.g. volatile vs nonvolatile) and consumer traits of interest, including search behavior and resulting functional responses (see Ref. [29••]), with the goal of yielding prescriptive knowledge that informs study designs (i.e. diversity manipulation matching consumer movement or behavior) that enhance predation (e.g. via increased herbivore movement; see Ref. [44]) or increased aggregation as in push-pull systems) or circumvent interference with predators. In addition, plant induced responses to herbivory can also interact with spatial features to shape phytochemical diversity effects by modifying plant chemistry and how its variation is spatially distributed [61,62] and thus deserve attention within this context.

#### iv) Temporal dynamics

The effects of phytochemical diversity on natural enemies exhibit time lags and are often transient, which can dampen top-down control (this is highlighted in some of the revised studies). A better understanding of plant and consumer traits contributing to the duration and stability of top-down control is needed. The use of plant chemotypes or species with complementary chemical and/or resource or reward-based traits (see *plant traits*), including nonoverlapping phenology, could contribute to maintain larger and more stable predator populations and communities. An overarching goal here is to favor predator establishment or retention (e.g. in conservation biological control; [39]) and in so doing promote the long-term persistence and effectiveness of top-down forcing. As above, plant induced responses can also feed into temporal variation in phytochemical diversity effects via interactions with consumer behavior and plasticity in other traits, a topic yet to be explored.

## Closing notes

Although the choices of plant chemical types (genotypes, species) and analytical methods are often constrained by various factors, some handle on the nature and amount of compound variation present among plant types is desirable to inform study design as well as decipher phytochemical diversity effects [63,64]. Plant traits (chemical and other types as well) together with consumer traits (and resulting trait combinations) must

be explicitly considered in building mechanistic frameworks to understand how effects propagate up food chains, drawing from community ecology (e.g. density- and trait-mediated effects) and other perspectives, such as information theory. Experimental studies making use of different manipulations (e.g. of plant-based spatial or physical features) and using trait-based knowledge to inform the selection of plant types and consumers (in the case of plants also informing on the design of diversity treatments) will help to identify interaction mechanisms and how they play out under different ecological contexts or systems. In addressing these challenges, we also stress the need for more studies involving predator manipulations (presence/absence, predator augmentations, behavioral manipulations, etc.) as a basic design feature that enables to test mechanisms of top-down control and separate them from bottom-up processes in explaining phytochemical diversity effects on herbivory and plant productivity. Finally, and despite the recognized importance of phytochemicals in mediating above-ground plant-insect interactions, our knowledge on phytochemical diversity effects on below-ground multitrophic interactions is sparse. Further research is needed to unravel interaction characteristics and mechanisms within this realm and their reciprocal linkages with above-ground interactions.

## Data Availability

No data were used for the research described in the article.

## Declaration of Competing Interest

The authors have no conflict of interest to declare.

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