



# Global change effects on plant–insect interactions: the role of phytochemistry

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Natural and managed ecosystems are undergoing rapid environmental change due to a growing human population and associated increases in industrial and agricultural activity. Global environmental change directly and indirectly impacts insect herbivores and pollinators. In this review, we highlight recent research examining how environmental change factors affect plant chemistry and, in turn, ecological interactions among plants, herbivores, and pollinators. Recent studies reveal the complex nature of understanding global change effects on plant secondary metabolites and plant–insect interactions. Nonetheless, these studies indicate that phytochemistry mediates insect responses to environmental change. Future research on the chemical ecology of plant–insect interactions will provide critical insight into the ecological effects of climate change and other anthropogenic disturbances. We recommend greater attention to investigations examining interactive effects of multiple environmental change factors in addition to chemically mediated plant–pollinator interactions, given limited research in these areas.

## Addresses

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## Introduction

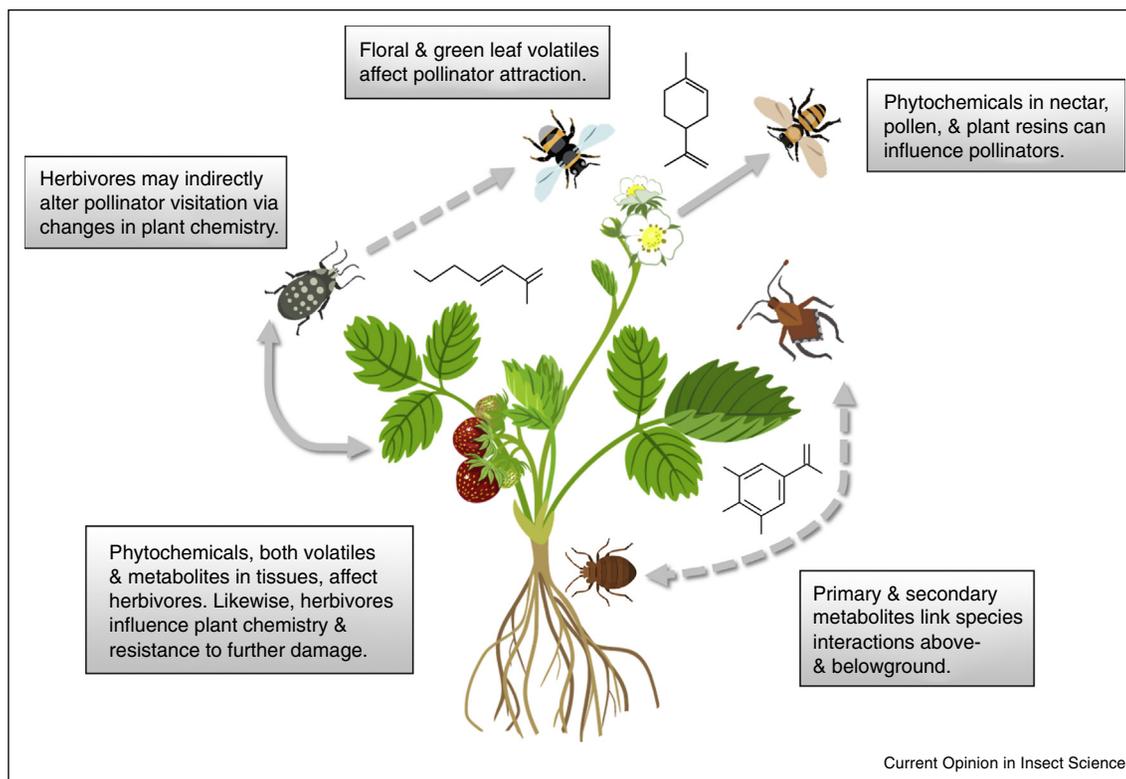
Global environmental change (GEC) can alter species' functional traits and ecological interactions with important population, community, and ecosystem-level consequences [1,2]. Many studies have documented the effects of various GEC drivers on herbivores [3–7,8\*\*] and pollinators [9–12]. In this review, we explore how GEC factors can modify plant–insect interactions by influencing the chemical ecology of plant–herbivore, plant–pollinator, and multispecies interactions (Figure 1). Our review focuses on recent research, in particular studies published in the last few years, that examine independent and interactive effects of five abiotic GEC drivers — climate warming, drought, elevated carbon dioxide (CO<sub>2</sub>), tropospheric ozone (O<sub>3</sub>) pollution, and increased nitrogen inputs (atmospheric NO<sub>x</sub>, N deposition, and soil N enrichment).

Plant chemicals, including primary and secondary metabolites, mediate plant–insect interactions (Box 1). While these phytochemicals often interact to influence herbivores and pollinators, we focus our review primarily on plant secondary metabolites (PSMs). GEC factors can alter the biosynthesis, composition, and levels of PSMs, which in turn, can affect plant herbivore defenses and pollinator attraction. Our understanding of the effects of global change on phytochemistry and plant–insect interactions, however, is often complicated by context-dependent responses, interactions among multiple GEC factors, and the challenge of disentangling direct and indirect effects of environmental variables on plants and insects (Box 2). As a consequence, it is difficult to make general conclusions about or predict the impacts of GEC drivers on plant–insect interactions. Nonetheless, recent studies provide new insight into GEC effects on chemically mediated plant–insect interactions, in particular with respect to the role of plant volatiles and the chemical ecology of plant–pollinator interactions.

## The chemical ecology of plant–herbivore interactions

Plant secondary metabolites play an important role in plant defense against herbivores by deterring feeding, reducing digestibility via direct toxicity, and by attracting natural enemies of herbivores [13]. Phytonutrients interact with PSMs to influence herbivores, although our understanding of interactive effects among these phytochemicals remains limited [14]. GEC drivers can alter the composition and concentration of PSMs in plant tissues and volatile emissions via changes in biosynthetic

Figure 1



Schematic of the chemical ecology of plant–herbivore, plant–pollinator, and multispecies interactions. Global environmental change (GEC) drivers, including elevated temperature, altered precipitation, elevated CO<sub>2</sub> and tropospheric O<sub>3</sub>, and increased nitrogen, can affect plant primary and secondary metabolites and thereby plant–insect interactions. Moreover, these GEC factors may act independently or interactively to alter plant chemistry, which in turn can have direct (solid lines) and indirect (dashed lines) effects on trophic dynamics and other ecological interactions among plants, herbivores, and other species influenced by phytochemical variation. Arrows indicate the direction of effect and illustrate examples of possible, but not all, interactions.

pathways, plant allocation patterns, and physiochemical properties of individual compounds. Such variation in PSMs due to GEC factors can affect insect herbivores and plant damage due to herbivory. A number of reviews have addressed the effects of global change on PSMs and plant–herbivore interactions [3,15–17,18<sup>\*</sup>], and specifically in regard to elevated temperature and altered precipitation [4], elevated CO<sub>2</sub> and tropospheric O<sub>3</sub> [5,6,8<sup>\*\*</sup>,19–22], and soil N enrichment [23,24<sup>\*</sup>].

#### Plant secondary metabolites and global environmental change

Similar to previous work, recent studies show that elevated temperature has variable effects on PSMs, and these effects are commonly idiosyncratic and context-dependent (Table 1; Box 2). For example, Zhao *et al.* [25] found that elevated temperature increased total phenolics, including condensed tannins and flavonoids in addition to saponins and alkaloids in black locust (*Robinia pseudoacacia*) seedlings. However, phytochemical responses depended on the plant tissue sampled (i.e., leaves versus

stems), month of sampling event, and interactive effects with heavy metal soil contamination. A number of studies have also found warming-induced increases in PSMs, including lignin [26<sup>\*</sup>], saponins [27], and volatile terpenes [28], while others have shown decreases in PSMs, including condensed tannins [25,29<sup>\*</sup>] and lignin [29<sup>\*</sup>]. Variation in PSM responses, within the same class of compounds or even the same compound, may be related to differences in plant phenology, plant development, or other environmental factors (e.g., water and soil nutrient availability) that influence plant metabolism and allocation to chemical defenses. For example, Jamieson *et al.* [29<sup>\*</sup>] found that experimental warming decreased condensed tannin and lignin concentrations in aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) juvenile trees during one year of a field study but not in a second year. The authors noted that differences in PSM responses corresponded with interannual climate variability. In this study, plant-mediated warming effects on an outbreak insect herbivore (*Malacosoma disstria*) were associated with shifts in both PSMs and phytonutrients.

**Box 1 Plant chemical traits affecting insect herbivores and pollinators**

**Plant primary metabolites:** Compounds essential for plant growth and development (proteins, amino acids, carbohydrates, lipids). Found in plant tissues (shoots, roots, flowers, phloem) and nectar. Important for herbivore and pollinator trophic dynamics and nutrition.

**Plant secondary metabolites (PSMs):** Specialized compounds, with no known essential function for plant growth and reproduction, but that play important and diverse functional roles, including as herbivore defenses and pollinator attractants. Some compounds may also attract specialized herbivores and natural enemies of herbivores or deter certain pollinator species. PSMs found in plant tissues, volatiles, and nectar affect herbivore and pollinator food preferences and performance. Major groups include nitrogen-containing compounds (alkaloids, cyanogenic glycosides, nonprotein amino acids), sulfur-containing compounds (glucosinolates), phenolics (phenolic acids, phenylpropanoids, tannins, flavonoids), and terpenoids (monoterpenes, diterpenes, sesquiterpenes, iridoids, cardiac glycosides).

**Biogenic volatile organic compounds (BVOCs):** Secondary metabolites emitted into the atmosphere by living organisms, primarily plants, including from roots, shoots, and flowers. Broadly, BVOCs include isoprene, terpenes, green leaf volatiles (GLVs), carbonyls, organic acids, halides, sulfur compounds, and benzenoid compounds [104]. BVOCs play important signaling roles in the interactions of plants with other organisms, especially herbivores and pollinators. Floral volatiles (or scents), a subset of BVOCs emitted from flowers, are of key importance in plant–pollinator interactions and these compounds are categorized by their biosynthetic origin [105].

Warming effects on host quality and plant–herbivore interactions depend on interacting biotic and abiotic environmental factors [4,7,26<sup>•</sup>,30–33]. In particular, water availability often interacts with temperature to influence plant growth and defense traits. For example, Couture *et al.* [26<sup>•</sup>] found that water stress increased common milkweed (*Asclepias syriaca*) cardenolides and decreased latex production, and temperature mediated the magnitude of response. Moreover, this study showed that Monarch (*Danaus plexippus*) larval growth was positively affected by elevated temperature and water stress via direct temperature effects in addition to phytochemical variation. In another study, drought stress increased glucosinolates in *Arabidopsis thaliana*, reduced *Mamestra brassicae* larval mass, and decreased *Myzus persicae* population growth [34<sup>•</sup>]. While altered glucosinolate levels did not explain negative effects on herbivores, the authors suggested that drought-induced changes in other phytochemicals, including flavonoid defense compounds, could have influenced herbivores. Increased drought intensity and frequency are key components of climate change that interact with warming and other GEC drivers to influence plant–herbivore interactions [4].

As with other GEC factors, the effects of elevated CO<sub>2</sub> and O<sub>3</sub> on plants and herbivores are frequently system-specific and context-dependent. Generally, elevated CO<sub>2</sub> and O<sub>3</sub> increase phenolics, such as some tannins and

**Box 2 Challenges to understanding global change effects on plant chemistry and plant–insect interactions**

**Context-dependent responses:** Plant and insect responses to global change depend on many factors, including species identity [29<sup>•</sup>,34<sup>•</sup>,40,74<sup>••</sup>,80<sup>••</sup>,89], phenology [28,101], interannual climate variability [29<sup>•</sup>], developmental stage of plants or insects examined [100,103], the magnitude of environmental change [34<sup>•</sup>,71,72,89,103], and other interacting abiotic and biotic factors.

**Interactive effects:** GEC drivers may interact in complex ways, though most studies evaluate a single environmental factor. A growing number of studies, however, are starting to consider how multiple interacting GEC drivers influence plant–insect interactions — including 2-way [26<sup>•</sup>,27,39–41], 3-way [97], and 4-way [28] interactions. Research indicates that the effect of one GEC factor often depends on another [26<sup>•</sup>,39,40,97]. Multiple environmental change factors may interact, potentially resulting in additive [41], synergistic [28], or antagonistic [39] effects on plants and insects.

**Direct and indirect effects:** Environmental change factors can directly and indirectly influence plants and insects. For example, herbivore physiology and performance traits may be directly affected by temperature and indirectly through warming-induced changes in plant chemistry [32]. Similarly, pollinator foraging activity can be directly affected by drought or indirectly via drought-induced changes in floral volatiles [74<sup>••</sup>]. These direct and indirect effects are especially difficult to disentangle in field studies.

flavonoids [5,6,8<sup>••</sup>,19,35]. Terpenoids tend to decrease with elevated CO<sub>2</sub> and increase with elevated O<sub>3</sub>, but different groups of terpenes demonstrate variable responses [6,19]. Phytohormones, including jasmonic acid (JA), ethylene (ET), and salicylic acid (SA), modulate the effects of elevated CO<sub>2</sub> and O<sub>3</sub> on plant chemical defenses. CO<sub>2</sub> enrichment tends to decrease chemical defenses regulated by JA and ET and increase SA-dependent defenses [8<sup>••</sup>]. Such changes in chemical defenses can result in positive, negative, or no effect on insects [8<sup>••</sup>,22], which presents challenges to predicting future shifts in herbivory. Elevated O<sub>3</sub> also tends to increase SA biosynthesis and upregulation of defense compounds involving the shikimic acid pathway, including some phenolic compounds [6,19]. However, there are a number of notable exceptions to the general trends described above. For example, Schneider *et al.* [36], found that leaf phenolics, including several flavonoids and a terpenoid in the tropical tree *Ficus insipida* were downregulated under higher O<sub>3</sub> conditions. For additional exceptions, see Table 1 and references noted above.

Increased soil nitrogen inputs often positively affect insect herbivores and increase herbivory [1,23,24<sup>•</sup>]. A recent review found that elevated N typically decreases tannins in trees, with little to no effect on other phenolic compounds [24<sup>•</sup>]. Frequently, N-enrichment decreases plant secondary metabolite concentrations, such as phenylpropanoid-derived compounds, though effects vary among major groups of PSMs [23,35]. For instance, nutrient (NPK) additions resulted in large increases in *Pinus*

Table 1

**Effects (+, –, 0) of global environmental change (GEC) drivers on plant chemical traits that mediate plant–herbivore and plant–pollinator interactions. This table highlights examples of changes in plant secondary metabolites (PSMs), known to play a role in plant–insect interactions, from recent studies (published in the last 5 years). Because few studies investigated PSMs in nectar, we show GEC effects on primary metabolites as well. Note that individual compounds and groups of compounds demonstrate idiosyncratic responses to GEC drivers (see Box 2 for factors that contribute to variation in PSMs). We note general trends, often with exceptions, in the review text. Phytochemical categories listed below are based on classifications presented in source references.**

GEC driver		Plant–herbivore	Plant–pollinator
<i>Temperature</i>			
Changes in plant chemistry	+	Flavonoids, condensed tannins, total phenolics, alkaloids [25], lignin [26*], saponins [25,27], volatile terpenes [28]	GLVs, volatile aromatic hydrocarbons [71], volatile terpenes [71,72]
	–	Condensed tannins [25,29*], lignin [29*]	Volatile aromatic hydrocarbons [71], volatile terpenes [71,72], GLVs [71,73], volatile benzenoids, volatile nitrogen containing compounds [73], nectar sugar concentration [89]
	0	Cardenolides [26*], lignin, condensed tannins, phenolic glycosides [29*]	Volatile terpenes, GLVs [73], nectar sugar concentration [88,89]
<i>Precipitation</i>			
Changes in plant chemistry	+	Cardenolides [26*], glucosinolates [34*], iridoid glycosides [39], volatile terpenes [53,54,56**], GLVs [54]	Volatile terpenes, GLVs, volatile benzenoids, & volatile aliphatics [74**]
	–	Volatile terpenes [54,56**,57,101], GLVs, volatile aliphatic ketones, volatile nitriles [56**], phenolics, monoterpenes and sesquiterpenes [100]	Volatile terpenes, GLVs, volatile benzenoids [74**]
	0	Lignin [26*], glucosinolates [34*], GLVs [54], volatile terpenes [54,56**,101], polyphenolics, condensed tannins, terpenes [100]	Volatile terpenes, GLVs, volatile benzenoids, volatile nitrogen containing compounds [74**]
<i>Carbon dioxide</i>			
Changes in plant chemistry	+	Glucosinolates [102], alkaloids, flavonoids, saponins [107]	
	–	Phenolics, condensed tannins [107]	Pollen protein [99**]
	0	Saponins [27]	Nectar sucrose concentration [91]
<i>Ozone</i>			
Changes in plant chemistry	+	Volatile terpenes [28,41,63], GLVs [41]	
	–	Phenolics [36], foliar terpenes [36], volatile terpenes [40,63]	Volatile terpenes [80**,81**], volatile phenolics [80**]
	0	Volatile terpenes, GLVs [41,63]	
<i>Nitrogen</i>			
Changes in plant chemistry	+	Volatile terpenes [28,37,41,101], iridoid glycosides [39], GLVs [41,101]	Volatile terpenes [78], nectar amino acids [93,94*]
	–	Tannins [24*], terpenes [37], iridoid glycosides [39], volatile terpenes [41,40]	Volatile terpenes [41,78,81**], GLVs [78]
	0	Phenolics [24*], iridoid glycosides [39], volatile terpenes [40,101], GLVs [101]	Nectar sugar concentration [93,94*]

*silvestris* monoterpene emissions [37], though the effect of N was not studied in isolation of other soil nutrients. Nitrogen enrichment can also alter plant allocation to above-ground and below-ground chemical defenses (e.g. [38]). And, similar to other GEC drivers, the effects of increased N on plant secondary metabolites depend on plant tissue (e.g. [38]) and on interactions with other environmental factors, such as water availability (e.g. [39]) and elevated O<sub>3</sub> (e.g. [28,40,41]).

Many studies document shifts in PSMs, but do not investigate subsequent effects on herbivores. Future research addressing how changes in PSMs affect herbivores as well

as how PSMs and plant nutrients interact to influence herbivory will enhance our understanding of chemically-mediated plant–herbivore interactions under global change. In addition to altering levels of PSMs in plant tissues, GEC factors can affect herbivore-induced plant volatiles with important consequences for plant–herbivore and multi-trophic interactions.

#### Herbivore-induced plant volatiles under environmental change

Plants emit ~10% of their recently assimilated carbon back into the atmosphere as biogenic volatile organic compounds (BVOCs; Box 1) under stressful conditions

[42]. These compounds play important roles in mediating both antagonistic and mutualistic multi-trophic interactions (Figure 1) as well as in determining the oxidative capacity of the troposphere, which in turn, can alter the effectiveness of BVOC-driven interactions. Specific blends of BVOCs are emitted in response to herbivores and pathogens. These blends offer critical information regarding plant location, quality, infestation history, and the presence of other insects [43–47]. Abiotic stressors, including GEC drivers considered in this review, can impact the BVOC response of plants to biotic interactions, thus modifying the way herbivores interact with host plants [48,49]. While it is understood that elevated temperature, decreased precipitation, and atmospheric pollutants impact herbivore-induced BVOC emissions, little is known about interactive effects of multiple abiotic stressors.

Even slightly elevated temperatures at the canopy level can cause a considerable and rapid increase in BVOC emissions [28,50], and herbivory has an additive effect [48,51]. Herbivore density interacts with temperature to influence BVOC blends, but differences in the solubility, volatility, and diffusivity of individual compounds result in varying profiles [52]. Herbivore  $\times$  temperature effects have been observed over longer time periods as well. For example, Kivimäenpää *et al.* [28] showed that previous-season herbivory increased monoterpene emissions in Scots pine (*Pinus sylvestris*) seedlings the following spring under elevated temperature while suppressing the increase of monoterpenes caused by O<sub>3</sub>.

Water stress often impacts BVOC-facilitated interactions. For example, previous exposure to drought may prime plants to a faster herbivore BVOC response, thus conferring greater resistance to herbivores [53]. Additionally, simultaneous herbivore and drought stress can affect a plant's indirect defenses via enhanced attractiveness [54] or deterrence [55] to parasitoids. Other work suggests that drought-stressed plants may be more susceptible to herbivore oviposition, but with no effects on larval performance or parasitoid host location [56\*\*]. Drought and/or release from drought stress can also influence herbivore-induced BVOCs on longer time scales. In piñon pine (*Pinus edulis*), high monoterpene emissions following early season herbivory were suppressed by midsummer drought, and the same trees exhibited a larger monoterpene flux following a release from drought stress, with implications for herbivore host location in the fall [57].

Elevated CO<sub>2</sub> inhibits isoprenoids [58,59], but a number of other herbivore-induced BVOCs (via jasmonic acid application) exhibit an increase under elevated CO<sub>2</sub> [60] with potential consequences for plant resistance to herbivory. Other studies have observed increased BVOC emissions in response to CO<sub>2</sub>  $\times$  herbivory but failed to observe an effect on parasitoid orientation and indirect

defense [61]. While the three-way interaction of elevated CO<sub>2</sub>, warming, and drought represents an important future climate scenario, these interactive effects on herbivore-induced BVOC emissions remain largely unexplored across plant–insect systems.

Ozone pollution can impact BVOC-mediated species interactions by altering host quality, reacting with volatiles and changing the level or composition of BVOC emissions, and/or interfering with insect signal perception. Enriched O<sub>3</sub> has been shown to alter a plant's susceptibility to oviposition by insect herbivores where females were unable to discriminate between plants exposed to BVOCs from damaged or undamaged neighbors [62], although the mechanism underlying this effect was not explicitly tested. Using a series of behavioral tests, Li *et al.* [63] demonstrated that *Plutella xylostella* larval attraction to herbivore-damaged cabbage (*Brassica oleracea* subsp. *capitata*) plants was reduced in elevated O<sub>3</sub> environments due to the degradation of terpenoids and green leaf volatiles as well as repellent properties of their oxidation products. Pinto *et al.* [64] found that O<sub>3</sub> also considerably altered herbivore-induced volatile blends, but this change did not affect the orientation of parasitoids, indicating a minimal role of oxidation products in signal perception for this system. In some cases, temporal dynamics of O<sub>3</sub> stress can be critical. For instance, O<sub>3</sub> alone did not induce BVOC emissions by *Brassica nigra*, but feeding by *Pieris brassicae* larvae following O<sub>3</sub> exposure resulted in greater emissions than feeding alone and, in turn, enhanced attraction by the parasitoid *Cotesia glomerata* [65\*].

Soil nitrogen availability can significantly alter the production and emission of BVOCs. Plants generally increase BVOC emissions under insufficient N, but the BVOC response appears to be system-specific, resulting in positive, negative, or no effects in response to N amendments [66]. Recent studies show that fertilization can increase monoterpene emissions [37], while low or exceedingly high levels of N can decrease monoterpene emissions and subsequently reduce parasitoid recruitment [55]. Kivimäenpää *et al.* [28] showed that increased soil N availability and elevated O<sub>3</sub> had positive additive effects on the emissions of several monoterpenes and total sesquiterpenes in Scots pine, but these effects were modified by herbivory. Positive additive effects of N and elevated O<sub>3</sub> on BVOC emissions have also been confirmed in other tree systems, especially following short-term O<sub>3</sub> exposure [41], but reduced BVOC emissions have been reported in leguminous species [40].

While many studies on BVOCs focus on the effects of abiotic or biotic factors in isolation, recent research reveals the importance of understanding interactive effects of multiple GEC drivers and herbivory. Additionally, these recent studies indicate a need to consider

GEC lag effects and spatiotemporal dynamics as well as mechanisms underlying system-specific responses. Furthermore, future studies would benefit from a multi-disciplinary approach to addressing how herbivory interacts with GEC factors to influence BVOC-mediated interactions. Specifically, work at the intersection of plant ecophysiology, atmospheric chemistry, and insect physiology will advance this research area.

### The chemical ecology of plant–pollinator interactions

Plant–pollinator interactions are essential to the health of natural ecosystems, and much of the human diet depends on insect pollination [12]. Components of GEC, including increasing temperatures, elevated CO<sub>2</sub> levels, and altered precipitation patterns, can directly affect plant–pollinator interactions by changing the phenology, physiology, and distribution of plants and insects [12,67–69]. Another important way that GEC factors can influence plant–pollinator interactions is by altering phytochemicals important for pollinator attraction, especially nectar and volatile chemistry. Here, we highlight recent studies in this young field of research examining chemically-mediated GEC effects on plant–pollinator interactions.

#### Floral volatiles and pollinator attraction under environmental change

Components of global change can alter floral BVOCs, which play a central role in pollinator attraction and plant–pollinator mutualisms. The effects of temperature on floral BVOCs have been most studied, with warming having a consistent positive effect on BVOC emissions [70–72] but see [73]. Interestingly, temperature can alter the rate of emission of some compounds more than others, leading to changes in the relative composition of compounds in bouquets [71,72], but with unknown influence on pollination, as no studies to our knowledge have examined how warmer temperatures affect pollinator attraction via shifts in floral BVOCs. A recent, exciting discovery is that rather than via passive diffusion, BVOCs are actively transported by a protein across the plasma membrane and expelled from *Petunia hybrida* flowers [106]. It is not known how GEC factors might affect activity of such proteins, but temperature and protein activity are often positively correlated.

Drought can alter the amount and composition of floral BVOCs and subsequent pollinator attraction in species-specific ways by decreasing or even increasing pollinator visitation to plants [74\*\*]. Interestingly, drought universally reduced visual apparancy via flower size and number in four forb species examined (*Campanula rotundifolia*, *Heterotheca villosa*, *Phacelia hastata*, and *Potentilla recta*), but had species-specific effects on BVOCs, with differences in the quantity and composition of volatiles across the four species tested. The general decrease in visual cues and increase in odor apparancy in response to

drought suggest that floral VOCs may be relatively more important than visual cues, such as floral size, for pollinators, particularly under changing environments [74\*\*,75].

Atmospheric pollutants can also affect floral BVOCs. For example, nitrogen deposition may have the potential to increase emission of some floral BVOCs and the frequency of floral visitors [76]. However, anthropogenic airborne contaminants, like ozone and diesel exhaust, can have a negative effect on pollinator foraging since they can degrade floral VOCs, once emitted, and increase foraging times of pollinators [77–79,80\*\*,81\*\*]. For example, Farré-Armengol *et al.* [80\*\*] found that realistic levels of ozone degraded *Brassica nigra* floral BVOCs in compound-specific ways, changing the ratio of compounds in the bouquet, which strongly inhibited attraction of the generalist bumble bee pollinator *Bombus terrestris*. It is becoming clear that airborne pollutants have significant negative effects on pollinator attraction to flowers, sometimes in unexpected ways (e.g. by altering BVOC ratios), but interactive and ecological effects remain largely unknown.

Relationships between GEC factors with floral BVOCs and subsequent plant–pollinator interactions are just beginning to be understood. Increases in atmospheric CO<sub>2</sub> is a principal GEC factor, but its effects on floral BVOCs have not been investigated to our knowledge. Extending studies of GEC factors on floral BVOCs to include effects on pollinators and plant fitness will improve our understanding community and ecosystem-level effects, but scaling-up will require creative methods and appropriate controls.

#### Floral rewards in a changing world

The quantity and composition of floral nectar plays a key role in mediating plant–pollinator interactions. Sugar and amino acids reward flower visitors, but nectar may also contain secondary metabolites that can reduce the length and number of pollinator visits, inhibiting pollination [82\*\*]. Nectar secondary metabolites can have negative, neutral (e.g. [83]), or positive (e.g. [84]) effects on pollinators, which may have community-wide impacts on pollination. The functional roles of PSMs in nectar are poorly understood, and warrant greater attention, given the potential for these compounds to play a role in pollinator health and pollinator-pathogen interactions (e.g. [84]). Moreover, the effects of global change drivers on nectar secondary metabolites are virtually unknown. Nectar secondary metabolites are often correlated with leaf secondary metabolites [82\*\*] and may therefore mirror changes in foliar chemical defenses under different GEC conditions. We are aware of only a single study that has examined GEC effects on nectar secondary metabolites. Halpern *et al.* [85] investigated the response of floral attraction and defense traits to leaf herbivory and

drought stress in *Nicotiana quadrivalvis* and found no effect of water availability on nectar nicotine.

In general, little is known about how nectar will respond to GEC factors. To date, research has focused on primary metabolites, while few studies have examined secondary metabolites. Nectar volume, sugar concentration, and sugar composition are shaped by temperature and water availability [86], but these factors have rarely been studied in the context of global change [87]. Studies using open-top chambers to increase temperature have yielded to mixed effects on nectar volume and sugar concentrations [88,89]. Greenhouse drought treatments can reduce nectar volume [85], while elevated CO<sub>2</sub> can increase [90] or decrease nectar production [91]. In a few studies and plant-systems, soil N enrichment had no effect on nectar volume [92,93,94\*] or sugar concentration [93,94\*,95] but see [92], but long-term N fertilization increased nectar production in field populations of *Ipomopsis aggregata* [95]. More consistently, N-enrichment increased nectar amino acid concentrations and changed amino acid composition [93,94\*,96]. Elevated N and temperature interacted to increase nectar amino acid and sugar concentrations, and elevated temperatures and CO<sub>2</sub> increased sugar concentrations in *Cucurbita maxima* [97].

Pollinator responses to GEC-related changes in nectar will likely vary by taxa. For example, changes in nectar amino acids may have implications for lepidopteran fitness [98], but how changes in nectar quantity and composition will affect other pollinators may depend on specific preferences and resource requirements. Further, interactions between GEC factors such as temperature, nitrogen and CO<sub>2</sub> can elicit different responses in nectar than single factors, which can have consequences for pollinator preference and longevity [97]. Despite extensive knowledge of the importance of nectar as a pollinator resource, few studies have examined how changes in nectar due to GEC factors will impact pollinators.

Finally, the impacts of GEC drivers on other floral resources have rarely been addressed. A few studies have demonstrated decreased pollen quantity [91] and protein quality [99\*\*] with elevated CO<sub>2</sub>, while long-term N fertilization did not influence per-flower pollen production and had weak, species-specific effects on *Ipomopsis aggregata* pollen quantity [95]. However, the effects of other GEC factors on pollen, which is the source of protein for many pollinators, are unknown. Further, impacts of global change on oils and resins, important resources for some insect pollinators, have received no attention. Changes in the chemical composition of floral resources due to biotic or abiotic stressors could have important implications for plant–pollinator interactions, warranting a need for greater research in this area.

## Conclusions and future directions

While the effects of global change on plant–insect interactions are well-studied, research to date has focused on phenology and species interactions with less consideration of plant chemical constituents that influence the food quality of plant resources for herbivores and pollinators. Compared to research on plant–herbivore interactions, far fewer studies have addressed the role of plant chemical traits on plant–pollinator interactions. We know little about the influence of plant secondary metabolites on pollinators and even less about how GEC factors affect the chemistry of floral volatiles, floral rewards, and, in turn, pollinators. Future research examining how herbivores interact with GEC factors to influence floral volatiles and pollinator visitation could provide important insight into understanding multispecies interactions under environmental change.

A large majority of the studies that consider GEC effects on plant chemical traits and plant–insect interactions examine either plant nutrition or plant secondary metabolites. Consideration of both nutrition and secondary metabolites, however, is necessary to enhance our understanding of global change effects on plant–insect interactions. While many studies evaluate environmental factors in isolation, a growing number of researchers are beginning to investigate multiple interacting factors (Box 2), which represent more realistic GEC scenarios. Research addressing the influence of multiple stressors on plant–herbivore, plant–pollinator, and multispecies interactions will provide critical information for assessing ecological consequences of anthropogenic environmental change.

## Conflict of interest

The authors declare no conflict of interest.

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