

# Plant Secondary Metabolite Diversity and Species Interactions

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## Keywords

plant–insect interactions, plant defenses, pollination, information theory, chemical information, herbivory

## Abstract

Ever since the first plant secondary metabolites (PSMs) were isolated and identified, questions about their ecological functions and diversity have been raised. Recent advances in analytical chemistry and complex data computation, as well as progress in chemical ecology from mechanistic to functional and evolutionary questions, open a new box of hypotheses. Addressing these hypotheses includes the measurement of complex traits, such as chemodiversity, in a context-dependent manner and allows for a deeper understanding of the multifunctionality and functional redundancy of PSMs. Here we review a hypothesis framework that addresses PSM diversity on multiple ecological levels ( $\alpha$ ,  $\beta$ , and  $\gamma$  chemodiversity), its variation in space and time, and the potential agents of natural selection. We use the concept of chemical information transfer as mediator of antagonistic and mutualistic interaction to interpret functional and microevolutionary studies and create a hypothesis framework for understanding chemodiversity as a factor driving ecological processes.

## 1. INTRODUCTION

Humans have utilized the diversity of plant secondary metabolites (PSMs) for thousands of years in medicine and pharmacology, but targeted analysis started only approximately 200 years ago with the isolation of morphine from the opium poppy, *Papaver somniferum* (Hartmann 2007). PSMs were differentiated from primary metabolites in that they “are formed during metabolism but . . . are no longer used in the formation of new cells” and their “importance . . . for the inner economy [primary metabolism] of the plant” (definition of secondary metabolites) (Sachs 1873, p. 541) is relatively minor. Although the initial isolation and identification of PSMs was driven by knowledge about their pharmacological functionality, they were, until the late 1950s, largely considered as detoxification or waste products of primary metabolism (Paech 1950, Reznik 1960) with only accidental biological function. In reflections on the history of the study of plant chemistry, Hartmann (2007) pointed out that biologists studying plant-herbivore-interactions had eventually suggested important biological functions of PSMs (Fraenkel 1959, Ehrlich & Raven 1964) and so laid the basis for the field of chemical ecology (Raguso et al. 2015).

At present, an estimated 200,000 PSMs have been isolated and identified. Although this number seems large, it is actually small relative to the approximately 391,000 described plant species, of which nearly 369,000 (94%) are vascular plants (Willis 2017). In a more specific example, 990 plant species have been analyzed for their floral emissions, and only approximately 1,720 compounds belonging to seven major compound classes have been isolated and identified from the floral headspace (Knudsen et al. 2006). The relatively low number of described PSMs is partly because the isolation, structural description and categorization of PSMs started much later than did the categorization of plants, and only a relatively small proportion of plants have been profiled (Hartmann 2007). However, most compounds and compound classes are widely expressed among members of different plant phyla. For example, terpenes (isoprenes) form one of the most diverse compound classes, are the major components of floral and vegetative volatile compound emissions, and have various ecological functions (Raguso 2008, Schiestl 2015). Some of those compounds such as  $\beta$ -caryophyllene, limonene, and linalool, together with the phenylpropanoids benzaldehyde and salicylic acid, are present in 50–70% of floral emissions of all plants studied (Knudsen et al. 2006). This strong overlap in plant metabolism among species as well as the often cited apparent paradox of PSM multifunctionality, on the one hand, and PSM functional redundancy, on the other (Kessler & Halitschke 2007), raises one of the longest-standing questions in the study of plant chemistry: Why do plants produce so many different compounds?

### 1.1. Biochemical Roots of Plant Secondary Metabolite Diversity

The proximate answer to why PSMs exhibit such great diversity is partially provided by advances in biochemistry and molecular biology. Researchers have hypothesized five major mechanisms that individually and multiplicatively contribute to biosynthetic diversity in individual plants and to differences in secondary metabolite bouquets among individuals and species.

1. Secondary metabolites are assembled from chemically simple precursors that derive from primary metabolism, which allows for a large number of possible combinations for those subunits. For example, two of the most diverse compound classes of terpenes and compounds containing aromatic rings derive from small isoprene or shikimate precursors, respectively (Dudareva et al. 2004).
2. Biosynthetic genes come in large gene families, and multiple genes usually encode functional enzymes of a similar type. For example, at least 32 genes in the *Arabidopsis* genome appear

to encode functional terpene synthases, which catalyze a diverse bouquet of hemi-, mono-, sesqui-, and diterpenes from common precursors (Tholl et al. 2005).

3. Some biosynthetic enzymes such as terpene synthases can produce multiple products out of the same precursor, and even small changes to the enzyme's active site can affect the proportional composition of the product bouquet (Köllner et al. 2004).
4. Modifying enzymes also come in large gene families, such as carboxyl methyl transferases and acetyltransferases, and can often use multiple substrates (Negre et al. 2003). This low substrate specificity may explain the rapid functional divergence of such enzymes (Pichersky et al. 2006) and may contribute to environmentally induced alterations in secondary metabolism.
5. Finally, spatially and temporally differential and organ-specific expression of biosynthetic genes can affect the diversity of compounds extractable from a plant (Dudareva et al. 2013, Pichersky et al. 2006). Thereby, the tissue-specific differential expression of secondary metabolite production can be adaptive by allowing plants to overcome conflicting effects of chemical information transfer, such as interactions with antagonists and mutualists mediated by the same information units (Kessler & Halitschke 2009).

## 1.2. Ecological Factors Driving Plant Secondary Metabolite Diversification

Since the early 1960s, PSMs were hypothesized as toxic, antidigestive, or antinutritive defense-mediating compounds (Ehrlich & Raven 1964, Fraenkel 1959) that repel approaching herbivores and/or reduce their quality as a resource (Duffey & Stout 1996) and so increase the fitness of plants (Kessler & Baldwin 2002). Furthermore, PSMs turned out to be inducible in response to environmental stresses, most notably to herbivory (Karban & Baldwin 1997). The induced metabolic changes, involving both primary and secondary metabolism, mediate changes in plant resistance to herbivores and transmit information to interacting organisms, such as neighboring plants, herbivores, and predators and parasitoids of herbivores (Dicke & Baldwin 2010, Heil & Karban 2010). These latter functions have been hypothesized mostly for herbivore-induced volatile organic compounds (VOCs) that, once emitted into the environment, provide ubiquitously available information on the physiological and metabolic status of the plant (Kessler 2015). Interestingly, Sprengel (1793), followed by Darwin (1862), had already proposed an ecological function of floral odors that attract pollinators and thus facilitate plant reproduction. Despite this early suggestion of a biological function for PSM, floral chemistry has only recently been recognized as a major mediator of species interactions that is also under selection by biological interactors (Adler 2000, Adler et al. 2012, Armbruster et al. 1997, Raguso 2008, Schiestl 2010).

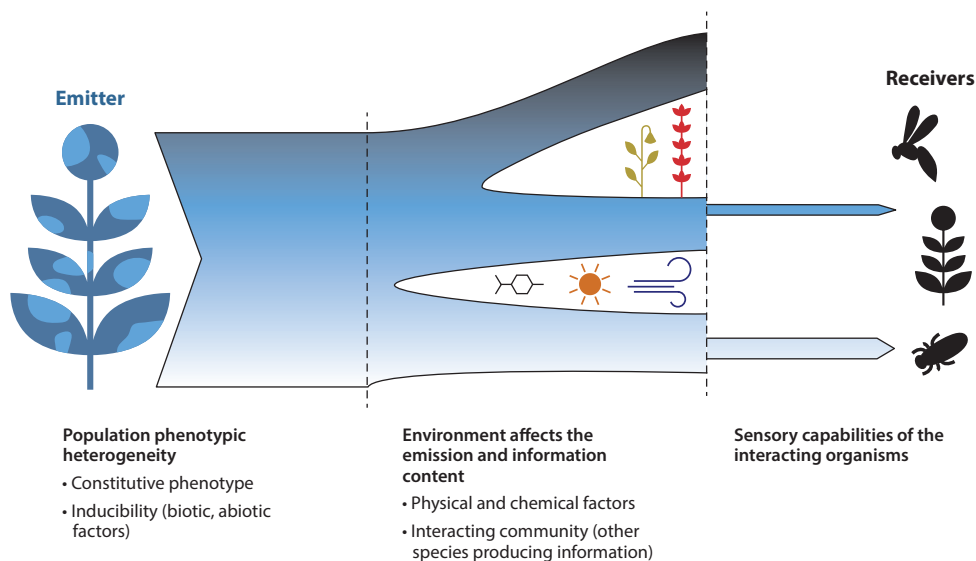
The current paradigm suggests a diversity of functions for PSM, ranging from allowing plants to cope with abiotic stresses (e.g., UV radiation, drought, heat) to mediating interactions with antagonists (e.g., herbivores, pathogens, neighboring plants) and mutualists (e.g., mycorrhizal fungi, rhizobium bacteria, predators/parasitoids of herbivores, pollinators) (Kessler & Halitschke 2007). Organisms interacting with plants can use bouquets of PSMs to identify appropriate hosts (Bruce & Pickett 2011); assess the physiological and metabolic state of the plant; and predict the presence of competitors, potential mates, antagonists, or, in the case of natural enemies of herbivores, the presence of prey/hosts (Kessler & Shiojiri 2016). By mediating these interactions, PSMs increase the arena in which interactions are played out from the cellular and plant level to the population and community level and so influence outcome and dynamics of ecological and evolutionary processes (Kessler & Baldwin 2002). Selection leading to microevolutionary changes in PSM composition and diversity can occur over only a few generations on timescales relevant to ecological interactions (Agrawal et al. 2012, Gervasi & Schiestl 2017, Uesugi & Kessler 2013).

While treating PSM production as information, we outline conflicting agents of natural selection and review the evidence for evolutionary and ecological processes related to PSM diversity at three levels ( $\alpha$ ,  $\beta$ , and  $\gamma$  chemodiversity).

## 2. PLANT CHEMISTRY AS INFORMATION AND EMERGING ECOLOGICAL CONFLICTS

### 2.1. Toxin, Repellant, and Detractant

Although information theory has long been applied to visual and auditory communication (Doyle 2009, McCowan et al. 1999), researchers have only recently begun to apply information theory to chemical information transfer (Kessler 2015, Wilson et al. 2015). Focused on understanding generation, transmission, storage, and processing of information (Shannon 1948), and applied to biological systems, information theory provides a framework to examine the effects of environmental and perceptual noise in shaping ecological interactions and the evolution of biological communication. Applying information theory to plant chemistry and to interactions with antagonists and mutualists means that any PSM can carry some information. It also implies that any compound not important in a specific transfer of information or any environmental alteration of the components of a signal can become noise that compromises the quality and transmission of information (Wilson et al. 2015) (**Figure 1**). Thus, the totality of PSMs produced by a plant or a plant population (fundamental chemical information space) and the proportion of PSMs that can be perceived by interactors (realized chemical information space), relative to the noise provided by



**Figure 1**

Chemical information and its noise. Communication system with plant as emitter of information, interacting antagonists and mutualists as receivers of information, and the environmental factors that compose noise in the transmission of chemical information. The noise altering the fundamental information emitted from a plant is composed of three categories that involve the population characteristics of the emitter, biotic and abiotic factors that alter the information content and provide the chemical context, and the sensory capabilities of the receiver organism.

the environment, determine which organism can interact with a plant by chemical means (Kessler 2015, Kessler & Shiojiri 2016).

Within this chemical information framework, PSMs can mediate direct defense of herbivores through three basic mechanisms, constituting three PSM categories.

1. Compounds can be toxic, antidiigestive, and antinutritive (direct chemical defenses), so in interacting with the availability of basic nutrients and physical defenses, they can reduce herbivore performance and affect plant fitness (Duffey & Stout 1996).
2. Compounds that are not directly harmful to herbivores can indicate bad food quality or limited accessibility, thereby repelling approaching herbivores (Bruce & Pickett 2011, De Moraes et al. 2001, Kessler & Baldwin 2001).
3. The presence or absence of particular compounds may render a bouquet of compounds incompatible with an herbivore's inherent or learned search pattern. As a result, they can detract attackers from a potential host plant (Hatano et al. 2015, Wright & Schiestl 2009).

All three mechanisms can theoretically be expressed constitutively and vary with plant genotype or species, or they can be phenotypically plastic and induced in response to previous damage by herbivores or other environmental stressors (Kessler & Baldwin 2002). Whereas compounds in category 1 directly affect herbivore performance and the outcome of interactions, those in categories 2 and 3 are exclusively chemical information that prevents direct interaction between plant and attacker. Thus, repellency (category 2) is based on an honest association between an existing direct chemical defense and a signal. By contrast, detractance (category 3) is based on the altered production of compounds that render host plant chemical information useless to an interacting organism (Kessler & Shiojiri 2016). This categorization results in a number of interesting hypotheses on the functional consequences of each of these mechanisms.

First, if we assume that preventing an initial attack (constitutive) and/or preventing subsequent attacks (inducible) to minimize damage is beneficial to plants, plants should advertise their defense status to the herbivore community. Such advertisement of plant defenses has been suggested for a number of physical defenses, including trichomes and thorns that feature aposematic coloration (Lev-Yadun 2009). Chemical aposematism, the use of chemical signals (e.g., VOCs) to advertise defenses and warn and repel approaching herbivores, has rarely been studied. A recent comparison of VOC emissions from 52 oak species found strong correlations between species identity and phylogenetic history, but not defense, which led the authors to reject the so-called aposematic fragrance hypothesis (Pearse et al. 2013). Although oaks may not be a group engaging in chemical aposematism or the wrong defense traits may have been measured as correlates with VOC emission (Pearse et al. 2013), these results raise interesting questions about the level (e.g., species, population, or community) at which such chemical aposematism can be expected. Resistance traits may vary in their efficiency in defending against different herbivore species such that resistance and defense become a function of the composition of the interacting community or identity of dominant herbivores (Poelman & Kessler 2016). Thus, chemical aposematism may evolve only in plant taxa with defense traits that efficiently exclude most of the fundamental community of antagonists that can affect plant fitness. In addition, herbivory-induced VOC emission can be viewed as fragrance aposematism when it is correlated with increased resistance and is functional in reducing subsequent herbivory (De Moraes et al. 2001, Kessler & Baldwin 2001).

Second, if herbivores use the complexity of chemical cues to guide their search for appropriate hosts (Bruce & Pickett 2011), plants can escape herbivory not only by evolving ever-new defense compounds (coevolutionary arms race and defense escalation) (Ehrlich & Raven 1964), but also by diverting chemical cues (information) away from a common host search pattern used by a potential herbivore. There are four basic mechanisms through which plants can alter the information

available and camouflage from herbivores. In the simplest form, plants could provide minimal cues and be invisible in an ocean of others. Such decreased attractiveness of less-emitting plants was observed in experiments with *Spodoptera frugiperda* caterpillars that preferred plants emitting herbivore-induced VOCs to less-emitting undamaged plants (Carroll et al. 2006). Similarly, the addition or subtraction of compounds to a composition of host search cues can render the information useless to a host-searching organism. Such an effect has been found in experiments with bumble bees, where the addition of individual compounds (1-hexanol) to floral VOC bouquets made bees avoid flowers in foraging (Wright & Schiestl 2009). In addition, lower attractiveness of plants lacking otherwise defensive feeding stimulants can be interpreted as evidence for the chemical camouflage hypothesis (Bartlett et al. 1996).

Third, plants can also produce compounds affecting the perceptibility of the host search cues, making the plant invisible to its attackers. A recent study of *Spodoptera littoralis* moths found that the herbivory-induced homoterpene (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) suppressed moth responses to otherwise attractive greenleaf VOC emissions [(*Z*)-3-hexenyl acetate] (Hatano et al. 2015).

Fourth, the chemical cues provided could mimic other plant species or organism and exclude a large proportion of the fundamental herbivore community. Decaying or fecal smells of food and brood-side deceptive flowers have been hypothesized as a mechanism to keep herbivores away (Lev-Yadun et al. 2009). However, we are not aware of examples of vegetative tissues emitting similar nonplant typical VOC bouquets, which would fully support a defensive function of this deceptive chemical information. There are also no clear examples of one plant species mimicking the chemical cues of a more defended plant species. However, there is an example of birch trees (*Betula* spp.) adsorbing and reemitting VOCs from neighboring *Rhododendron tomentosum* with resistance effects on birch herbivores (Himanen et al. 2010). This is a potentially common but rarely studied mechanism of associational resistance and a case of environmentally acquired chemical camouflage.

The ecological function of all four information-altering mechanisms as well as chemical aposematism are frequency dependent on both the population and the community level (see Section 4.2). Moreover, because of the ubiquitous availability of chemical information, different interactors using information differently can have conflicting effects on the plant and thus cause diffuse natural selection on the respective traits (Schiestl 2015). Moreover, chemical information is context dependent, and its value may vary with the biotic and abiotic circumstances.

## 2.2. Conflicting Functions of Chemical Information Exchange

Chemical information transfer can cause conflicts when the same information affects plant mutualists and antagonists simultaneously. The literature commonly refers to such effects as a type of ecological costs (Strauss et al. 2002). These costs are apparent with PSMs in general and plant VOCs in particular because of the ubiquitous availability of the information they encode (Kessler & Halitschke 2007). Conflicts at the ecological level can translate to divergent patterns of natural selection. Accordingly, conflicting selection on PSMs has been reported from interactions between generalist and specialist herbivores (Castillo et al. 2014, Lankau 2007), pollinators and herbivores (Knauer & Schiestl 2017), and two differently effective pollinators (Gervasi & Schiestl 2017) (Table 1). Large conflicts can also arise from crosstalk between plant signaling pathways that can make a plant responding to one attacker more vulnerable to another. Ecological costs resulting from phytohormone pathway crosstalk have been extensively discussed elsewhere (Bostock 2005, Koornneef et al. 2008, Pieterse & Dicke 2007). Thus, we focus on four major conflicting interactions that involve PSM-mediated information transfer.



**Table 1** Empirical evidence for selection acting on or being affected by the three levels of chemodiversity

Type of selection		Reference	Results	Level of chemodiversity relevant to selection <sup>a</sup>
Conflicting/divergent selection	Specialist and generalist herbivores	Lankau 2007	Generalist mollusks selected for higher sinigrin (allyl-glucosinolate) concentration in <i>Brassica nigra</i> ; specialist aphids ( <i>Brevicoryne brassicae</i> ) exerted stabilizing selection for intermediate sinigrin concentration	$\alpha$
		Castillo et al. 2014	Specialist beetles <i>Lema daturaphila</i> and generalist grasshoppers <i>Spbenarium purpurascens</i> , respectively, exerted negative and positive indirect selection on scopolamine (tropane alkaloid) in <i>Datura stramonium</i>	$\alpha$
	Herbivores and pollinators	Knauer & Schiestl 2017	Bumble bees ( <i>Bombus terrestris</i> , pollinator) and cabbage butterflies ( <i>Pieris brassicae</i> , pollinator and herbivore) caused conflicting selection on floral volatile phenylacetaldehyde in <i>Brassica rapa</i>	$\alpha$
	Two pollinators	Gervasi & Schiestl 2017	Bumble bees ( <i>B. terrestris</i> ) and hoverflies ( <i>Episyrphus balteatus</i> ) caused divergent selection on three floral volatiles (methyl benzoate, <i>p</i> -anisaldehyde, benzyl nitrile) in <i>B. rapa</i>	$\alpha$
Disruptive selection		Johnson et al. 2009	Disruptive selection on quercetin glucuronide (flavonoid) in <i>Oenothera biennis</i> under ambient herbivory	$\alpha$
G × E	Genotypic variation of the population affects selection	Parker et al. 2010	Deer herbivory selected for lower total shoot phenolics in a genetically diverse <i>O. biennis</i> neighborhood but not in monocultures	$\beta$
	Neighboring species modify selection on traits	Lankau & Strauss 2007	Selection on sinigrin (allyl-glucosinolate) in <i>B. nigra</i> was positive in a community dominated by heterospecifics and switched to negative when community was dominated by conspecifics	$\gamma$
		Lankau & Strauss 2008	Direction and intensity of selection on sinigrin (allyl-glucosinolate) in <i>B. nigra</i> varied depending on identity of neighboring plants and presence of specialist and generalist herbivores (mollusks and aphids)	$\gamma$
Balancing selection		Kroymann et al. 2003	Detection of balancing selection for insect resistance conferring <i>GS-Elong MAM2</i> gene (methylthioalkylmalate synthase) among different <i>Arabidopsis thaliana</i> ecotypes	$\alpha$

Examples include phenotypic selection and molecular studies.

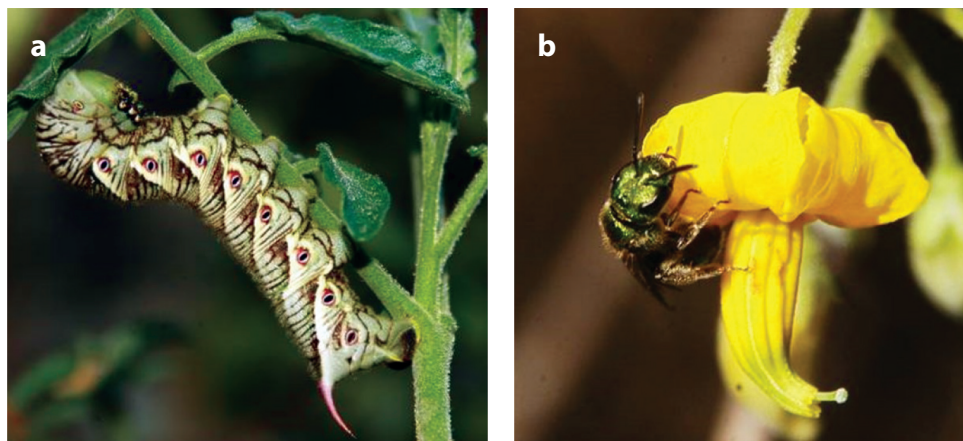
<sup>a</sup>Lowest or most relevant level of chemodiversity for corresponding example is identified, where applicable. Selection outcome can affect all levels of chemodiversity.

**2.2.1. Conflict between direct and indirect defense.** Indirect plant defenses are traits that reduce herbivory through the facilitation of third trophic level interactions and benefit the plant. There are two major categories of indirect defenses: resource mediated (e.g., extrafloral nectaries, food bodies, and shelter in ant plants) and information mediated (e.g., herbivore-induced VOC emission) (Kessler & Heil 2011). Because our review focuses on PSMs, we concentrate on information-mediated indirect defenses. Multiple plant systems have shown herbivore-induced VOC emission attracts natural enemies, such as predators and parasitoids of herbivores (Dicke & Baldwin 2010). Typically, herbivore-induced VOC emission is part of a plant's transcriptional and metabolic reconfiguration, so herbivore-induced direct resistance is commonly found accompanying changes in the plant's fragrance after herbivore attack (Kessler & Baldwin 2002). Therefore, induced direct defensive traits can negatively affect indirect defense function either by immediately affecting predators and parasitoids or secondarily through plant defensive compounds sequestered by potential prey or hosts (Barbosa et al. 1991). Moreover, induced VOC emission may not only attract natural enemies of herbivores, but also make plants more apparent to herbivores. Indeed, there are numerous cases in which herbivores are attracted to induced VOC emission and may even use it as an aggregation cue (Carroll et al. 2006, Raffa 2001). Thus, although previously damaged plants may be less susceptible to herbivores and may come with higher predation pressure, the ease with which they are found can override the potential costs for a host-searching herbivore (Carroll et al. 2006). However, there are also multiple examples in which herbivores use induced VOC emission to avoid plants of poor quality and high predation pressure. In these cases, herbivore repellency and predator attraction synergistically reduce the plant's herbivore load (De Moraes et al. 2001, Kessler & Baldwin 2001). However, new studies on the effects herbivore-induced VOC emissions from cabbage plants have on hyperparasitoids suggest that effects at the fourth trophic level can cancel out those at the third trophic level (parasitoid) and render indirect resistance ineffective (Poelman et al. 2012).

**2.2.2. Conflict among herbivore defense, pollination, and seed dispersal.** Various studies show that both herbivores (Agrawal et al. 2012, Berenbaum et al. 1986, Huber et al. 2016, Mauricio & Rausher 1997, Uesugi & Kessler 2013) and pollinators (Schiestl et al. 2011) function as agents of selection on the abundance and diversity of compounds. Floral fragrances or compounds contained in nectar and pollen affect the size and composition of a pollinator community capable of interacting with a plant, in the same way that vegetative secondary metabolism restricts the herbivore community interacting with a plant (Adler 2000, Raguso 2008). Recent studies found direct evidence that whole-plant-induced responses to herbivory can affect pollinator behavior and, consequently, plant fitness (**Figure 2**) (Kessler et al. 2011, Schiestl et al. 2014). Similarly, floral signals can make plants more apparent to herbivores or provide information about host plant quality to herbivores (Adler et al. 2006, Theis et al. 2014).

These observations have led to the hypothesis that the plant mating system (e.g., dependence on animal vectors of pollen, self-compatibility versus self-incompatibility) evolved in interaction with plant defense strategies (Kessler & Halitschke 2009). Support for this hypothesis comes from experiments with inbred and outbred lines of horsenettle *Solanum carolinense*. Inbred plant lines had a consistently lower secondary metabolite diversity, which was associated with reduced constitutive resistance to herbivores, the major cause of inbreeding depression in this system (Campbell et al. 2013). Interestingly, inducibility of resistance was also compromised in inbred plants versus outbred plants (Campbell et al. 2014). On a macroevolutionary level, comparison of 56 species in the Solanaceae family found a strong correlation between plant mating system and herbivore defense. Self-incompatible species had a higher constitutive resistance than did self-compatible species, which also showed a higher inducibility of resistance (Campbell & Kessler





**Figure 2**

Conflict between herbivore defense and pollination. (a) In the wild tomato *Solanum peruvianum*, leaf herbivory by herbivores such as hornworms *Manduca* sp. (Sphingidae) induces increased volatile organic compound (VOC) emission from both leaves and flowers. (b) Pollinators such as *Corynura* sp. (Halictidae) use induced VOC emission to avoid flowers on herbivore-damaged plants. This herbivory-induced pollinator limitation comes with fitness costs for the plant (Kessler et al. 2011), but models show it also reduces the probability of extinction for interacting populations (Glaum & Kessler 2017).

2013). Accordingly, inducibility of resistance has been hypothesized as one of the mechanisms to overcome the conflict between attracting pollinators and repelling herbivores, by producing compromising secondary metabolites only when needed, for example, in case of an actual herbivore attack. Other potential mechanisms include temporal separation of flowering from times of peak herbivory (Burdon et al. 2015, Parachnowitsch et al. 2012a), spatial and regulatory separation of floral and leaf secondary metabolism (private channel), and inducible changes in mating system (induced reproductive assurance) (Kessler & Halitschke 2009). Future research should investigate diversity, inducibility, and tissue compartmentalization of defensive and information-mediating secondary metabolite production as a function of mating system. Similar conclusions can be applied to the apparent conflict between plant chemical defenses and fruits/seed dispersal. As with flowers, the chemistry of fleshy fruit affects the community of potential seed dispersers (Whitehead & Bowers 2014), and leaf herbivory can affect fruit chemistry and seed dispersal (Whitehead & Poveda 2011).

**2.2.3. Mycorrhizal fungi and parasitic plants.** Another important example of a conflict mediated by plant chemical signaling is the belowground interaction of plants with mycorrhizal fungi and root-parasitic plants (Bouwmeester et al. 2007, López-Ráez et al. 2017). Plants depend on certain symbiotic interactions, for example, between legumes and rhizobacteria or between most plant taxa and mycorrhizal fungi. Both of these types of interactions are mediated through chemical signaling. For example, colonization of legume roots and the subsequent initiation of nodules by nitrogen-fixing rhizobacteria are triggered by plant-root-secreted flavonoids (Bais et al. 2006) and are also affected by other secondary metabolites (López-Ráez et al. 2017). Similarly, the interaction between plant roots and mycorrhizal fungi depends on diverse secondary metabolites, including strigolactones and terpene lactone carotenoid derivatives. These compounds are secreted by host roots and stimulate branching and growth of the fungus hyphae, thereby increasing the probability of plants coming into contact and establishing a symbiotic relationship with the fungus

(Akiyama et al. 2005, López-Ráez et al. 2009). The fungus can provide essential mineral nutrients and allow plants to be competitive in suboptimal environments (Harrison 2005, Karandashov & Bucher 2005). Arbuscular mycorrhizal fungi, in turn, depend on carbon provision by the plant (Bécard et al. 2004).

However, compounds like strigolactones also have phytohormonal properties (Gomez-Roldan et al. 2008, Umehara et al. 2008) and trigger germination and attachment of obligate parasitic plants of the genera *Striga* sp. (witchweeds) and *Orobancha* sp. (broomrapes) (Akiyama & Hayashi 2006). These root parasites can have devastating effects on plant fitness and yield in agricultural crops (Gressel et al. 2004). Parasitic plants (antagonists) benefit from a chemical cue that their hosts cannot live without, because it is used for another essential interaction with a mutualist (e.g., arbuscular mycorrhizal fungus). How plants overcome this apparent conflict associated with chemical signaling has not been addressed directly. However, production of strigolactone as well as other root exudates is reduced either when soil conditions make interactions with mycorrhizal fungi less important (Elias & Safir 1987, Nagahashi & Douds 2004) or when fungal arbuscules have already formed in plant roots (Bouwmeester et al. 2007, Gworgwor & Weber 2003, Lenzemo et al. 2005). Thus, plants can avoid attracting parasitic plants by emitting the revealing chemical signal only when needed and in response to an environmental stressor such as limited nutrient availability. Strong selection by parasitic plants should also promote private channel communication with the mutualist fungi.

**2.2.4. Competition and defenses against herbivores.** A special but potentially most common case of chemical signaling occurs between neighboring plants. The root exudates discussed above as well as the direct interaction between roots and aboveground tissues can affect plant growth and interaction with other organisms (Bais et al. 2006, Bouwmeester et al. 2007). To a large extent, this conflict between defending against fitness-reducing herbivores and pathogens and investing in competition with neighbors, better known as the “dilemma to grow or to defend” (Herms & Mattson 1992), has spurred much research into plant defenses in general (Stamp 2003). In addition, competing plants can use chemical information from their neighbors to gain an advantage. A prime example is the response of plants to VOCs emitted from herbivore- or pathogen-attacked neighbors. Exposure to a damaged-neighbor cue can prime or directly induce changes in receiver defense metabolism preparing them for a potentially oncoming antagonist (Heil & Karban 2010). This phenomenon has been observed in many plant species and is usually referred to as “eavesdropping” on a neighbor’s induced VOC cues. This assumes that only the receiver gains a benefit from the exchange of chemical information.

As in the examples above, plants could avoid the conflict of chemical information exchange by providing private channels of communication. Indeed, in one of the best-studied examples, sagebrush (*Artemisia tridentata*) plants respond only to volatiles emitted from herbivore-attacked close relatives but not to those from distant relatives. Thus, information exchange is highly specific to the plant genotype, not necessarily to the attacking herbivore (**Figure 3**) (Karbon et al. 2013). Furthermore, relatively high chemotype diversity should be maintained at the population level, which was found in the *A. tridentata* system, thus supporting the eavesdropping hypothesis (Karbon et al. 2014).

In contrast to eavesdropping, a mutual benefit would result if information transfer between two or more plants helps spread the risk of herbivory evenly across the plant population, with each individual receiving minimal damage. A similar benefit would result from the initially damaged plant creating via VOC communication a patch of resistant plants into which it is less likely for an herbivore to enter. In this case, chemical information shared should be under selection to be universally “understandable” (open channel of communication) among members of a population,



**Figure 3**

Conflict between competition and herbivore defense. (a) Volatiles emitted from clipped sagebrush *Artemisia tridentata* induce strong herbivore resistance in close kin but not in nonkin neighbors (private channel). This accords with the hypothesis that plants eavesdrop on their neighbor's chemical wound signal to prepare for oncoming herbivores (Karban et al. 2013). (b) In contrast, in tall goldenrod *Solidago altissima*, both emitters and receivers seem to benefit from sharing chemical information about oncoming herbivory via herbivore-induced volatile organic compounds (Morrell & Kessler 2017, Rubin et al. 2015). This observation supports the hypothesis of mutual benefit from sharing chemical information.

thus converging on a common language. Although more specific studies are needed, recent experiments on tall goldenrod *Solidago altissima* (Figure 3) found a risk-spreading effect of chemical information exchange between plants (Morrell & Kessler 2017, Rubin et al. 2015). Moreover, chemical information becomes more similar upon induction among plants within a population (Morrell & Kessler 2017, Uesugi et al. 2013), which accords with the prediction of selection for a common language.

### 3. PLANT SECONDARY METABOLITES AS TARGETS OF NATURAL SELECTION

Two hypotheses have been proposed to explain the high diversity of PSMs found in most plants. The screening hypothesis by Jones & Firn (1991) posits that a diverse profile of biologically inactive, inexpensive compounds increases the likelihood of evolving active compounds. Natural selection “screens” the array of inactive compounds for biologically active compounds. This hypothesis was likely derived from the notion that PSMs are first and foremost by-products of primary metabolism; it also addressed the mechanism of generating compound diversity, rather than compound function. Recent studies found that genes encoding PSM pathways are grouped in biosynthetic gene clusters, which suggests strong selection on efficient, functional compound production that is not derived from a simple breakdown process (Nützmann et al. 2016).

Another widely cited hypothesis suggests that PSM diversity is beneficial in a diverse abiotic and biotic environment (Berenbaum & Zangerl 1996). According to this “interaction diversity” hypothesis, interacting with a diverse community of mutualists and antagonists selects plants for a diverse suite of PSMs. The ecological consequences of potential ecological conflicts involving the PSMs discussed in Section 2.2 provide potential selection scenarios in line with the interaction

diversity hypothesis. In a more specific example, elevated chemical diversity in *Piper* species was associated with a more diverse and more specialized community of herbivores and lower overall damage (Richards et al. 2015).

A frequently discussed expression of the diversity hypothesis is compound synergism, where the effectiveness of a defense compound increases in the presence of another (Berenbaum & Zangerl 1991, McKey 1979). In one of the first examples of synergism, Berenbaum & Neal (1985) showed that myristicin radically enhances the toxicity of xanthotoxin against the moth *Helicoverpa zea*. Similar effects have subsequently been demonstrated in other study systems (Dyer et al. 2003, Leckie et al. 2016, Steppuhn & Baldwin 2007). Synergistic effects can also be specific to herbivore species or type. Meta-analyses suggest that synergistic effects of secondary metabolites are effective more often against generalist than specialist insect herbivores (Richards et al. 2016).

### 3.1. Evolvability of Plant Chemical Diversity

Heritability of chemical traits in plants, in general, is high compared with morphological, phenological, and life-history traits (Geber & Griffen 2003). For chemical traits, high heritability likely reflects high evolvability (Moore et al. 2014), even though measures of heritability can be sensitive to environmental variation (Houle 1992). High or moderate estimates of heritability of PSM production have been found for all plant tissues studied, including leaves (Agrawal 2005, Berenbaum et al. 1986, Delphia et al. 2009, Johnson et al. 2009, Karban et al. 2014, Zangerl & Berenbaum 1990), roots (Parker et al. 2010, Van Dam & Vrieling 1994), woody stems (Moreira et al. 2013), seeds (Berenbaum et al. 1986, Zangerl & Berenbaum 1997), flowers (Zu et al. 2016), and fruits (Rowan et al. 2009). The high variability and ease of diversification of PSMs may contribute to high heritabilities and suggests there is ample genetic variation available for selection.

Compared with other traits affecting herbivore preference and performance, such as morphological or life-history traits, PSMs may be under weak evolutionary constraints (Carmona et al. 2011, Hartmann 2007). Accordingly, relatively weak selection can lead to adaptive changes when evolutionary constraints are not limiting the response to selection, thus contributing to high PSM diversity. Consistent with this hypothesis, macroevolutionary comparison of *Inga* species showed that chemical defense traits had evolved independently of developmental (leaf expansion rate and chlorophyll content) and indirect ant defenses (Kursar et al. 2009). However, it is unclear whether the weak constraints are universally true, as PSM traits can be genetically linked to other plant traits. For example, selection for increased and decreased iridoid glycosides in *Plantago lanceolata* resulted in correlated changes in plant size over four generations (Marak et al. 2000). Similarly, in *Brassica rapa*, artificial selection for height caused changes in floral scent and leaf glucosinolates (Zu & Schiestl 2017). Furthermore, pleiotropic effects among secondary metabolites are relatively common (Zu et al. 2016). Recent transcriptome analyses revealed that selection for particular scent compounds resulted in upregulation of genes upstream from the metabolic pathways (Cai et al. 2016). Despite pleiotropic effects and linkage disequilibrium, PSM evolution may still be relatively free of constraints because of lower production costs, relative to those associated with structural and phenological traits (Cai et al. 2016).

### 3.2. Evidence for Rapid Evolution of Plant Secondary Metabolites

Rapid evolution can result in changes within populations over time spans of less than 100 years or 10 generations, making it a potentially important contributor to the outcome of ecological interactions (Thompson 1998). Owing to their high diversity, heritability, and measures of phenotypic selection, PSMs may be highly evolvable, making them good candidates for rapidly evolving traits.



Artificial selection studies have shown that selection can result in increases and decreases in non-volatile leaf PSM or floral volatile production over only 2–4 generations (Lankau & Kliebenstein 2009, Lankau & Strauss 2007, Marak et al. 2000, Siemsen & Mitchell-Olds 1998, Siemsen et al. 2002, Zu et al. 2016). Some selected plant lines have also been used to confirm the realized defensive as well as other functions of the target metabolites (e.g., Biere et al. 2004, Marak et al. 2000).

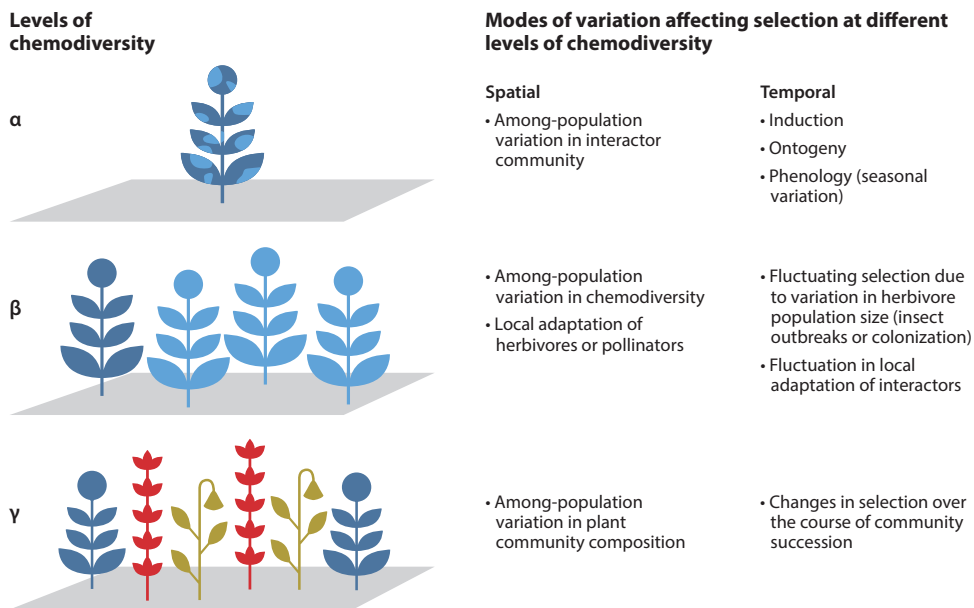
Over the past decade, long-term experimental evolutionary studies manipulating the agent of selection have demonstrated rapid evolution of PSMs in response to herbivores and pollinators. These studies are valuable in demonstrating that rapid evolutionary changes occur in PSMs. They are also important in identifying the selective agents and discovering some of the secondary effects of manipulating those agents. Generalist and specialist aphid selection regimes resulted in different proportions of glucosinolate chemotypes in *Arabidopsis thaliana* over 5 generations (Züst et al. 2012). Similarly, multiyear insect removal treatments resulted in a decline in fruit ellagitannin concentration in *Oenothera biennis* (Agrawal et al. 2012) and altered the leaf diterpene acid and phenolic compound concentrations in *S. altissima* (Uesugi et al. 2016, 2017). Floral volatile bouquets in *B. rapa* evolved several differences in bumble bee and hoverfly pollination selection treatments after 11 generations (Gervasi & Schiestl 2017). As evident from these studies, PSM diversity can be maintained through selection by herbivores and pollinators, and ecological interactions can drive rapid evolutionary changes in PSM production. Nevertheless, several other potential sources of selection on PSMs as well as the conditions that promote the observed high diversity of PSMs remain to be tested (Züst et al. 2012).

## 4. FUNCTIONAL LEVELS OF PLANT CHEMODIVERSITY

In biodiversity research, three functional levels of diversity can be differentiated (Whittaker 1972). Whereas  $\alpha$  diversity describes the mean species diversity at a local scale,  $\beta$  diversity describes the species turnover from one to another community as the ratio between regional and local species diversity. Treated either as the product or the sum of  $\alpha$  and  $\beta$ ,  $\gamma$  diversity describes the total species diversity in a landscape. Moore et al. (2014) proposed a similar categorization of PSM diversity to describe the levels at which compound diversity could be measured and is likely functional. Accordingly,  $\alpha$  diversity describes compound diversity of a single sampling unit, a single plant, or even only a specific tissue, whereas  $\beta$  diversity describes the differences in compound diversity among different individual units, and thus the diversity of plant chemotypes within a population (Moore et al. 2014). Different from Moore et al. (2014), we define  $\gamma$  diversity as the total diversity of compounds of all plant populations within a plant community, analogous to the species diversity of all habitats within a landscape. We propose this change to the original use of the different levels of compound diversity to evaluate the functionality of PSM diversity from the perspective of the interacting organism and so as a trait that is under differential selection, depending on the chemical context in which a population of chemotypes is presented (**Figure 4**).

### 4.1. $\alpha$ Chemodiversity

PSM  $\alpha$  diversity is foremost a function of the biochemical properties of a plant. However, compound multifunctionality, on the one hand, and the complexity of ecological communities, on the other, are likely the main drivers maintaining  $\alpha$  chemodiversity. It can be under positive selection if compound diversity per se is functional through additive and/or synergistic effects. Or, it can be under negative selection if only certain individual compounds are functional and the costs of secondary metabolite production high. Disruptive selection acts to increase variation in a trait under selection. Johnson et al. (2009) reported disruptive selection on a flavonoid compound, quercetin



**Figure 4**

Modes of spatial and temporal variation affecting natural selection on plant chemodiversity at different levels.

glucuronide, in *O. biennis* (Table 1). Depending on the magnitude of ubiquity of the information or effects thereof, selection can vary from specific to diffuse. Accordingly, the more private the communication channel is, the lower the compound diversity of the perceptible proportion of the signal. For example, deceptive orchids of the genera *Ophrys* and *Chiloglottis* can rely on a very small number of compounds that mimic the sex pheromone blends of their pollinators (Schiestl 2005). The reverse could be true if multiple interacting species select for different traits, analogous to multiple communication channels. This could result from conflicting selection on the same traits or differential selection on multiple traits, both of which occur in either plant-herbivore or plant-pollinator interactions (Table 1). In both cases, a major prediction of this hypothesis of diffuse selection is that chemical diversity is a function of the diversity of interactions, mediated by PSM traits. To our knowledge, no direct tests of these predictions have been conducted. However, positive correlations between PSM diversity and associated arthropod community diversity strongly supporting this hypothesis were recently found in *Piper* spp. (Richards et al. 2015).

## 4.2. $\beta$ Chemodiversity

As a reflection of the number of plant chemotypes found in a population,  $\beta$  diversity raises the question of which mechanisms maintain phenotypic diversity within a population. Spatial and temporal heterogeneity of the environment allows differential fitness for different phenotypes and promotes the maintenance of high genetic diversity through  $G \times E$  interactions (Moore et al. 2014). Furthermore, the genotypic and chemotypic diversity of the population can affect selection for PSM diversity. Parker et al. (2010) showed that deer selection on shoot phenolic production in *O. biennis* depends on the genotypic diversity of the experimental population (Table 1).

Similarly, frequency-dependent selection associated with the local adaptation of interactors can explain the maintenance of PSM  $\beta$  diversity. In antagonistic interactions, uncommon phenotypes



can benefit through negative frequency-dependent selection. There is some evidence for negative frequency-dependent selection acting in plant systems in mechanical defense traits and floral traits. Rare trichome morphs had an advantage in *Arabidopsis balleri* subsp. *gemmifera* when herbivores were present (Sato et al. 2017), owing to the feeding choice of the flea beetle *Phaedon brassicae* (Sato & Kudoh 2017). Other studies have reported rare morph advantages in floral display (Ågren et al. 2013) and seedling survival, which also promoted genetic diversity (Browne & Karubian 2016). There is still little experimental evidence for maintenance of chemical diversity through density-dependent selection in natural populations. However, local adaptations of herbivores to host plant chemistry are certainly an important prediction of this hypothesis and have been demonstrated in some study systems (Garrido et al. 2012, Laukkanen et al. 2012).

Under the chemical information framework, plants can benefit from maximizing the noise due to their differences and distort search patterns commonly used by interacting organisms such as herbivores (Bruce & Pickett 2011). The resulting  $\beta$  chemodiversity of such populations is then expected to be larger and the covariation between compounds in a blend (or phenotypic integration) lower than in populations without the selecting agent (e.g., herbivore), and local adaptation patterns should be minimal. This chemical noise or chemical camouflage hypothesis is mechanistically related to the so-called moving target hypothesis used to explain the evolution of induced responses to herbivory (Adler & Karban 1994). Phenotypic plasticity to previous damage, to VOCs from neighboring plants, or to any environmental factor makes plants unpredictable food sources, a moving target for attackers that frequently need to adjust their digestive metabolism to changes in food quality. In either hypothesis, phenotypic change or population-level phenotypic differences, respectively, in secondary metabolism are effective in mediating resistance rather than the production of toxic metabolites (Adler & Karban 1994).

Both variable selection and the frequency-dependent selection hypothesis could explain the maintenance of genotypic and phenotypic chemical diversity within plant populations. Interestingly, both hypotheses also provide clear predictions for the evolution of inducibility. Population-level PSM patterns of induced plants should be more dissimilar (higher  $\beta$  diversity), and have lower phenotypic integration, than those of undamaged plants. Phenotypic integration has rarely been measured for secondary metabolism traits. However, a recent meta-analysis of phenotypic integration of VOC profiles from different plant tissues and across multiple study systems found partial support for the above hypotheses. For example, phenotypic integration was, on average, smaller (or  $\beta$  diversity higher) for herbivore-induced VOC bouquets than among undamaged plants (Junker et al. 2017). Thus, induced VOC emission may function primarily as a deterrent, rather than being involved in indirect resistance or as a chemical aposematism (Kessler & Heil 2011).

The chemical noise-maximizing mechanisms described above could work well in keeping away interactors, but they would be very disruptive when information exchange is beneficial for the plant, such as when attracting pollinators or for agents mediating indirect resistance. In such interactions or if plants benefitted from advertising bad food quality (chemical aposematism), we would likely observe positive frequency-dependent natural selection toward a common communication phenotype (a common chemical language) (Raguso & Kessler 2017) and, thus, increased population-level phenotypic integration. A recent analysis of herbivore-induced VOC emission in *S. altissima* found higher phenotypic integration among herbivore-damaged plants, thus supporting the hypothesis of functional chemical information transfer (Morrell & Kessler 2017). In this system, induced VOC emission and the associated information transfer from plant to herbivore and from plant to plant strongly impact the distribution of herbivores within the population (Rubin et al. 2015).

Similarly, chemically mediated interactions with mutualists, such as pollinators, are likely to select for private population-level communication channels. For example, high pollinator constancy is expected to select for common local interaction phenotypes in a positive

frequency-dependent manner, as described for local patterns of floral VOC emission in *Penstemon digitalis* (Parachnowitsch et al. 2012b). Although reduced at the local scale,  $\beta$  chemodiversity via this mechanism may be dramatically increased for the meta-population owing to larger differences between populations. This may also explain why a recent meta-analysis found lower average phenotypic integration in floral versus leaf VOC emission (Junker et al. 2017). Moreover, natural selection can act only on chemical information that is perceived and processed by the respective agent of natural selection. In particular, with respect to private channel communication, only the neurophysiologically perceivable proportion of a secondary metabolite bouquet may follow these patterns (Bruce & Pickett 2011).

### 4.3. $\gamma$ Chemodiversity

If the specific information space occupied by an individual plant or a population of plants determines the realized community of interacting organisms, the more or less overlapping chemical information space of neighboring plant species composes the biotic environmental noise that can affect the outcome of interactions (Wilson et al. 2015). As with  $\beta$  chemodiversity,  $\gamma$  diversity allows plants to advertise their qualities to potential interactors or remain relatively undetectable within the noise of a diverse environment. Broadly, this would include associational resistance and susceptibility effects that are mediated by chemical traits (Barbosa et al. 2009, Root 1973). The more common, or more apparent, a species is in its community, the less noise should impact its communication systems. Furthermore, the strength of natural selection on chemical communication by antagonists should increase the more dominant a species becomes. Accordingly, Glassmire et al. (2016) showed that *Piper kelleyi* plants surrounded by a greater diversity of other *Piper* species had lower phytochemical defenses. Two studies on *Brassica nigra* suggest a role for community diversity or intraspecific neighbors in selection on phytochemical defense: Selection on sinigrin changed from negative to positive as the proportion of heterospecifics in the proximity of the focal plant increased (Lankau & Strauss 2007), and intraspecific competition modified selection by generalist and specialist herbivores on sinigrin concentration (Lankau & Strauss 2008) (**Table 1**). Although these studies did not explicitly manipulate the chemodiversity of the community, their results are consistent with the hypothesis that variation in chemodiversity due to diversity of heterospecifics can modify selection on one species.

Although rare species can benefit disproportionately from associational resistance or autotoxicity (Speed et al. 2012), they may also face a problem attracting certain interactors, such as mutualists, through chemical communication. For example, rarity disadvantage due to pollinator-mediated competition has been observed for *Limnanthes douglasii* subsp. *rosea* in the presence of its congener *Limnanthes alba* (Runquist & Stanton 2013). Such competitive interactions can result in differential natural selection on floral traits as a function of frequency and apparency of coflowering communities (Wassink & Caruso 2013). Even though this selection has not been observed for plant chemical cues, floral scent is frequently suggested as one of the major traits under selection by interactors (Geber & Moeller 2006, Raguso 2008), and at least one study on *P. digitalis* found it was under similar or stronger natural selection than were morphological flower traits (Parachnowitsch et al. 2012b).

## 5. PLANT-INDUCED RESPONSES: TEMPORAL VARIATION IN CHEMODIVERSITY

The great genetic diversity of PSMs within and across individuals underlies induced changes following biotic interactions such as herbivory (Dicke & Baldwin 2010, Karban & Baldwin 1997)

and pollination (Kessler & Halitschke 2009). This induction increases PSM diversity in time, which may be one reason induction is beneficial as plants become “moving targets” for their enemies (Adler & Karban 1994). Increased variability in food quality for herbivores following induction can function as an added defense, and recent studies illustrate the importance of PSM variability on herbivore performance (Pearse et al. 2018, Wetzel & Thaler 2016). Induction can result in greater  $\alpha$  chemodiversity if induced responses to herbivory are highly localized (Kurban 2011). Accordingly, induced variation in glucosinolate concentrations between leaves within individuals was greater than was variation among individuals in wild radish *Raphanus raphanistrum* (Shelton 2005). Furthermore, lower phenotypic integration of the volatile bouquet in induced versus control plants in a multispecies comparison (Junker et al. 2017) suggests that induction may increase both  $\alpha$  and  $\beta$  chemodiversity.

Temporal increase in chemodiversity upon induction can expose genetic variation to selection that is not observed in the constitutive state. Wild radish exhibits high and significant heritability for glucosinolates only in damaged plants (Agrawal et al. 2002). There are also multiple examples for adaptive variation in inducibility (Moreira et al. 2013, Van Dam & Vrieling 1994, Zangerl & Berenbaum 1990). In a macroevolutionary comparison of milkweeds (*Asclepias* spp.), induction of toxic cardenolides was highest in plants from lower latitudes, suggesting that selection for induction increases with the intensity of biotic interactions (Rasmann & Agrawal 2011). The evidence for induction as an alternative to high constitutive PSM diversity is equivocal. In a phylogenetic comparison of Solanaceae, induced and constitutive resistances were negatively correlated (Campbell & Kessler 2013), and higher constitutive phenolic compound diversity conferred higher resistance in one species (Campbell et al. 2013). However, in milkweeds, highly inducible species produced constitutively more diverse and more toxic cardenolides (Rasmann & Agrawal 2011).

## 6. CONCLUSION

Although new advances in analytical chemistry, metabolomics, and complex data computation (Hartmann 2007) increasingly allow us to treat PSM diversity much like individual traits with high sample throughput, the hypothesis framework needs to be adapted. What we have compiled here makes it possible to address functional hypotheses on compound diversity by treating plant chemistry in an information theory framework. All the hypotheses presented above focus on how chemodiversity on three levels ( $\alpha$ ,  $\beta$ ,  $\gamma$ ) (**Figure 4**) affects interactions between organisms. The large question emerging from this framework regards how far chemical information, in particular, and information exchange, in general, between organisms affect population and community dynamics and, thus, ecosystem processes. Does consideration of information transfer change our views on how populations and communities are structured and persist? For example, a recent game theory model broadly applied the concept of ownership to biological systems. Within this framework, active prevention of competition can be understood as making a contract about owning a resource (Hare et al. 2016). Such contracts have to be mediated by direct exchange of information between interactors. Plants seem to use chemical handshakes to recognize kin and consequently do not compete for resources (make an ownership contract) with close relatives (Biedrzycki & Bais 2010, Dudley & File 2007). Such chemically mediated active avoidance of competition could be far more common and expand beyond kin, potentially selecting for optimal neighborhoods within populations and communities.

Similarly, the induction of PSMs in response to environmental stresses and associated direct or indirect resistance to herbivores can affect the realized carrying capacity of plant populations as a resource, thereby affecting outbreak cycles of attacking herbivores (Kessler et al. 2012, Stieha et al. 2016). By contrast, the use of the same chemical information across multiple trophic levels

can cancel out effects on plant fitness (Poelman et al. 2012) or stabilize interacting populations (Figure 2) (Glaum & Kessler 2017). Understanding the relative importance of such processes is not only important for understanding the ecological dynamics of natural systems, but also helpful for optimizing biocontrol technologies through the targeted manipulation of information transfer between plants and their antagonists and mutualists to maximize yield (Pickett & Khan 2016).

## DISCLOSURE STATEMENT

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