

The raison d'être of chemical ecology

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Abstract. Chemical ecology is a mechanistic approach to understanding the causes and consequences of species interactions, distribution, abundance, and diversity. The promise of chemical ecology stems from its potential to provide causal mechanisms that further our understanding of ecological interactions and allow us to more effectively manipulate managed systems. Founded on the notion that all organisms use endogenous hormones and chemical compounds that mediate interactions, chemical ecology has flourished over the past 50 years since its origin. In this essay we highlight the breadth of chemical ecology, from its historical focus on pheromonal communication, plant–insect interactions, and coevolution to frontier themes including community and ecosystem effects of chemically mediated species interactions. Emerging approaches including the -omics, phylogenetic ecology, the form and function of microbiomes, and network analysis, as well as emerging challenges (e.g., sustainable agriculture and public health) are guiding current growth of this field. Nonetheless, the directions and approaches we advocate for the future are grounded in classic ecological theories and hypotheses that continue to motivate our broader discipline.

Key words: *biological control; community and ecosystems ecology; genomics; indirect effects; information transfer; mechanisms of species interactions; mutualisms; nonconsumptive effects; signals; toxins.*

INTRODUCTION

As *chemical ecologists*, we seek to understand how the distribution and abundance of organisms, as well as their complex interactions, mutualism and parasitism, predator–prey cycles, community assembly, are mediated by chemical agents across different spatial and temporal scales. The organic compounds that comprise these agents, such as signals, cues, toxins, anti-nutritives, resins, inks, latex, and other chemical contrivances, represent a vast biochemical space that includes molecules of diverse size, polarity, mode of action, and biosynthetic origin. From its birth as a field, chemical ecology has always had a strong interdisciplinary flavor. The rigorous identification of causal chemical agents requires sophisticated analytical techniques, whereas the

careful demonstration of their ecological functions demands the use of manipulative experiments, typically in the form of iterative “bioassay-guided fractionation” (Whittaker and Feeny 1971, Harborne 1993), and more recently in the form of genetic manipulation of trait expression (Baldwin 2010). This combination of approaches has been crucial in documenting the chemical mediation of species interactions in both model and non-model systems in ecology.

Chemical ecologists continue to break new scientific ground, from the identification of chemically novel substances produced in biofilms of marine bacteria that trigger the larval settlement and metamorphosis of larval biofouling tubeworms (Shikuma et al. 2014) to the demonstration that mice infected with malarial parasites emit a different suite of volatile compounds, which are more attractive to the mosquito vectors of this disease (De Moraes et al. 2014). Thus, in addition to identifying novel bioactive molecules, chemical ecologists utilize strong-inference to identify causative agents and their ecological functions, a logical approach that provides a necessary counterpoise to the immense, untargeted data sets being generated in the present informatics age (Pickett 2014). Thus, the explanatory power, and

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promise, of chemical ecology as a discipline stems from its potential to provide tangible mechanisms where conventional ecological approaches might simply indicate patterns, “effects,” or the context-dependency of specific interactions (Schoener 1986, Peacor and Werner 2001).

In the last two decades, new technical and conceptual tools have enabled chemical ecologists to integrate studies of the functional analysis of chemical traits, on multiple organizational levels, with studies of fundamental evolutionary questions. At the same time chemical ecology has expanded from a largely terrestrial, insect–plant biased enterprise concerned with pheromone chemistry, predator avoidance, and plant–herbivore coevolution, to a global exploration of multi-trophic interactions, including mutualism, across all ecosystems and domains of life. Increasingly, the study of chemical ecology has embraced the multi-organismal reality of such interactions (Raffa et al. 2008, Stallforth et al. 2013). We anticipate continued and fundamental changes as phylogenetics and comparative genomics, systems biology, metabolic engineering, and neuroscience provide a new generation of tools with which to explore chemically mediated interactions between organisms (Kang and Baldwin 2008).

In this essay, we discuss the conceptual foundations of chemical ecology and their potential to elucidate important mechanisms in natural and human-modified ecosystems across the full range of subjects relevant to the readers of *Ecology*. First, we address the information content of natural products by considering the universal recognition of key signals and cues by biological systems and the modification of their meanings through biochemical and ecological context (Dicke and Sabelis 1988). We also discuss toxins, substances that cause disease, dysfunction, or death, as drivers of biotic interactions, as well as their potential to lend structure to ecological “landscapes” of information. We then take a closer look at how ecological chemistry provides important links that bind together members of communities and alter their properties in ways that affect ecological diversity, stability, productivity, nutrient flow, and ecosystem function (Hay 2009). These discussions are interspersed with glimpses into the future of chemical ecology, in the context of emerging fields (e.g., genomics-enabled field ecology [Baldwin 2010]) and emerging ecological challenges (e.g., sustainable large-scale agriculture [Cook et al. 2007]) in an increasingly human-dominated biosphere.

INFORMATION CONTENT, ECOLOGICAL FUNCTIONS, AND GENOMIC BASES OF CHEMICAL TRAITS

Small molecules mediate information transfer

We live by our eyes and ears and tend generally to be oblivious to the chemical happenings in our surrounds. Such happenings are ubiquitous. All organisms engender chemical signals, and all, in their respective ways, respond to the chemical emissions of others.

With these words, Eisner and Meinwald (1995) reflected on the rise of chemical ecology as a field, with widespread recognition of the importance of chemistry in mediating terrestrial organismal interactions and the maturation of the analytical techniques needed to identify them. Shortly thereafter, the parallel application of chemical ecological approaches to marine biology reached a critical mass, revealing the ubiquity of chemically mediated ecological interactions in coral reefs, benthic, and pelagic marine environments, and expanding the universe of chemical structures known to display such functions (Hay 1996, Pohnert et al. 2007). We now expect, and observe, chemically mediated interactions everywhere, from the microbial biofilms assembling in deep-sea thermal vents and within our own digestive systems to the herds of ungulates gathering at Serengeti watering holes, along with their competitors, predators, and parasites.

The surprising diversity and ubiquity of ecologically active chemical structures compel a fundamental question: what kinds of information do they convey? One answer to this question is rooted in the basic laws of cellular metabolism and the history of life, in which nutrient uptake, excretion of waste, movement, replication, growth, and other fundamental processes are mediated through biochemistry. The distinctive functional groups and structural properties of different molecular classes (sugars, nucleic acids, amino acids) endow them with specific information content: how to store chemical energy, how to transcribe and translate the genetic code. In the parlance of animal behaviorists, these primary metabolites are “index cues,” truly honest indicators of the fundamental processes that they mediate (Maynard-Smith and Harper 1995). Scaled up to multicellular organisms and populations thereof, natural communities across the biosphere are rife with index cues of their members’ presence, abundance, and activities. These cues inform habitat selection, foraging decisions, predator avoidance, courtship, and territoriality by other community members, and thus enhance their fitness (Hay 2009). When *Daphnia* water fleas and *Rana* tadpoles show developmental plasticity in the presence of fish and larval dragonfly predators, respectively, they are responding adaptively to chemical index cues from their predators’ bodies or secretions (Agrawal 2001). Similarly, a large number of toxic, digestion-affecting or repellent chemical cues indicate the presence of potential prey, hosts, or mutualists (e.g., allelopathy [Bais et al. 2006]). By convention, signals are distinguished from cues in that they confer fitness benefits to the source organism (sender) by altering the behavior of the receiver, and are inferred to have evolved in the context of the sender–receiver interaction (Maynard-Smith and Harper 1995). Mutually beneficial communication between senders and receivers is shaped by reciprocal selective pressures between them, along with selection to evade eavesdropping third parties (competitors, predators, parasites) and to be detectable within the environmental context in which they are transmitted

(Endler 1993). In sum, a diverse assemblage of small molecules can be viewed as potential information that is available to any biological entity, from single cells to kelp forests, that can decode the information in an appropriate context (Box 1).

Further insight can be gained from considering the degree to which chemical signals mediate specialized vs. generalized interactions. Using pollination as an example, we expect private channels of novel chemical signals to mediate the obligate relationship between figs and fig wasps, due to strong selection to stabilize their mutualism while excluding destructive third parties (Dufaÿ and Anstett 2003, Hossaert-McKey et al. 2010). However, more generalized plant–pollinator interactions tend to be mediated by generic volatiles that are innately attractive to diverse groups of pollinators, or are easily learned by them in association with nectar- or pollen-based floral resources (Raguso 2008). Furthermore, the diversity of visitors to generalized flowers appears to select for multifunctional compounds (volatile or not) that simultaneously repel enemies and attract pollinators or adaptively modify their behavior (Galen et al. 2011, Kessler et al. 2012*b*). Multifunctionality is emerging as one of the most important and common attributes of natural products, which is surprising in the light of their great structural diversification.

The challenge of understanding the causes and consequences of multifunctionality extends beyond signals and cues to toxic compounds that may directly influence community composition and dynamics. For example, tetrodotoxin (TTX) is an alkaloidal neurotoxin that causes paralysis by blocking sodium channels, and thus constitutes a powerful defense in the marine microbes, fishes, mollusks, terrestrial amphibians, and other organisms that can produce or sequester it. For these creatures, resistance to TTX combined with high chemosensory sensitivity has allowed the evolution of additional functions, including sex pheromone, predator avoidance cue, acquired antipredator resistance, and, as a venom, a means of subduing prey (Zimmer and Ferrer 2007). The classical literature on butterfly–host plant coevolution is replete with similar examples of toxic plant defense compounds (cyanogenic glycosides, glucosinolates, cardenolides, pyrrolizidine alkaloids) that are overcome by specialist herbivores for whom they play additional roles as feeding and oviposition stimulants (Renwick 2002), sequestered antipredator defenses (Weller et al. 1999), nuptial gifts (Gonzalez et al. 1999) and condition-dependent sex pheromones (Landolt and Phillips 1997). Similarly, plant compounds initially thought to mediate plant resistance (e.g., glucosinolates, terpenoids) appear to serve multiple functions, either in resource storage (Heath et al. 2014) or in plant endogenous signaling in response to different environmental stressors (Liu et al. 2013, Martinez-Ballesta et al. 2013). These examples emphasize the multi-functionality of many ecologically important chemical substances

Box 1: Signals and Functions

Adopting a view of small molecules as carriers of information (Maynard-Smith 2000) can lead to a deeper understanding of yet another fundamental question in chemical ecology: how and why do small molecules evolve multiple or conditional ecological functions? Among behaviorists, these are known as “conventional signals,” because they are not absolutely constrained to specific index functions (Maynard-Smith and Harper 2003), and they may play very different roles in different ecological contexts or on different levels of organization. Understanding small molecules primarily as information can help to explain a compound’s evolution from a primary function on a particular level of organization (e.g., ATP synthase in chloroplasts) to a very different function on another level (e.g., the ATP synthase-derived peptide inceptin, which elicits plant responses to herbivory when present in the oral secretions of an herbivore [Schmelz et al. 2006]). Presumably, the information reliably conveyed by inceptin as an ATP synthase fragment is self-recognition of damaged tissues (Heil 2009). Thereby, the functions of a molecule are determined by its detectability and information content for a particular process on a particular level of organization. Similarly, certain compounds attract some organisms while repelling others, the latter seemingly because either innate or learned repellence (e.g., aposematism) reduces the risk of disease or mortality due to the repellent itself or its association with a toxin.

(Note: although nutritional ecology has historical links to chemical ecology through the study of chemical defenses and is directly relevant to our discussion of ecosystem-level processes below, a full discussion of nutrients per se is beyond the scope of this essay.)

across multiple organizational levels, and the futility of seeking to determine their “primary” or “original” functions without knowledge of their deep phylogenetic history.

The causes and consequences of chemodiversity

Why do organisms produce so many chemical substances that are not directly involved in primary metabolism? Over a half century since Fraenkel’s (1959) groundbreaking treatise on the *raison d’être* of secondary metabolites, questions concerning the ultimate causes of their diversity and function continue to stir debate among chemical ecologists (Moore et al. 2014). Despite the historical success of bioassay-guided fractionation, it remains challenging to determine specific

Box 2: Information Landscapes and Community Dynamics

While the role of chemical traits in mediating community dynamics seems relatively evident, the study of the effects of chemical information on the general attributes of communities and ecosystems as complex systems provides new opportunities for ecological synthesis and the generation of novel, integrative hypotheses. Examples of such opportunities include:

- 1) Chemically mediated associational resistance and susceptibility (Barbosa et al. 2009).
- 2) Different habitats/communities selecting for different signals (Hebets and Papaj 2005).
- 3) Chemical signaling between multiple trophic levels as a determining factor for competitiveness and thus persistence in a particular community (Poelman et al. 2011).
- 4) The role of chemical signals in aiding/preventing disease or pest outbreaks and affecting their dynamics (Kessler et al. 2012a).
- 5) The potential for invasive species to alter chemical interactions between organisms, leading to alternative stable states of chemical information transfer (Cappuccino and Arnason 2006).

biological functions for the multitude of identified natural products. Jones and Firn (1991) proposed the “screening hypothesis” to address the paradox that although many plants show high chemical diversity, relatively few of their metabolites have demonstrated biological activity. They reasoned that higher standing levels of chemical diversity, if not prohibitively costly to produce, should increase the probability of activity against a novel herbivore or pathogen. Like an immune system, the metabolic machinery that generates chemodiversity is the trait favored by selection in this model.

High compound diversity and plasticity (i.e., induced changes in the diversity and/or relative dosages of secondary metabolites) have been suggested to be functional in their own right, due to additive or synergistic effects among compounds (Richards et al. 2010). Hilker (2014) has asked whether chemodiversity itself is an organizing principle or an emergent property of ecological interactions, conferring benefits at a micro-community scale akin to those attributed to biodiversity (e.g., stability and productivity) at larger ecological scales. This view is intriguing in light of the relevance of small-molecule information content across multiple organizational levels, as discussed previously. Moreover, it expands the conceptual framework of chemical communication to consider the impact of information

transfer on community processes when they are approached as complex adaptive systems. Information transfer could thus have major impacts on commonly considered attributes of complex systems, such as self-organization, alternative stable states, and nestedness (Wessels 2013). Chemical ecological studies of plant–insect interactions provide support for this view. Specifically, when the chemical information landscape is altered through phenotypic (Viswanathan et al. 2005) or genotypic manipulations (Halitschke et al. 2008) of one or multiple components in the interaction network, there are significant consequences for community dynamics. For example, the arthropod herbivore community found on *Brassica oleracea* plants is structured both by the identity of the initial damaging herbivore species, which induces changes in plant chemistry, as well as by the plant genotype (Poelman et al. 2010). Similarly, the diverse community of parasitoids and hyperparasitoids in this system varies with the volatile emissions specifically induced by parasitized vs. unattacked host herbivores (Poelman et al. 2012), which in turn affects the host plant choices made by one of the major herbivores in the system, the diamondback moth, *Plutella xylostella* (Poelman et al. 2011). Studies of community-wide effects of the chemical information landscape, while still rare, suggest significant fitness consequences for the species involved (Poelman et al. 2008, Kessler et al. 2011). The observation of such fitness consequences suggests strong selection on chemical information and the potential for rapid evolution of chemical traits in response to the removal of a community component (see Box 2). An important development in recent years is the opportunity to manipulate chemodiversity genetically and thereby to measure its ecological importance. We consider this advance and its potential in the following sections.

Genomics and the exploration of metabolic functions

The traits of interest to chemical ecologists span life history attributes, primary metabolism (i.e., growth and allocation), and those traits involved in interactions (e.g., diet choice, production of secondary compounds, and responses to chemical defenses). To address the causes and consequences of variation in such traits, one needs to start not only with natural variation, but also with the ability to phenotype many individuals, and to determine the genetic basis for their expression. For instance, local adaptation of Drummond’s rock cress (*Boechera stricta*) was linked to recent evolutionary changes in cytochrome P450 enzymes that influence the production of glucosinolate compounds, which mediate resistance to herbivores, in conjunction with geographic variation in the selective environment (Prasad et al. 2012).

High throughput DNA sequencing methods are opening up new opportunities for investigating the underlying genetic mechanisms that mediate chemical ecological interactions. As a preview of future possibil-

ities, we consider current approaches in the investigation of high-value crop plants such as maize. Through low-coverage DNA sequencing of several thousand inbred maize lines, genome-wide association studies (GWAS) can identify genetic loci affecting complex traits like pathogen resistance, flowering time, and seed composition (Buckler et al. 2009, Cook et al. 2012). As the sequencing of whole genomes becomes more routine, genetic mapping and the identification of linked genes will provide a superb complement to the diverse sets of phenotypic assays that are currently used to characterize natural populations.

The identification of genetic loci that underlie the chemical traits mediating interactions between organisms provides ecologists with expanded opportunities to generate testable predictions. Just as seeds in some crop plant breeding programs are now genotyped before they are planted in the field, the genetic makeup of partners in an ecological interaction can be investigated before they interact. Then, based on the genotypes, it should be possible to generate predictable hypotheses regarding which traits might be favored in the particular environment that is being investigated. Once candidate genes have been identified by genetic mapping, they can be validated through knockdown by RNA interference, overexpression, or targeted modification of the genome sequences in the organisms of interest (Kang and Baldwin 2008). This approach has translated successfully to field experiments on chemically mediated plant defense and reproductive ecology in wild tobacco (*Nicotiana attenuata*) (Baldwin 2010, Schäfer et al. 2013). An additional benefit of such studies is that selective trait-silencing may reveal unexpected ecological interactions that are pre-empted by wild-type trait expression. When Kessler et al. (2004) selectively silenced genes mediating direct and indirect defenses of *N. attenuata*, the predicted increase in herbivory by tobacco specialists and reduced induction of nicotine were accompanied by an unexpected increase in damage by generalist leafhoppers not regularly observed on wild tobacco. Selective knockdown of floral nicotine modified pollinator behavior, as predicted from bioassays with artificial flowers, but also increased nectar-robbing behavior by carpenter bees and florivory by noctuid moth larvae (Kessler et al. 2008). These and similar experiments (Kessler et al. 2012b), made possible through increased understanding of complex biosynthetic pathways, reveal the hand of chemistry in shaping both the presence and absence of links in complex ecological networks.

Returning to the question of multifunctionality, the identification of biosynthetic genes will create new opportunities for targeted manipulation to study ecological function of individual plant metabolites, which mediate interactions between organisms in ways that extend beyond their toxic or deterrent effects. For instance, volatile indirect plant defenses can have conventional signaling functions in attracting specialized herbivores or predators (Pivnick et al. 1994, Turlings et al. 1995). Less well studied are the nondefensive

functions that many common secondary metabolites can have within the plants that produce them. Regulation of primary metabolism and important functions such as flowering time may be triggered by the production of specific metabolites known also to have defensive functions. Two of the best-studied classes of plant defensive metabolites, glucosinolates in *Arabidopsis thaliana* and benzoxazinoids in maize, can function as signaling molecules to initiate other plant defenses (Clay et al. 2009, Ahmad et al. 2011). Other classes of defensive plant metabolites likely have similar functions, which can be elucidated once the biosynthetic enzymes have been identified and manipulative experiments can be implemented. Broad characterization of changes in the transcriptomes and metabolomes of these plants will help to identify additional functions of secondary metabolites that extend beyond direct defense against herbivores and pathogens.

CHEMICAL MEDIATION OF COMMUNITY STRUCTURE, ECOSYSTEM DYNAMICS, AND HUMAN INTERESTS

Having outlined the modes of action of chemical signals, cues, and toxins, along with their information content and genomic-biosynthetic provenance, we now shift our focus to the question of how semiochemicals can structure communities and ecosystems. An important development in the field of chemical ecology in recent years has been its expansion to encompass community level interactions and processes (see Box 3). Recognition that chemical agents mediate organismal interactions and the flow of nutrients at community and landscape scales, combined with identification of the specific chemicals mediating such processes, provides opportunities for the growth of ecological theory and its application to solving pressing problems in human-managed ecosystems.

Small molecules affect top-down and bottom-up community interactions

The core direct (dyadic) interactions in plant-herbivore-natural enemy communities are strongly influenced by chemical factors. In addition to being the energetic base of most food chains, plants have strong chemically mediated interactions with their attackers and their attacker's natural enemies. Plants actively respond to attack, and there is a deep literature on the types of induced responses and their consequences for the fitness of plants, herbivores, and pathogens (reviewed by Hunt et al. 1996, Karban and Baldwin 1997, Farmer 2014). We are still learning how plants detect and respond to herbivores and pathogens. For example, some plants recognize herbivores using specific chemicals in female oviposition secretions (Hilker and Meiners 2011) and in insect saliva to induce both direct (Schmelz et al. 2009) and indirect (O'Doherty et al. 2011) defenses. Recent studies show that plants use the earliest available information to detect attackers in their environment. How rapidly a plant detects and responds to a pathogen

Box 3: A Research Agenda for Advancing Community Chemical Ecology

Below we present a series of points suggesting future research approaches that recognize the importance of chemistry and complex multi-species interactions.

- 1) Recognize that most organisms produce highly complex blends of biosynthetically diverse compounds, which are likely to have multiple functions. We suggest integrated field studies using model systems and their non-model relatives, in their natural communities, preferably using specific genotypes, silenced, or inbred lines to perturb chemical phenotypes and measuring community responses. As has been shown for wild tobacco, the dominant alkaloid nicotine is a substantial part of its ecological story, but certainly not the whole story (Kang and Baldwin 2008).
- 2) Endogenous hormones and exogenous allelochemicals interact. We are learning more about behavioral interactions, even in plants, mediated by hormones, receptors, and allelochemicals, and which are likely critical for species interactions and community outcomes (Glinwood et al. 2011). We are primed for conceptual and experimental synthesis between endogenous (hormonal) chemical ecology and interspecific (allelochemical) chemical ecology. Indeed, not only do hormonal cues mediate the production of allelochemicals, but conversely, many interspecific interactions impact hormone expression (Zhang et al. 2007).
- 3) Despite the promise of the genomics approaches outlined above, we recognize that -omics approaches alone are unlikely to solve all outstanding problems in ecology. In particular, we will need nuanced experiments to reveal emergent (nonlinear or non-additive) properties mediated by complex chemical mechanisms at the community level. We anticipate the resurgence of natural history, theory, and observation of strong interactions in the next generation of chemical ecological research.
- 4) Comparative biology, especially in combination with a manipulative approach, can be a vehicle both for generalization and for identifying the exceptions that prove the rule. For example, a triumph of chemical ecology in the last 20 years has been the elucidation of the highly conserved hormonal signaling pathways of plants (Thaler et al. 2012). Alternatively, if closely related species have highly divergent chemistries (or interactions) this may be a very powerful way to initiate a research program, especially if manipulations are possible or if a broad swath of species can be surveyed (Heil et al. 2004).

can make the difference between resistance and susceptibility (Greenberg 1997), and rapid detection may also be important in defense against herbivores. For example, goldenrod plants can detect sex pheromones from herbivorous flies (Helms et al. 2013), and *Arabidopsis* responds to chemicals in the slime of herbivorous slugs (Orrock 2013) as advance warning of future herbivory. These recent discoveries exemplify that diverse and currently under-studied index cues from attackers provide information in plant–herbivore–pathogen interactions. On the flip side, attackers use chemicals to manipulate plants to decrease plant defense responses and increase resource quality (Musser et al. 2002). Diverse plant attackers, including whiteflies (Zhang et al. 2009), lepidopteran eggs (Bruessow et al. 2010) and *Pseudomonas* bacterial pathogens (Cui et al. 2005) have been shown to tap into the plant's own hormonal signaling system to prevent the induction of effective defenses. In sum, given the wealth of information available to plants and their attackers, and the potential for coevolutionary dynamics, we remain limited in the generality of predictable species interactions. A deeper understanding of the kinds of information available to each partner will allow us to test predictions about when specific or rapid responses are beneficial. For example, plants detect both below- and aboveground herbivores,

and whether or not these are integrated at the whole-plant level may depend on the similarity of attackers and the predictability of attack across the two modules (Bezemer and van Dam 2005).

Our understanding of herbivore–predator interactions has changed dramatically in the last decade, as we now know that approximately half of the ecological impact of predators on their prey and the prey's resources arises from nonconsumptive effects, that is, the prey's detection of and response to predators, independent of predation (Preisser et al. 2005). As discussed above, there is growing evidence that predator-specific chemical index cues are used, not only in aquatic fish and invertebrate systems, but also in terrestrial invertebrate systems (Lefcort et al. 2006, Hermann and Thaler 2014). Alternatively, sometimes the chemical cues triggering prey responses are from the bodies of conspecifics, and so could arise generally from any predator consuming a given species. The chemical identification of these cues remains a frontier in predator–prey ecology. Although much has been learned from manipulative studies on the ecological effects of predator cues as experimental treatments (Peacor and Werner 2001, Relyea 2004), knowing the chemical identity of these cues could help elucidate a predictive framework for the temporal consequences of predator presence, the extent of the community that will

be affected, and whether a prey will recognize an introduced predator (Weissburg et al. 2014).

The importance of chemical information in mediating top-down and bottom-up effects has several consequences for multi-species interactions. First, as discussed earlier, the information content can generate high specificity, not only in plant–herbivore–parasitoid systems, but more broadly in other predator–prey interactions. Second, by altering the outcome of these fundamental binary interactions, semiochemicals have the potential to generate chemically mediated indirect effects through trophic cascades, such as TTX-mediated food webs (Ferrer and Zimmer 2012). And third, the spatial and temporal patterns of interactions mediated by chemicals are different than those generated by direct contact. A predator must contact its prey to eat it, but the presence of the predator alone can affect the prey over larger spatial and temporal scales (Peckarsky et al. 2002). Ecology's early interest in consumptive and competitive interactions focused us on negative species interactions. However, nonconsumptive links also consist of mutualistic interactions.

The ubiquity of chemically mediated mutualistic links

Although trophic relationships have dominated our thinking about chemically mediated species interactions, most non-trophic relationships, including mutualism, also are mediated at some level by chemistry. However, only recently have mutualistic links become more widely recognized and integrated into ecological and evolutionary theory (Bruno et al. 2003). The obligate nature (and associated cost–benefit landscape) of mutualistic interactions varies enormously across the biosphere, often with conditional fitness consequences (Bronstein 1994). Of critical importance to the role of mutualisms in community interactions is the need for stabilizing mechanisms that prevent runaway cheating or runaway population explosion of mutualists (Axelrod and Hamilton 1981). It is here where chemical ecology has tremendous potential to impact our understanding of nonconsumptive links in food webs.

Partner choice and sanctions are two mechanisms by which ecologists have proposed that mutualistic interactions may be policed against two prevalent forms of exploitation: cheaters, which fail to deliver a service to the partner; and parasites, which overexploit the resources provided by the partner (Bull and Rice 1991). One of the first empirical examples of such policing came from work on obligate yucca–yucca moth pollination interactions, where high oviposition by moths induces selective fruit abortion, demonstrating the plant's strong check against selfish behavior by moths (Pellmyr and Huth 1994). Similar sanctions against “uncooperative” rhizobia (those that did not provide nitrogen to plants) have been demonstrated in legumes (Kiers and Denison 2008). A priority for future research is to understand how the chemical basis of partner choice in these associations is linked with

functional consequences, relating to patterns of interactions with the wider ecological community and the evolutionary trajectories of the participating organisms.

Given the conflicts of interest inherent to nearly all mutualistic interactions, there is some potential for one partner to impose costs or negative fitness impacts on the other (Bronstein 2001). Consider the role of ant-protectors of *Acacia* trees. Although such trees may invest less in chemical defense than their counterparts without ant-defenders, they still engage in various chemically mediated interactions for reproductive purposes. In particular, some African *Acacia* species emit (*E,E*)- α -farnesene, a volatile emanating from pollen that repels ants during the key window of pollination by andrenid bees, as a way to suppress ant-mediated costs of deterring pollinators (Willmer et al. 2009). In this system, natural selection on plant allocation and chemistry has yielded an interacting network of direct and indirect (ant-mediated) defenses, and volatile and nonvolatile floral attractants and deterrents. Deciphering the spatial and temporal variation in expression of these traits, let alone the production costs vs. ecological costs of different strategies, will be an important step in understanding within-plant chemical networks and how they mediate complex species interactions.

In the analysis of partner choice in mutualistic interactions, the concept of specificity is key, as some chemical signals may be uniquely produced and perceived, while others may be quite general, as discussed above in the context of plant–pollinator interactions (Raguso 2008). Interestingly, both kinds of signals are involved in one of the most important terrestrial mutualisms, the establishment of nitrogen-fixing rhizobial symbioses in legume root nodules. Like figs and fig wasps, these specialized bacteria are attracted to specific legume hosts by flavonoids in their root exudates, and the bacteria, in turn, produce nod factors, substituted lipo-oligosaccharide molecules that grant access to a root hair and initiate nodule development. Although flavonoids are a common class of molecules that can mediate a full spectrum of interactions with other plants, root herbivores, fungi, and bacteria (Bais et al. 2006), structurally distinct isoflavonoids like luteolin mediate host-specific recognition by rhizobia (Peters et al. 1986). In contrast, nod factors are chemically unique, highly complex molecules that mediate species-specific nodulation between different legumes and their rhizobial partners through complex cascades of gene expression (Broughton et al. 2000). Arbuscular mycorrhizal (AM) fungi engage in another important rhizosphere mutualism with plants, in which plant roots exchange up to 20% of their photosynthetic carbon with symbiotic AM fungi in exchange for phosphorus. Like plants with generalized pollination systems, plant–mycorrhizal interactions exhibit high connectance, including direct links to noncooperative or even pathogenic fungi and, through this network, indirect links to other plants. Thus, partner choice

mechanisms are bound to be more nuanced and conditional in such a system, for which models of dyadic cooperation and defection are inadequate (Kiers and Denison 2008).

It is clear from these examples that specificity is defined both from the sender's and receiver's perspectives. How is the same chemical signal produced by the sender depending on its biotic or abiotic environment? And does the effect of a particular chemical signal depend upon the identity (species, genotype, nutritional needs, receptor tuning) of the receiver? Returning to *Acacia* trees, some Central American species have evolved an elegant chemical filter as a means to specifically attract their obligate *Pseudomyrmex* ants while excluding facultative ant species. Quite simply, their extrafloral nectar contains high invertase (sucrose-digesting) activity and thus is dominated by hexose sugars, which are nutritionally unavailable or unattractive to most ant species, but are preferred by *Pseudomyrmex*, whose own gut invertase activity is meager (Heil et al. 2005). Under the right circumstances, a generic and ubiquitous compound may be sufficient to mediate a highly specific mutualism.

Over the past decade, network analysis has revolutionized the way that ecologists think about complex community interactions, including those between plants, pollinators, and other visitors in floral markets (Bascompte and Jordano 2007). However, only recently has the impact of chemistry on such interactions been investigated. Junker and Blüthgen (Junker and Blüthgen 2010, Junker et al. 2011) have combined field observations, behavioral bioassays, and chemical analyses to demonstrate on a community scale that floral scents generally are attractive to obligate floral visitors, including legitimate pollinators, but the same volatile blends are repellent to facultative and thieving flower visitors (Junker et al. 2011). Of particular importance is that these analyses explained natural patterns of floral visitation in complex natural communities, but also relied on behavioral bioassays under more controlled conditions. Similarly, a recent study by Tewksbury et al. (2008) identified multiple and divergent functions for capsaicin and related alkaloids in the fruits of wild chili peppers, in which these pungent compounds balance complex interactions with birds (preferred seed dispersal agents), mammals (seed predators), fungal pathogens, and their insect vectors along a latitudinal gradient in Bolivia. Geographic variation in these kinds of complex community interactions and the selective pressures that shape them, connected over landscape scales by dispersal, migration, and abiotic factors, compels us to consider below how chemical ecology affects ecosystem dynamics.

Small-molecule-mediated interactions as links between ecosystems

In previous paragraphs, we have considered how the ecology of individual organisms can be shaped by small

molecules produced by other organisms. Such interactions are also evident at the scale of the ecosystem, such that the traits of an entire ecosystem (productivity, nutrient flux, robustness, and other traits) can be influenced by small molecules derived from another ecosystem. The study of ecosystem-scale chemical ecology is still in its infancy, and its practitioners would not necessarily identify themselves as chemical ecologists. Even so, ecosystem chemical ecology is crucial for any comprehensive explanation or prediction of ecosystem processes and ecosystem response to perturbation.

Between-ecosystem transfer of small molecules and their ecosystem-scale consequences can be investigated most readily in nested ecosystems, because, by definition, the inner ecosystem(s) is contained within, and interacts exclusively with, the outer ecosystem. Plants and animals participate in nested ecosystems: the inner ecosystem of complex microbial communities associated with the root system, gut, and other parts, and the outer ecosystem defined by the resources and conditions in the habitat in which the plant/animal resides. The significance of small molecules produced by the inner ecosystem on outer ecosystem processes can be substantial and diverse. For example, ergot alkaloids produced by endophytic fungi in the European grass *Lolium arundinacea* play a major role in the invasiveness of *L. arundinacea* introduced to the Midwestern prairies of USA, by promoting selective herbivory on native plants and the resultant suppression of plant succession (Rudgers et al. 2007). In a very different type of interaction, volatiles derived from bacterial inhabitants of the scent glands of hyenas have been implicated in social communication within and between groups (Theis et al. 2013), with likely cascading effects on the social organization of hyena populations and, consequently, the impact of these abundant carnivores on the dynamics of grassland and woodland ecosystems in Africa.

Individual small molecules can also link ecosystems at the largest spatial scales. Dimethyl sulfide (DMS), generated in vast amounts by lysing cells of the ocean's phytoplankton and released into the atmosphere (Charlson et al. 1987), offers a vivid example. Hotspots of DMS emission by phytoplankton being consumed by krill (small crustaceans in the surface waters of the oceans) are utilized as a foraging cue by krill-feeding procellariiform sea birds (albatrosses, petrels, etc.), with ecosystem-level consequences. Specifically, the DMS-mediated foraging by these pelagic sea birds is a key driver of between-ecosystem nutrient transfer: their feces are inferred to promote the retention of limiting nutrients, especially iron, in the surface waters of the nutrient-poor Southern Ocean (Savoca and Nevitt 2014). During the nesting season, the nutrient transfer is from the ocean to land, with ramifications for microbial-mediated nutrient flux in terrestrial soils (Fukami et al. 2006). Although the chemistry and scale of this phenomenon differ from those of terrestrial

systems, Savoca and Nevitt (2014) remind us that the phytoplankton–krill–seabird interaction is formally equivalent to chemically mediated tri-trophic interactions through indirect defense, with profound biogeochemical consequences.

These important studies notwithstanding, the scale of chemically mediated information transfer between ecosystems has not been studied systematically and therefore the overall significance of these processes is uncertain. However, the potential implications of these interconnections are substantial because chemicals in one ecosystem can have cascading effects on an otherwise unconnected (or weakly connected) ecosystem. The species producing these chemicals may not be important to the ecosystem in which they reside, but crucial to the function of a distant ecosystem. Identification of these long-distance interactions is a high priority, enabling us to explain and predict the full consequences of perturbations in one ecosystem and potentially to utilize these semiochemicals in ecosystem restoration. These considerations are relevant to a great diversity of ecosystems, from the impacts of resident microorganisms on human health (recognizing that medicine is the restoration of the perturbed ecosystem in our multi-organismal selves) to the connections between the terrestrial and marine ecosystems at the planetary scale.

Chemical ecology and pest management

Just as chemical agents are important in shaping natural communities and ecosystems, they play crucial roles in the interactions occurring in human-managed systems such as agriculture, forestry, and aquaculture. Chemical ecologists have always applied their knowledge to agricultural systems, to understand insect pest distribution patterns (Root 1973), and to manipulate naturally occurring chemical signals such as pheromones to create traps to monitor and control pests in agricultural settings (Wright 1964). There are different ways in which chemical ecological principles can be used to control and manipulate pests. Very broadly we could characterize two main modes of action in which chemical compounds can be used in production systems: (1) behavioral modification and (2) direct toxic effects.

Behavior-modifying practices are based on the use of cues or signals for intraspecific as well as interspecific communication. A classic example that exploits intraspecific chemical cues is the use of insect sex pheromones (Witzgall et al. 2010). Due to their importance in mate finding and therefore in reproduction, sex pheromones can be used to modify pest behavior, not just in agricultural systems (El-Sayed et al. 2006) but also to control forestry pests such as bark beetles (Borden and Lindergren 1988), trap mosquito populations to decrease the impact of their vectored diseases (Syed and Leal 2009), and manage invasive aquatic organisms such as crayfish (Gherardi et al. 2011). Traps with lures based on synthesized pheromones can be used to attract and

kill males of targeted pest species (Witzgall et al. 2010). Pheromones can also be used for mating-disruption practices, in which the release of synthetic pheromones homogenizes the chemical information landscape, preventing male insects from finding conspecific females with which to mate (Witzgall et al. 2008). In comparison to traditional pesticide use, these practices have the added advantage of conserving the natural enemies of the pests in the agricultural systems, which leads to mitigation of pest pressure thanks to a reduction in mating and the build-up of the natural enemy population (Jones et al. 2009). Interspecific chemical communication can be used to modify the behavior of organisms via chemical repellents or attractants (Cook et al. 2007). For example, agriculturalists have begun to use plants that constitutively emit volatile profiles similar to those released by herbivore-attacked plants. This practice exploits the natural behavior of gravid female pest insects to avoid ovipositing on those plants, with the benefit of pesticide-free crop protection (Khan et al. 2000, 2014; see Box 4). Those same volatile blends can serve as a lure for natural enemies that are attracted to them as signals that indicate the presence of an herbivore (Turlings et al. 1995, Takabayashi and Dicke 1996), as long as the herbivores sought by such enemies are present. The potential benefits of behavioral manipulation are not limited to plant volatiles. Chemical cues emitted by waterbucks (*Kobus defassa*) repel tse-tse flies (*Glossina* spp.) (Gikonyo et al. 2003), and currently are being tested in repellent collars to reduce levels of sleeping sickness in livestock in East Africa (ICIPE).⁶ Alarm pheromones such as (*E*)- β -farnesene (EBF) emitted by aphids also can be sprayed on crop plants to repel other aphids from settling on them, and to attract natural enemies of aphids to the crop (Hardie and Minks 1999, Bruce et al. 2005). Furthermore, aphids living on plants that constitutively emit EBF give rise to progeny habituated to EBF as an alarm, and these progeny suffer increased mortality from coccinellid beetle predators (de Vos et al. 2010).

Toxic compounds from diverse sources can confer plant resistance against pests and have been widely used in agricultural production. For example, pyrethrins derived from *Chrysanthemum* flowers were long used as insect repellent and insecticides, and are the basis for commercially available pyrethroid insecticides (Katsuda 1999). Insecticidal extracts from other plants (e.g., neem (*Azadirachta indica*), Isman 2006), as well as crystalline protein toxins from bacteria (e.g., Bt from *Bacillus thuringiensis* [Koziel et al. 1993]) play central roles in current pest control strategies and illustrate how chemical ecology fuels agricultural innovation (Kota et al. 1999).

Above, we discussed the ecosystem-level effects of ergot endophytes in an invasive grass, which are

⁶ <http://www.icipe.org/index.php/news/657-how-the-stink-of-a-waterbuck-could-prevent-sleeping-sickness-in-kenya.html>

Box 4: Push–Pull Agriculture: the Power of Behavioral Manipulation

The simultaneous deployment of repellent and attractive cues constitutes the “push–pull” strategy, in which a combination of measures renders the protected organism or crop unattractive for pests (push) while directing them toward another, more attractive resource (pull) that is unsuitable for pest survival (Cook et al. 2007). In East Africa the push–pull approach has been widely adopted for the control of stem-boring moth species that impose a major constraint on maize cultivation (Khan et al. 2000, Hassanali et al. 2008). Intercropping with a repellent plant in combination with border strips of a trap plant decreases herbivore pressure, doubles yields, and has been adopted by more than 68 000 farming families (Khan et al. 2008, 2014). This push–pull strategy increases crop yields not only due to behavioral manipulation of insect pests but also due to control of weeds. Witchweed (*Striga hermonthica*, Orobanchaceae) is a root-parasitic plant that decimates maize production in many regions of Africa. When developing the push-pull strategy for stem borer control, researchers at ICIPE discovered that intercropping with *Desmodium uncinatum* and *D. intortum*, used as a repellent for the stem borers, also reduced the presence of witchweed (Khan et al. 2002, Hassanali et al. 2008). Further analysis of the chemical ecology of this interaction showed that *Desmodium* plants caused suicidal germination of witchweed seeds. *Desmodium* roots exude a germination stimulant for *S. hermonthica* while at the same time producing allelopathic substances that inhibit haustorial development, effectively killing the parasitic plant (Khan et al. 2014). Thus, chemical ecological approaches have identified further ecological benefits to be reaped from a leguminous plant long appreciated for its N-fixing capabilities as an intercrop (Henzel et al. 1966).

exacerbated in disturbed, human-impacted habitats. Agro-ecosystems provide similar kinds of empirical evidence for the community-wide effects of the expression of bioactive compounds in the environment. An illustrative example is the use of Bt-modified crops at large scales in agroecosystems. The transfer of the genes that encode the Bt insecticidal properties from bacteria into maize, potato, and cotton reveals the consequences that a toxic chemical substance can have on the insect community in large-scale agro-ecosystems. For example, the constitutive expression of Bt in cotton reduced the presence of a generalist pest, the cotton bollworm

(*Helicoverpa armigera*), not only on cotton but also on a series of neighboring crops (Wu et al. 2008). Moreover, populations of lacewings, ladybird beetles, spiders, and other natural enemies increased in time due to reduced insecticide sprays in regions where Bt-cotton is used (Lu et al. 2012). These findings suggest that whole insect communities can respond at a regional level to localized expressions of a toxic substance (Wu et al. 2008). However, the use of Bt-cotton created unforeseen problems with secondary pests in the same region. Mirid bugs reached pest status on cotton and other associated crops (Lu et al. 2010), exemplifying that responses at the community level, and not just of the target pest, can result from the expression of a novel toxin. Another outcome of the over-expression of toxic compounds such as Bt is the evolution of pest resistance (Ferre and Van Rie 2002), which has been documented for at least 13 major agricultural pest species (Tabashnik et al. 2013). These findings confirm that herbivores are capable of adapting to a wide variety of toxins, even compounds that are normally synthesized outside the plant kingdom, as has been previously shown for the evolution of resistance to pesticides.

The examples presented in this section demonstrate how we already use chemical ecological principles to manage our production systems in agriculture and forestry. Similar practices, and challenges, typify the current state of aquaculture, in the development of integrated control strategies for sea lice in salmon farms (Torrissen et al. 2013). For example, recent field trials demonstrate the effectiveness of 2-aminoacetophene, a compound isolated from non-host fish, in reducing sea louse infestation of salmon in fish farms (Hastie et al. 2013). Even human and animal disease management is influenced by chemical ecology. However, there are still serious challenges to overcome, such as the evolution of resistance to toxic substances. Developing pest management strategies that facilitate behavioral manipulation of the whole community (microbial as well as multicellular members, above- and belowground) to maximize yield is one of the largest challenges currently faced by the field of applied chemical ecology. The complexity of natural systems appears to hold important clues for ensuring long-term, sustainable production of the goods and services we need to survive as a growing human population (Vandermeer et al. 2010).

CONCLUSIONS

The goal of the early practitioners of chemical ecology was to characterize the diversity of chemical natural products and determine their ecological functions, primarily within the realms of toxins, pheromones, and chemically mediated coevolution. Present-day chemical ecology has expanded to the study of information exchange, not only at intra- and interspecific levels, but also within complex communities, natural, and managed ecosystems, including human-dominated habitats across the biosphere. A number of recurring themes

emerged in our review. First, most ecologically important chemical agents appear to be multifunctional, and our traditional focus on toxicity and defense has prevented us from reaching a broader understanding of non-defensive functions. Second, information landscapes, spatial and temporal variation in the distribution of chemical agents, appear to play central roles in shaping community structure and ecosystem dynamics, especially in the highly modified agricultural, silvicultural, and aquacultural habitats that dominate much of earth's surface. Third, traditional, targeted methods for studying chemically mediated, dyadic interactions are giving way to unbiased approaches that leverage informatics tools and, importantly, acknowledge the multiorganismal reality of ecological interactions at all scales. The incorporation of chemical ecological concepts and approaches provides opportunities to discover, perturb, and manipulate the mechanisms that mediate complex ecological interactions, to reveal hidden patterns not obtainable using correlational studies, and to frame novel, testable hypotheses for how such interactions evolve. The chemical ecology approach leads not only to a deeper understanding of ecological principles, but provides us with tools to address the urgent ecological problems of a hungry, and growing, human population.

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