

The Ecological Importance of Allelopathy

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Abstract

Allelopathy (i.e., chemical interaction among species) was originally conceived as inclusive of positive and negative effects of plants on other plants, and we adopt this view. Most studies of allelopathy have been phenomenological, but we focus on studies that have explored the ecological significance of this interaction. The literature suggests that studies of allelopathy have been particularly important for three foci in ecology: species distribution, conditionality of interactions, and maintenance of species diversity. There is evidence that allelopathy influences local distributions of plant species around the world. Allelopathic conditionality appears to arise through coevolution, and this is a mechanism for plant invasions. Finally, allelopathy promotes species coexistence via intransitive competition, modifications of direct interactions, and (co)evolution. Recent advances additionally suggest that coexistence might be favored through biochemical recognition. The preponderance of phenomenological studies notwithstanding, allelopathy has broad ecological consequences.

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...the mere presence of a material which, when extracted, is toxic to other plants may not necessarily be of any ecological significance.

—Muller & Muller (1956, p. 359)

1. INTRODUCTION

Allelopathy was coined by the Czech-Austrian botanist Hans Molisch [2001 (1937)] in his book *The Influence of One Plant on Another: Allelopathy*. Molisch provided a long list of examples of inhibitory and stimulatory ways by which plants affect each other through chemicals released into the environment. To Molisch, reciprocal (*allelo*) perception (*pathy*) encapsulated the idea that plants can sense and interact with each other positively and negatively via mechanisms other than through the direct effect of resource uptake (see Schenk et al. 1999). But over time, *pathy* became construed exclusively as suffering or harm (e.g., Keeley 1988). This semantic shift in the definition of allelopathy has been debated (Rice 1984, Keeley 1988), but currently allelopathy is defined as a broad suite of chemically derived negative interactions (Muller 1966, Hierro & Callaway 2003, Inderjit et al. 2011, Cipollini et al. 2012).

Even this modern narrow definition of allelopathy is hard to classify as a general interaction. Defining allelopathy solely in the context of suffering puts it in the competition category, but it is neither mediated by nor even necessarily coupled with resource uptake, which is the sine qua non for competition in ecology (Begon et al. 2006). Thus, allelopathy can be a form of nonresource-based interaction between plants (Mahall & Callaway 1991), or interference (Reigosa et al. 1999, Begon et al. 2006, Gurevitch et al. 2006). Interference unifies the language of animal and plant ecology (Begon et al. 2006, Gurevitch et al. 2006) but has also been used as a label for general negative interactions between plants, thus allowing us to define allelopathy and competition as different types of interference (Muller 1966, Harper 1977, Ridenour & Callaway 2001) (Table 1).

Semantics acknowledged and set aside, over the last 20 years an astonishing array of studies have reported plants interacting via mechanisms that suggest reconsidering and applauding Molisch's prescient notions. There is a great deal of evidence that plants interact both negatively and positively via the release of biochemicals that act as inhibitors, promoters, and complex signals that can be induced in response to the environment and that are even reversible in some cases (Metlen et al. 2009). Thus, chemical communication between plants goes beyond the release and

Table 1 Alternative views of allelopathy, the type of interaction that those views represent, the nature of effects exerted by species on each other, and examples of references in which different views have been adopted

View	Interaction	Effects	References
Original	Chemical communication	+, −, 0	Molisch 2001 (1937), Rice 1984, Reigosa et al. 2002, this review
A type of competition	Interference competition—as an alternative to exploitative competition	−	Jackson & Buss 1975, Begon et al. 2006, Gurevitch et al. 2006, Lankau et al. 2011, Aschehoug et al. 2016
A type of interference	Allelopathy interference—as an alternative to competition interference	−	Muller 1966, Harper 1977, Wardle et al. 1998, Schenk et al. 1999, Ridenour & Callaway 2001

Although allelopathy originally included positive, negative, and neutral interactions, over time allelopathy evolved to be considered as a purely negative interaction by most authors.

impact of toxins (see Preston & Baldwin 1999, Schenk et al. 1999, Renne et al. 2014, Novoplansky 2019, Callaway & Li 2020). However, because of this etymological evolution of *allelopathy*, we have no word for this broader group of processes. Despite this semantic limitation, in the spirit of Molisch, this review embraces the broad suite of ways that plants may chemically interact, including signaling and communication, and thus compete with and facilitate each other. To avoid confusion, we attempt to be explicit about net chemical consequences (positive, negative, neutral) for interactions. We focus on plants because of the overwhelming preponderance of plants in the relevant literature, but allelopathy is not restricted to plants (e.g., Jackson & Buss 1975), is common among microbes (Gonzalez et al. 2018), and can be a mechanism by which microbes affect plants and vice versa (Inderjit 2005, Cipollini et al. 2012).

Most studies of allelopathy are phenomenological—the application of extracts or isolated chemicals to seeds or plants—and there may be thousands of studies showing that such compounds can be inhibitory in controlled conditions. Instead, we focus on the potential ecological significance of allelopathy. Searching for ecological significance guided early studies of spatial distributions in California coastal sage scrub and chaparral (Muller et al. 1964, Muller 1966) and in abandoned fields (Rice 1964). Since the 1960s, interest in allelopathy as an organizing ecological mechanism in plant communities has accelerated, and researchers have tackled concerns about methodological approaches, inconsistencies between laboratory assays and field patterns, and alternative explanations for patterns ascribed to allelopathy (Bartholomew 1970, Harper 1977, Stowe 1979, Keeley 1988, Inderjit & Nilsen 2003, Lau et al. 2008). In addition to influencing local species distribution, allelopathy plays an important role in nonnative plant invasions (Zhang et al. 2020, Kalisz et al. 2021) and the striking biogeographic differences in the abundance of species in native and nonnative ranges (Callaway & Aschehoug 2000), in line with earlier notions suggesting that the strength of allelopathic interactions is conditioned by species coevolution (Rabotnov 1974). Also, intraspecific variation in the intensity of allelopathic effects has been proposed to promote coexistence (Lankau & Strauss 2007), and allelopathy appears to drive coevolution between native and nonnative plant species (Lankau 2012). Allelopathy has been frequently reviewed (e.g., Muller 1966, Whittaker & Feeny 1971, Wardle et al. 1998, Hierro & Callaway 2003, Cipollini et al. 2012, Ehlers et al. 2020), but here we target the potential roles of allelopathy in determining species distributions, regulating the conditional nature of interactions among plant species, and maintaining local species diversity. That is, we focus on the conceptual areas in ecology to which we think allelopathy has contributed the most.

2. DISTRIBUTION OF SPECIES

2.1. Ecological Scales

G. Evelyn Hutchinson (1957) provided a strong theoretical basis for studying species distributions by integrating the importance of limiting abiotic and biotic factors in the context of niches. He posited that the range of abiotic conditions in which populations could persist could be depicted as fundamental niches of species, whereas biotic interactions, such as predation and competition, reduced fundamental niches to produce realized niches. In the 2000s, incorporating facilitation into ecological theory led to the proposal that biotic interactions can also increase fundamental niches (Bruno et al. 2003). In practice, niches are visualized as the ecological or biogeographical spatial extents at which species occur (Lomolino et al. 2017). Hutchinson's ideas rapidly inspired empirical studies designed to assess how abiotic and biotic forces establish species distributions in the field (e.g., Connell 1961). In this context, allelopathy emerged on the ecological map when

the release of toxins from some plants was reported to determine the local distribution, or spatial niche, of other plant species in California shrublands (Muller et al. 1964).

2.2. Biogeographical Scales

At large spatial scales, niches are manifest in geographic ranges of distribution, with realized ranges determined not only by negative biotic interactions but also by limits to dispersal (Lomolino et al. 2017). To our knowledge, no research has shown that natural distributional ranges are limited by allelopathy.

2.3. Distribution and Allelopathy

In the foundational study of the ecological importance of allelopathy, Muller and colleagues (1964) argued that direct allelopathy was responsible for zones devoid of herbaceous vegetation around aromatic shrubs in chaparral and coastal sage scrub. They found that volatile compounds from shrubs inhibited root growth of herbaceous seedlings in the laboratory and proposed that those toxins were in dew that condenses on seedlings in the field. Importantly, aerial delivery would allow toxins to reach neighboring plants effectively without being neutralized by soil microbial decay, adsorption to soil colloids, or xeric conditions (Muller & Muller 1956). However, an alternative explanation for the bare zones soon emerged. In a clear case of apparent competition (Holt 1977), Bartholomew (1970) demonstrated that the same shrub species harbored small mammals and birds that consume herbaceous plants near the shrubs, and when those herbivores were experimentally excluded, herbs recovered in bare zones. Despite a large body of other evidence for the allelopathic effects of chaparral shrubs (e.g., Muller & Del Moral 1966, McPherson & Muller 1969, Christensen & Muller 1975), allelopathy as a general mechanism for vegetation patterns in the field was largely rejected (Harper 1977, Keeley 1988). Rejection did not, however, impede four subsequent decades of research on the consequences of allelopathy for the distribution of species (e.g., Stowe 1979; Mahall & Callaway 1991, 1992; Pakeman et al. 2006). And in a new twist, recent research on chemical interactions between shrubs and their neighbors indicates apparent predation—herbivory on *Artemisia tridentata* appears to inhibit the germination of neighbors by increasing the production of volatile toxins (Karban 2007). Thus, a substantial body of work supports allelopathy as contributing to ecological-scale plant distributions in shrublands, chaparral (**Figure 1**), and elsewhere (e.g., Whittaker & Feeny 1971, Weidenhamer & Romeo 1989, Wardle et al. 1998, Hunter & Menges 2002).

The invasive grass genus *Sorghum*, more than any other genus, may provide a thorough mechanistic understanding of allelopathy and its influence on distributions. Detailed studies show that fine roots of *Sorghum bicolor* store and release large amounts of the chemical sorgoleone and that sorgoleone can be taken up by other species, after which the compound interferes with photosynthesis (for more detail, see Dayan et al. 2010). Sorgoleone is also produced by the invasive *Sorghum halepense* (Czarnota et al. 2001), and the comprehensive understanding of sorgoleone corresponds with evidence from field measurements and experiments indicating that allelopathy may contribute to strong effects of *S. halepense* on the distributions of other species. Rout et al. (2013) found that leachate from shoots and roots of *S. halepense* strongly suppressed the growth and reproduction of *Schizachyrium scoparium* when applied only to the soil in field experiments. Correspondingly, rhizome-driven expansion of *S. halepense* into *S. scoparium*-dominated native grassland occurred at roughly 0.5 m per year, and over time expansion dramatically decreased native diversity and virtually eliminated *S. scoparium*. In other cases, increased distribution of global invaders such as *Fallopia × bobemica* (Parepa et al. 2013) and *Acacia* species (Yanelli et al. 2019)

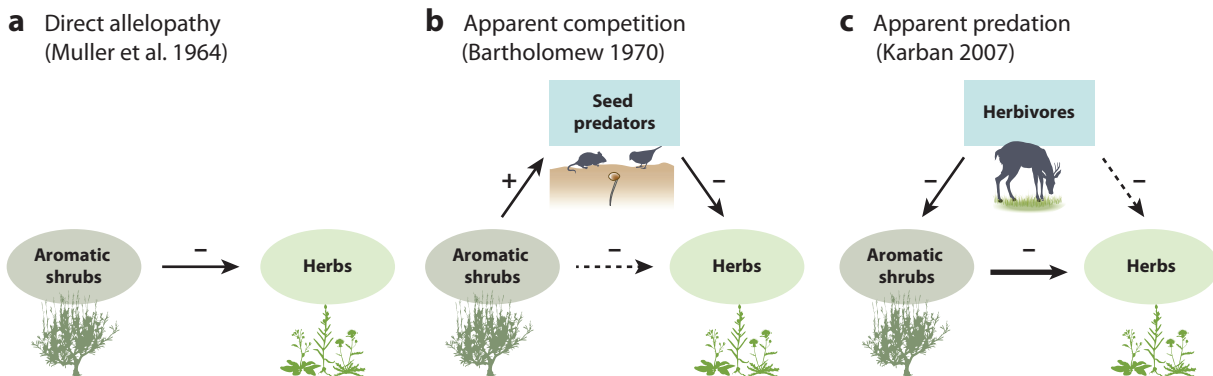


Figure 1

Alternative explanations for the formation of bare zones around desert and chaparral shrubs. (a) Muller et al. (1964) proposed that these zones resulted from direct allelopathic effects of aromatic shrubs on neighboring forbs and grasses through the production of volatile toxins. (b) Bartholomew (1970) showed instead that shrubs provide shelter to small mammals and birds that consume seeds of herbaceous vegetation near the shrubs. (c) Finally, in renewed support for a role of allelopathy in the distribution of herbaceous plants in the chaparral, Karban (2007) found that volatile compounds from shrubs inhibit seed germination of herbaceous neighbors and that experimental clipping increases the production of inhibitors. Solid and dashed lines indicate direct and indirect interactions, respectively. The thickness of the lines indicates the strength of the interaction.

in nonnative ranges has been proposed to be chemically facilitated by soil biota and other plants, respectively.

Root-based allelopathy has also been proposed as a mechanism for spatial segregation among roots and thus aboveground territoriality (the defense and exclusive use of space) in plants (Schenk et al. 1999). The most comprehensive body of evidence for such territoriality is for the North American desert shrub *Larrea tridentata*. There are four integrated sources of evidence. First, in many parts of its range, *L. tridentata* adults are remarkably regularly spaced (Fonteyn & Mahall 1978). Second, excavations demonstrate that *L. tridentata* adults show discrete spatial root segregation, four to five times more than predicted by unconstrained growth from the main stems (Brisson & Reynolds 1994). Third, Fonteyn & Mahall (1978) found that removal of neighboring *L. tridentata* shrubs around target conspecifics indicated virtually no competition for water, corresponding to the little overlap among roots of different individuals (Brisson & Reynolds 1994; but see Mahall et al. 2017 for long-term results). Fourth, Mahall & Callaway (1991, 1992) found that the root growth of *L. tridentata* dramatically decreased when roots approached roots of conspecifics and that this effect was reduced by adding activated carbon to the experimental soils. This result suggests that the regular spatial distribution and root segregation may be due to allelopathic effects of root exudates. This allelopathic effect was also manifest against another commonly co-occurring species, *Ambrosia dumosa*, which appears to be competitively excluded by *L. tridentata* over time (McAuliffe 1988). *A. dumosa*, which has a clumped distribution (Fonteyn & Mahall 1978), showed strong intraspecific root–root contact inhibition that was not affected by activated carbon and thus was due to a recognition process more akin to self–nonself recognition and Molisch’s perspective on allelopathy. As for *L. tridentata*, *A. dumosa* did not demonstrate short-term intraspecific competition in field removal experiments (Fonteyn & Mahall 1978), suggesting that root recognition may segregate resource exploitation belowground. Similarly, contrasting root responses of *Glechoma hederacea* (avoidance) and *Fragaria vesca* (intrusive) to one another (Semchenko et al. 2007) were proposed to drive their clumped and dispersed distributions in the field, respectively (de Kroon 2007).

3. CONDITIONALITY OF SPECIES INTERACTIONS

3.1. Ecological Scales

Species interactions vary in strength and direction with spatial and temporal environmental conditions (Bronstein 1994). In the classic studies of *Tribolium* beetles, competitive outcomes were temperature dependent (Park 1954). Mycorrhizal effects can be conditional, ranging from mutualistic to parasitic depending on phosphorus in soils (e.g., Hoeksema 2010). Competition among plants in the absence of herbivores may shift to facilitation when herbivores are present (Callaway et al. 2005a).

The stress gradient hypothesis (SGH) frames the idea that conditionality between competitive and facilitative interactions varies with the degree of abiotic and biotic stress in the environment (Bertness & Callaway 1994). The SGH considers competition and facilitation in their most general nonmechanistic meanings, but stressful conditions can also increase the production of secondary compounds (Selmar & Kleinwächter 2013) and abiotic stress has been proposed to regulate the strength of allelopathic interactions between plants (Reigosa et al. 2002).

3.2. Biogeographical Scales

Conditionality in species interactions may operate at large temporal and geographical scales (Bronstein 1994). Over evolutionary time, interacting species may prompt reciprocal adaptive changes to each other—they can coevolve. Because coevolution occurs between the phenotypic traits of interacting species (Hoeksema 2010), and because trait expressions vary across space, coevolved interactions are also expected to display geographical variation and be conditioned by the environment (Thompson 2005). This idea set the stage for the geographic mosaic theory of coevolution (GMTC) (Thompson 2005). The GMTC pivots around three fundamental evolutionary hypotheses: geographic selection mosaics, coevolutionary hotspots, and trait remixing. The geographic selection mosaics hypothesis posits that reciprocal selection on species traits depends on the local environment in which populations occur; that is, there is a genotype \times genotype \times environment interaction affecting the fitnesses of interacting species. The coevolutionary hotspots hypothesis proposes that reciprocal selection on traits in interacting species is present only within particular communities (coevolutionary hotspots) that are embedded in regions where natural selection is not reciprocal (coevolutionary coldspots). Finally, trait remixing posits that communities, with species traits coevolving in hotspot or coldspot fashions, are genetically connected throughout the region, so that the genetic structure of local populations is influenced by mutations, gene flow, genetic drift, and local extinctions that occur within the region (**Figure 2a**). Biogeographically based coevolution has been considered as a major biological factor affecting the intensity of allelopathic interactions (Rabotnov 1974, Reigosa et al. 1999, Callaway & Aschehoug 2000, Renne et al. 2014, Huang et al. 2018), and the GMTC provides an exceptional framework for organizing empirical evidence for conditionality and advancing our understanding of the ecological significance of allelopathy.

3.3. Ecological Variation in Allelopathy

Allelopathy may increase with abiotic stress (Rice 1984), which led to the stress hypothesis of allelopathy (SHA) (Reigosa et al. 2002). Consistent with the SHA, plants subjected to stressful conditions increase the production of secondary compounds (Top et al. 2017), including allelochemicals, in a well-understood physiological process (Selmar & Kleinwächter 2013). More importantly, some studies have shown that plants under both biotic (Thelen et al. 2005, Karban 2007) and abiotic (Ruan et al. 2016) stress display increased allelopathic effects. However, the

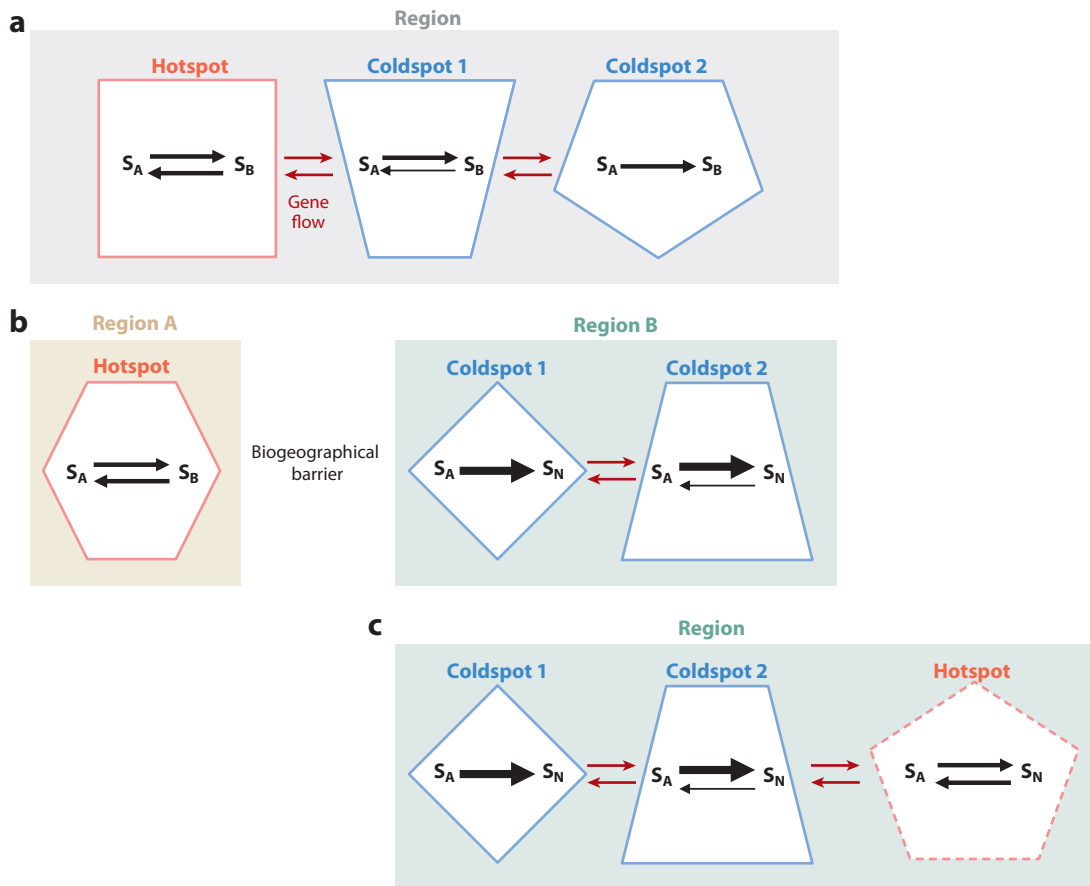


Figure 2

(a) Schematic representation of the geographic mosaic theory of coevolution (GMTC). Coevolutionary mosaics (represented by different shapes) occur within regions and are genetically interconnected (red arrows). Coevolutionary hotspots are mosaics where natural selection on traits in interacting species is reciprocal, whereas coevolutionary coldspots are mosaics where natural selection is not reciprocal. Black arrows inside mosaics show selection exerted by a pair of species on each other, with different thicknesses representing different selection strengths; in the pentagon for coldspot mosaics, selection occurs only through species A (S_A) on species B (S_B). (b) Allelopathic research on species invasions in the context of the GMTC. Species with a common evolutionary past (S_A and S_B in region A) exert more similar reciprocal selection on each other, particularly within coevolutionary hotspots, than do species with no coevolutionary past [S_A and species N (S_N) in region B]. S_A originated in region A and was introduced by humans into region B, where S_N is native and also naive to S_A phytochemicals. (c) The formation of coevolutionary hotspots. Allelopathy studies suggest that coevolutionary hotspots may arise over time (mosaic with dashed border) within the region where species have only recently interacted. Figure inspired by Thompson (2005) and Hoeksema (2010).

generality of the SHA remains unclear, and research along natural environmental gradients would be crucial (Pedrol et al. 2006). Similarly, little is known about how the SHA applies to the geography of allelopathy; that is, according to that idea, allelopathic interactions can be expected to be more frequent, stronger, or both in unfavorable environments, such as arid, semiarid, and high-altitude systems. Much of our knowledge about conditionality in allelopathy at ecological scales is still largely idiosyncratic (Aschehoug et al. 2014, Parepa & Bossdorf 2016, Meiners et al. 2017), and experiments or large-scale spatial tests of the SHA are needed. The SHA has the potential to broaden our understanding of general shifts in competitive and facilitative

plant interactions. It predicts that stress will promote negative interactions through allelopathy, whereas the SGH predicts increases in positive interactions with stress. This difference may be in part because general stress-related facilitation appears to be a by-product of the physical presence of other species that provide shelter, shade, and water retention, the effects of which can supersede their competitive effects. In contrast, chemically based parallels to facilitative by-products are not known. Regardless, because positive and negative interactions generally act in concert, integrating allelopathic responses along stress gradients may provide more detailed insight into how the abiotic environment controls species interactions.

In this context, mycorrhizae and allelopathic intensity deserve attention. Because mycorrhizal mutualists help plants capture soil resources, mycorrhizae are particularly important in stressful environments (Latef et al. 2016) and can increase negative allelopathic interactions by facilitating belowground connectivity among plants (Barto et al. 2011). Thus, mycorrhizal associations have the potential to contribute to increases in allelopathic intensity with stress.

3.4. Biogeographical Variation in Allelopathy

At biogeographical scales, allelopathy may be conditional due to an evolutionary history that is shared, or not, among interacting species (Rabotnov 1974; Reigosa et al. 1999, 2002; Callaway & Aschehoug 2000; Lankau 2012; Renne et al. 2014). This idea originated with the Russian ecologist Tikhon Rabotnov (1974), who proposed that allelopathic interactions are insignificant or neutral in coevolved plant communities (among species sharing a native biogeographical range) but important or strong in communities whose members share no evolutionary past. Rabotnov's insights were later conceptualized in the novel weapons hypothesis (NWH) (Callaway & Aschehoug 2000) and the biochemical recognition hypothesis (BRH) (Renne et al. 2014). Importantly, these latter hypotheses do not reject strong allelopathic interactions in any community, regardless of evolutionary history, but instead postulate that the odds of unusually intense allelopathic interactions increase when species encounter biochemicals new to them.

3.4.1. Novel weapons hypothesis. Humans can exert tremendous evolutionary selection, and a notable example is anthropogenic dispersal to new geographical ranges—species invasions. Human-mediated dispersal drives encounters among biota with no shared evolutionary past. In doing so, humans might create coevolutionary coldspots. That is, species invasions might give rise to situations in which selection between species is not reciprocal but strongly unidirectional, at least initially (**Figure 2b**). Investigating allelopathy experimentally in the context of species invasions and human-made coevolutionary coldspots gave new life to Rabotnov's ideas.

Callaway & Aschehoug (2000) reported that allelopathic effects of the invasive Eurasian *Centaurea diffusa* were more intense on North American species than on Eurasian congeners. This difference corresponded with a far stronger chemically based inhibition of phosphorus uptake in the Eurasian congeners than in the North American congeners. Together, this evidence suggested that some nonnative invasive species might exude chemicals that are relatively ineffective against well-adapted neighbors in communities where they originated, perhaps in the well-known context of nutrient acquisition (Li et al. 2016), but that happen to be highly inhibitory to nonadapted plants in communities where they were introduced. If so, contrasting allelopathic effects might have major ecological consequences, as they cause some species to experience marked increments in relative abundance in nonnative ranges compared with native ranges, perhaps providing a mechanism for nonnative plant invasion. The NWH has received substantial experimental support derived from many species and systems (e.g., Callaway et al. 2008, Qin et al. 2013, Svensson et al. 2013, Zheng et al. 2014, Becerra et al. 2017). In addition, two recent reviews found that most of the nonnative invasive species considered “produce allelochemicals with the potential to negatively affect

native plant performance” (Kalisz et al. 2021, p. 367) and that “native plants suffered more from leachates of naturalised alien plants than from leachates of other native plants” (Zhang et al. 2020, p. 348). But perhaps because successful invasions provide much more obvious potential study systems than do unsuccessful invasions, reciprocal inhibitory effects of native species on nonnative species have received little attention. A good example of the latter is the suppression of the South American nonnative grass *Paspalum notatum* by an allelopathic shrub native to Florida, *Polygonella myriophylla* (Weidenhamer & Romeo 1989; for other examples of native plants allelopathically suppressing nonnative plants, see Zheng et al. 2014 and Ning et al. 2016). Additionally, leachates and degraded litter of the nonnative grass *Bothriochloa ischaemum* reduced germination, growth, and survival of the native grasses *Andropogon gerardii* and *S. scoparium*, and leachates and degraded litter of *A. gerardii* reduced the biomass of *B. ischaemum* but not of *S. scoparium* (Greer et al. 2014), again suggesting that evolutionary history matters for the intensity of allelopathic interactions.

3.4.2. Biochemical recognition hypothesis. Chemical communication can occur among seeds. Seeds can sense competitors (Preston & Baldwin 1999, Renne et al. 2014), facilitators (Yanelli et al. 2019), and symbiotic hosts (Plakhine et al. 2009) via phytochemicals released by conspecific or heterospecific neighbors. Sensing the biotic and abiotic environment may provide critical information for germination or induce an individual to remain dormant until better conditions arrive. This is crucial because germination is irreversible and has profound consequences for fitness and therefore is expected to be under strong selection (Cohen 1966). Similar to Rabotnov (1974) and Callaway & Aschehoug (2000), but in specific reference to germination, Renne et al. (2014) suggested that shared evolutionary histories may increase the odds that seeds from some species recognize phytochemicals from other species and then adaptively germinate or defer germination depending on neighbor identity. Accordingly, species with a shared evolutionary past are predicted to adjust their germination responses to each other’s presence better than species with no evolutionary history (Renne et al. 2014). To our knowledge, the BRH, *sensu* Renne et al. (2014), has been evaluated once. Assuming that delayed germination is advantageous in competitive environments, Renne et al. (2014) assessed whether phytochemical leachates from co-occurring species in Argentinean versus North American grasslands reduced seedling emergence more than phytochemical leachates from species with no historic association. They found that some species exhibited reduced emergence following leachate exposure of sympatric relative to allopatric species, supporting species-specific biochemical recognition. Importantly, leachate origin did not affect seedling biomass, suggesting the possibility of a nontoxic biochemical effect on germination reduction but not growth. Thus, sympatric plant association might contribute to the evolution of species-specific biochemical recognition. Recently, general stimulatory effects of leachates from sites invaded and uninvaded by nonnative *Acacia* species on germination of acacias and native species were suggested to also support the BRH (Yanelli et al. 2019); however, some positive germination responses occurred irrespective of shared evolutionary pasts between species. Further testing the BRH requires increasing the number of study systems, using putative chemicals that are or are not recognized by seeds, and identifying mechanisms underlying germination decisions. Many previous studies, specifically those of the effects of leachates on seed germination, might, however, be reconsidered in the context of recognition and not toxicity.

3.4.3. Formation of coevolutionary hotspots. Nine years before the articulation of the NWH, Lawrence et al. (1991) found that individuals of seven native species that had not encountered nonnative *Ailanthus altissima* in the field were more susceptible to *A. altissima* toxins than were conspecifics that occurred with the invader. Moreover, seeds produced by unexposed populations were more susceptible to *A. altissima* toxins than were seeds produced by previously

exposed populations, suggesting that phytotoxic susceptibility/tolerance is heritable. Similarly, Callaway et al. (2005b) found that some grass species from sites invaded by *Centaurea stoebe* (experienced) exhibited increased resistance to *C. stoebe* and that the differential effects of the invader were ameliorated by activated carbon. Conversely, some experienced grass congeners exerted stronger competitive effects on *C. maculosa* biomass than did inexperienced congeners.

Plant species may evolve either reduced or increased production of allelochemicals in their nonnative ranges, depending on trade-offs between fitness advantages and production costs of toxins. That is, if phytotoxins are costly, then individuals that release them at low concentrations may be favored because reduced doses may suffice to inhibit neighbors that are not adapted to the toxins. Low levels could also be advantageous when toxins are ineffective against neighboring plants even at high concentrations. Alternatively, if phytotoxins confer fitness advantages, and if that benefit is greater than the production cost, then selection may favor individuals with increased phytotoxicity, as proposed in the allelopathic advantage against resident species (AARS) hypothesis (Callaway & Ridenour 2004).

To our knowledge, only two studies have used both native and nonnative genotypes to explore evolved allelopathic responses in novel environments. In the first study, Prati & Bossdorf (2004) found that native European genotypes of *Alliaria petiolata* reduced germination of both North American *Geum laciniatum* and European *Geum urbanum* in similar proportions. However, nonnative North American *A. petiolata* reduced the germination of only naive North American *G. laciniatum* and had no effects on experienced European *G. urbanum*. These puzzling results might be explained by findings from a later study in which nonnative populations of *A. petiolata* evolved reduced production of sinigrin, an allelochemical with antimycorrhizal properties, along an invasion chronosequence in response to shifts in ambient competition (Lankau et al. 2009). The study authors found that as nonnative populations age, communities become increasingly dominated by *A. petiolata* and competition moves from interspecific to intraspecific, and under those conditions, natural selection drives down the production of sinigrin. This is because, in contrast to other species in the community, *A. petiolata* is nonmycorrhizal and sinigrin production is costly. Nonnative populations sampled by Prati & Bossdorf (2004) may have been from sites where *A. petiolata* is abundant and thus with low sinigrin production. Reduced concentrations of sinigrin could be effective against new naive neighbors but insufficient against old experienced ones. We do not know, however, how variation in sinigrin production in nonnative populations compares with that in native populations. Furthermore, there are strong biogeographical differences for the effects of *A. petiolata* on mycorrhizal colonization and mutualistic performance (Callaway et al. 2008), complicating direct plant-to-plant allelopathy.

In the second study, Yuan et al. (2013) found that nonnative genotypes of *Solidago canadensis*, relative to native genotypes, increased the production of allelochemicals and produced extracts that increased the suppression of seed germination and biomass of a naive new neighbor. These results are consistent with the AARS hypothesis. However, knowledge about variation in allelopathic traits between native and nonnative populations is limited, and more studies are needed to understand how phytotoxicity might evolve in nonnative ranges.

One important, yet poorly studied, further step in assessing shared evolutionary history in allelopathic interactions is exploring mutual adaptive responses between native and nonnative species. In the first study to document coevolution between native and nonnative plants, Lankau (2012) showed that populations of the native *Pilea pumila* that co-occurred with evolved high-sinigrin populations of the nonnative *A. petiolata* (Lankau et al. 2009) were more tolerant of competition from *A. petiolata* than from *P. pumila* populations growing at sites with low-sinigrin populations of the invader.

The evolution of increased resistance to novel plant toxins (Lawrence et al. 1991, Callaway et al. 2005b), increased competitive abilities in native species (Callaway et al. 2005b), reduced phytotoxicity in nonnative species (Lankau et al. 2009), and reciprocal responses between natives and nonnatives (Lankau 2012) suggests that coevolutionary hotspots might rapidly arise in environments where species with no evolutionary history meet (**Figure 2c**). The development of such hotspots, in which species progressively interact more evenly, may provide a powerful mechanism for species coexistence in those environments.

4. COEXISTENCE OF SPECIES

4.1. Coexistence Theory

Coexistence theory explores ecological and evolutionary processes that affect the interactions of species with their local biotic and abiotic environments and that determine relative abundances of species within communities (Lankau 2011, HilleRisLambers et al. 2012). Central to coexistence theory is understanding the mechanisms that maintain the diversity of species that co-occur at the same trophic level. Chesson (2000) organized these mechanisms into two categories: equalizing and stabilizing. Equalizing mechanisms reduce inherent fitness differences between species, whereas stabilizing mechanisms increase negative intraspecific interactions relative to negative interspecific interactions. In other words, equalizing mechanisms cause species to limit themselves more than they limit others, and stabilizing mechanisms have traditionally been related to the idea of niche differences (Adler et al. 2007). A key distinction between these categories is that stabilizing mechanisms depend on species abundance, but equalizing mechanisms do not (HilleRisLambers et al. 2012). The abundance-dependent nature of stabilizing mechanisms promotes abundance when species are rare and decreases it when species are common. In practice, distinguishing between these mechanisms is difficult (see HilleRisLambers et al. 2012), likely because they do not operate independently of each other. Communities in which species within the same trophic level interact by chemical means have provided exceptional, but rare, study systems for testing modern coexistence theory (Lankau 2011, Levine et al. 2017, Soliveres & Allan 2018). Below, we review the empirical evidence derived from those systems and how this contributes to our understanding of coexistence.

Chesson's (2000) ideas also emphasize that niche differences alone do not ensure stable coexistence. That is, coexistence in Chesson's framework also depends on the magnitude of the fitness difference between species (Adler et al. 2007). Equalizing (fitness similarity) and stabilizing (niche differences) mechanisms operate in opposing directions, such that in the absence of fitness differences between species (strong equalizing mechanisms), as in neutral models, small niche differences (weak stabilizing mechanisms) suffice to achieve coexistence; in contrast, under large fitness differences (weak equalizing mechanisms), species coexistence requires large niche differences (strong stabilizing mechanisms). Species coexistence thus results from the balance between fitness similarities and niche differences, and whereas stabilizing niche differences promote coexistence, relative fitness differences lead to competitive exclusion (see figure 2 in Adler et al. 2007, figure 1 in MacDougall et al. 2009, and figure 3f in HilleRisLambers et al. 2012). For example, fitness advantages of nonnative species based on novel chemical traits are predicted to exclude native species unless niches of natives and nonnatives do not overlap (MacDougall et al. 2009).

4.2. Intransitive Competition and Modification of Interactions

Most studies of more than two species assume competitive interactions to be hierarchical or transitive (Soliveres & Allan 2018). In the simplest three-species scenario, transitive competition is

represented as species A > species B > species C < species A. Competitive interactions can, however, be nonhierarchical, or intransitive, such that species A > species B > species C > species A, forming competition loops. Communities in which no species is competitively superior to all other species can be conceptualized as rock-paper-scissors systems (Kerr et al. 2002). But complete competitive loops are not required to establish strong indirect interactions that promote coexistence among groups of species, which is important, as few true loops have been experimentally identified (see Aschehoug et al. 2016, Levine et al. 2017, Soliveres & Allan 2018). Intriguingly, some species modify interactions among other species without creating a loop, yet still drive strong indirect interactions. Intransitive competition and the modification of interactions by a third species have gained attention (Metlen et al. 2013, Levine et al. 2017, Soliveres & Allan 2018), but the mechanisms (i.e., equalizing versus stabilizing) driving coexistence within species networks remain poorly explored. Communities with allelopathic interactions are among the exceptions, and work in those communities has provided insights into intransitivity (Lankau 2008, 2009; Armas & Pugnaire 2011; Metlen et al. 2013).

4.3. (Co)evolution

A full understanding of how species diversity develops and is maintained must incorporate evolutionary changes that arise from species interactions (Lankau 2011). Perhaps the best example of the importance of evolution in coexistence is character displacement (Dayan & Simberloff 2005), the emergence of niche differentiation caused by competition. Evolution can promote species coexistence through processes that can increase not only niche differences but also fitness similarities between species (for a comprehensive review, see Lankau 2011). Attempts to integrate evolution into Chesson's framework are only emerging, and notably, allelopathy is again playing a role in those efforts (Huang et al. 2018).

4.4. Coexistence via Intransitive Competition

Communities with allelopathic interactions inspired early studies of intransitive competition. The groundbreaking study was with sessile invertebrates on coral reefs, not plants. Jackson & Buss (1975) argued that species-specific allelopathic effects of sponges and ascidians on ectoproct species promoted the formation of competitive networks (i.e., intransitive competitive relationships) that precluded any single species from monopolizing the most limiting resource in marine hard-substrate environments—space. Though hard to measure experimentally, such intransitive allelopathy could maintain high species diversity even in the absence of disturbance or consumer effects. Similarly, Kerr et al. (2002) demonstrated that three strains of *Escherichia coli* coexisted through intransitive allelopathy. In this system, *E. coli* strain C produces colicin, a toxin that kills the susceptible *E. coli* strain S, but colicin is ineffective against the resistant *E. coli* strain R. However, strain R grows at faster rates than strain C because producing colicin is costlier than being resistant to colicin, and strain S grows faster than strain R because susceptibility confers nutrient-uptake advantages. Consequently, strains of *E. coli* are engaged in the rock-paper-scissors game described above. Importantly, this study reveals conditions needed for intransitive competition: Competitive reversal is caused by production of a toxin, the presence of susceptible and resistant genotypes, a balanced cost that favors toxin resistance over toxin production, and the action of different types of negative interactions (i.e., allelopathy and exploitative competition; also see Lankau 2011). Because similar conditions might be present in natural plant, sessile marine invertebrate, fungal, and bacterial communities (Kerr et al. 2002), intransitive competition may be an important mechanism for coexistence in nature (e.g., Soliveres & Allan 2018), and allelopathy, relative to resource competition, might be a key mechanism for intransitivity (Armas & Pugnaire 2011).

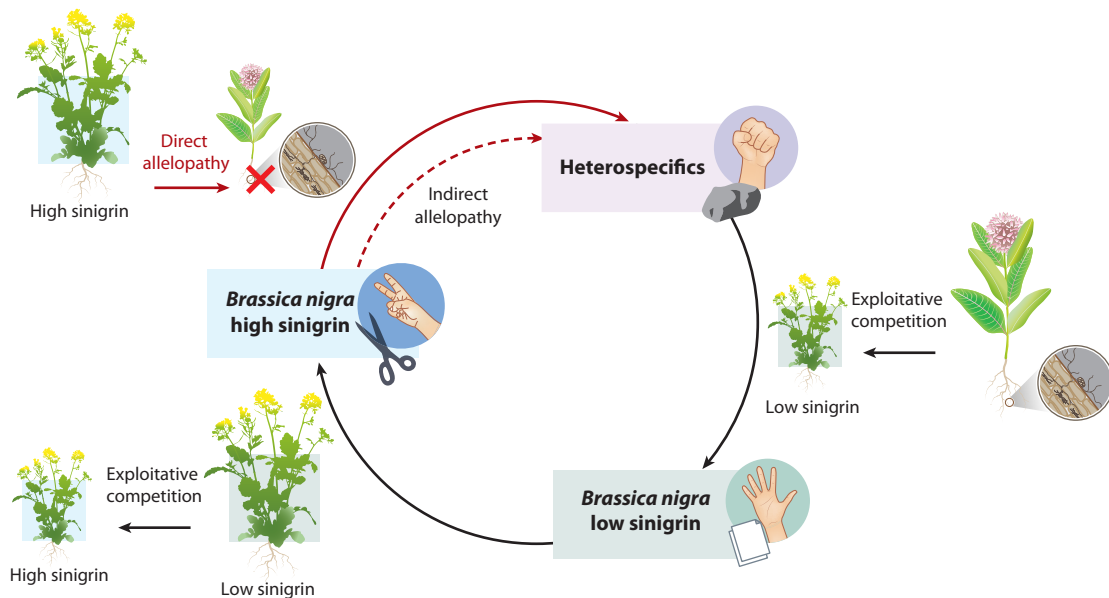


Figure 3

The intransitive competition network composed of *Brassica nigra* and neighboring plants (heterospecifics). This type of cyclic dynamics is also described as a rock (heterospecifics)–paper (*B. nigra* low sinigrin)–scissors (*B. nigra* high sinigrin) system. *B. nigra* expresses variation in the concentration of the allelochemical sinigrin; individuals with high sinigrin concentration outcompete heterospecifics but are outcompeted by conspecifics with low sinigrin concentration, which in turn are outcompeted by heterospecifics. Negative effects of sinigrin on heterospecifics are partially mediated by inhibiting mycorrhizal associations. Sinigrin production is costly, and *B. nigra* is nonmycorrhizal, generating a trade-off between intra- and interspecific competitive ability. Heterospecifics overcome *B. nigra* with low sinigrin levels because mycorrhizae enhance their uptake of soil resources. This competition loop maintains the diversity of both species and genotypes. Coexistence in this study system is caused by the production of a toxin, the presence of susceptible and resistant community members, a trade-off between toxin production and competitive ability, and the operation of resource- and nonresource-based interactions. Similar conditions have been reported for a system typified by three strains of *Escherichia coli*.

Empirical studies of intransitive competition are rare, and evidence that intransitivity is mediated by plant allelopathy is rarer. To our knowledge, Lankau and collaborators, studying interactions between *Brassica nigra* and neighboring plant species, provide the key example. Lankau & Strauss (2007) reported that intransitive competitive networks, based in part on allelopathy, promote not only the diversity of species but also genotypic diversity. *B. nigra* expresses variation in the concentration of the allelochemical sinigrin, and individuals with high sinigrin concentration outcompete neighboring species. However, high-sinigrin individuals are outcompeted by conspecifics with low sinigrin concentrations, and they are outcompeted by heterospecifics (Figure 3). Given the inhibitory effects of sinigrin on arbuscular mycorrhizal fungi (AMFs), negative effects of *B. nigra* on neighbors may be partially mediated by reductions of fungi that mutualistically associate with heterospecifics (Lankau & Strauss 2007, Lankau 2011, Lankau et al. 2011). Members of the Brassicaceae do not establish mutualistic associations with AMFs, so sinigrin confers little advantage in intraspecific competition. In contrast, producing high levels of sinigrin can be a disadvantage when individuals are competing with conspecifics because, similar to colicin (Kerr et al. 2002), sinigrin production is costly. Moreover, producing sinigrin seems to generate a trade-off between intra- and interspecific competitive ability (Lankau 2008). As a result, selection should favor genotypes with high sinigrin concentration in interspecific competition, whereas genotypes low in sinigrin should be favored in intraspecific

competition. This trade-off increases the abundance of *B. nigra* genotypes when genotypes are rare; consequently, it is a stabilizing, niche-based coexistence mechanism (Chesson 2000, Lankau 2008). Finally, heterospecifics can overcome low-sinigrin *B. nigra* individuals because AMFs enhance soil resource uptake by neighboring plant species (i.e., classic exploitative competition; Lankau et al. 2011). The phylogenetic distance between the *B. nigra* and *E. coli* systems is large, but the ecological and evolutionary resemblance is remarkable in that toxin production trades off with competitive ability, sensitive and nonsensitive actors are involved, and resource and nonresource interactions occur. Further studies should address the importance of those shared features for developing intransitive dynamics and maintaining species diversity.

Lankau & Strauss (2007) also suggest major consequences for conservation, as their results show that conserving species may require conserving genotypes. In another fascinating example of the potential mutual dependency between genetic and species diversity, intraspecific variation in the chemical diversity of monoterpenes in *Pinus sylvestris* was also positively correlated with the species richness of the vegetation growing beneath individual trees (Iason et al. 2005). Mechanisms driving that association are not known, however.

4.5. Coexistence via Modification of Interactions

Parker & Muller (1979) reported a scenario in which a native herb, *Pholistoma auritum*, establishes monodominant stands under *Quercus agrifolia* trees in California savannas. They found that annual grasses surrounding the tree canopies grew well under trees without *P. auritum*, but that *P. auritum* completely excluded grasses via the effects of litter and leachates. Their field measurements and experiments suggested exceptionally strong indirect interactions potentially mediated by allelopathy. Metlen et al. (2013) found that the invasive forb *Centaurea stoebe* had strong competitive [possibly allelopathic (Ridenour & Callaway 2001)] effects on the invasive grass *Bromus tectorum* in grassland without pine canopies. *Pinus ponderosa* canopies had no effects on *C. stoebe* and *B. tectorum* when they were grown alone, but the competitive effects of *C. stoebe* on *B. tectorum* did not occur under *P. ponderosa*, where chemicals from pine litter appear to modify interactions between those invasive species. Shade also reduces the allelopathic effects of *C. stoebe* (Chen et al. 2013). Similar dynamics have been reported for interactions between *P. ponderosa*, *C. stoebe*, and the native grass *Pseudoroegneria spicata* (Metlen & Callaway 2015). A next step would be to explore whether the modification of interactions affects coexistence through equalizing or stabilizing mechanisms.

4.6. Coexistence via (Co)evolution

The idea that the strength of allelopathy is conditioned by evolutionary history shared by community members (Rabotnov 1974, Reigosa et al. 1999, Callaway & Aschehoug 2000) implies that coevolution between species in the same trophic level might reduce the proportion of strongly unbalanced interactions and promote coexistence (Callaway et al. 2005b, Lankau 2012). The adaptive response of populations to chemicals released by neighbors (Lawrence et al. 1991, Ehlers & Thompson 2004, Callaway et al. 2005b, Grøndahl & Ehlers 2008), as well as responses that have reciprocally evolved between them (Lankau 2012), can facilitate species coexistence via equalization or stabilization, contingent on the abundance-dependent nature of responses (Chesson 2000, Adler et al. 2007, HilleRisLambers et al. 2012). Huang et al. (2018) conducted an elegant experiment designed to explore mechanisms for coexistence in the coevolved interaction between *A. petiolata* and *P. pumila* (Lankau 2012). They found that the coexistence of those species was promoted more by increases in stabilizing (increased niche differences) than in equalizing (reduced fitness differences) processes. The NWH has been classified as a fitness difference-based

hypothesis for invasion because novel biochemicals confer large advantages on nonnative species compared with native species (MacDougall et al. 2009). Consequently, those results are important because they emphasize that fitness differences are precluded from leading to competitive exclusion via a mechanism that stabilizes coexistence (i.e., niche differentiation; see Adler et al. 2007). More research is needed on coexistence mechanisms hidden behind (co)evolved responses such as those discovered by Huang et al. (2018). A recent review of allelopathic interactions found a negative relationship between allelopathic intensity and the phylogenetic distance between species, indicating that allelopathy might contribute to coexistence of closely related species (Zhang et al. 2020).

4.7. Coexistence via Chemical Recognition and the Role of Chemical Communication in Overyielding

Accumulating evidence indicates that the mutual perception of plants by means of chemical messengers, as conceived by Molisch [2001 (1937)], can be sophisticated to the point where plants appear to discriminate substances released from self from substances released from nonself and even kin versus nonkin (Dudley 2015), both aboveground (Karban & Shiojiri 2009) and belowground (Novoplansky 2019). The ability of plants to selectively detect and respond to chemical signals from other plants is likely to promote species coexistence (Callaway & Li 2020), but that mechanism awaits demonstration, as the study of chemical recognition in plants has focused on the response of individuals. Furthermore, other than the research on plant distributions described above (Mahall & Callaway 1991, 1992; de Kroon 2007), research on the ecological significance of phytochemical recognition is only now emerging. For example, increased productivity (overyielding) in mixtures of *P. spicata* populations compared with population monocultures could not be explained by traditional mechanisms such as resource complementarity and, more recently, soil pathogens (Atwater & Callaway 2015); instead, intraspecific overyielding in *P. spicata* may be affected by root recognition (Yang et al. 2015). That is, root elongation rates of *P. spicata* decreased more after contacting roots of plants from the same population than after contacting roots of plants from a different population, which could translate into reductions in the volume of soil occupied by roots and concomitant higher acquisition of resources in monocultures than in mixtures (Yang et al. 2015). The possibility that such root recognition responses influence overyielding in other systems should be studied (see Mommer et al. 2010).

We are unaware of studies linking chemical interactions to overyielding in mixtures in natural communities, but recent work with crops indicates that root exudates contribute to overyielding in intercropping systems. *Vicia faba* (fava beans) increased biomass and grain production by *Zea mays* (maize) when grown in low-phosphorus soil by releasing organic acids and protons that acidified soil and mobilized phosphorus. This release promoted maize uptake of phosphorus, for which maize has a high requirement (Li et al. 2007). In turn, root exudates from maize enhanced nodulation and N₂ fixation in fava beans, enhancing their productivity (Li et al. 2016). These stimulatory effects were specific, as root exudates from *Triticum aestivum* (wheat) and *Hordeum vulgare* (barley) did not promote nodulation in fava beans (Li et al. 2016). Species-specific responses are an intriguing aspect of the fava bean–maize system because chemical facilitation occurred between species with distant geographic origins [the Near East for fava beans (Caracuta et al. 2016) and the Americas for maize (Piperno & Flannery 2001)], and it was not observed between species with similar geographic origins, as both wheat and barley are thought to have also originated in the Near East (Heun et al. 1997, Badr et al. 2000). We do not know, however, whether coevolution conditions those positive chemical effects as it might for negative allelopathic effects (e.g., Callaway & Aschehoug 2000). Such root chemical facilitation has not been reported for wild plants.

SUMMARY POINTS

1. Recent advances in the study of chemical interactions suggest value in a return to the original view of allelopathy as the mutual inhibitory and stimulatory perception among plants.
2. Allelopathy influences local plant distributions in grasslands, shrublands, and forests around the world.
3. Simple addition or removal experiments can provide clear experimental evidence that general negative or positive interactions affect distributions. However, evidence for allelopathy (or nutrient depletion for that matter) as a mechanism affecting distributions is necessarily built through accumulation of correlative evidence, not a decisive experiment. In other words, we can show that species A suppresses species B, that species A produces a powerful toxic chemical, and that this chemical when applied realistically suppresses species B. But we cannot eliminate all other potential mechanisms.
4. The strength of allelopathy may be conditioned by coevolution, providing the basis for novel allelopathic traits facilitating the invasion of nonnative species.
5. Adaptive responses of native species to nonnative chemicals and those of nonnative species to native chemicals suggest that coevolutionary hotspots can rapidly emerge in regions where species with no shared evolutionary history meet.
6. Allelopathy in phylogenetically distant systems where competition loops have been established suggests that allelopathy can contribute to intransitive competition and species coexistence.
7. Allelopathy has much to contribute to fundamental ecological concepts.

FUTURE ISSUES

1. Predictive models for how ecological conditions affect the strength and direction of allelopathic interactions are needed.
2. Integrating allelopathic responses along stress gradients may provide further insight into how the abiotic environment controls shifts in species interactions.
3. Further studies should address the general importance of features shared by the *Escherichia coli* and *Brassica nigra* systems for developing intransitive dynamics and maintaining species diversity.
4. Allelopathic interactions between native and nonnative species can provide models that incorporate evolution into coexistence theory.
5. Studies of negative and positive chemical recognition and communication between plants have the potential to broaden our understanding of the ecological and evolutionary importance of allelopathy.

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Is one of the best empirical studies of intransitive competition.

Is the first study to document coevolution between native and nonnative plant species.

Provides an excellent example of intransitive competition, by which maintaining species diversity requires conserving genotypes and vice versa.

Seems to be the first report of adaptive responses of native species to nonnative chemicals.

First exploration of chemical root recognition between conspecifics and heterospecifics.

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Is a foundational study of the ecological importance of allelopathy.

Seems to be the first manuscript proposing that coevolution conditions the strength of allelopathy.

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Errata

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