ESSAY REVIEW
Interactions among plants and evolution

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Summary

1. Interactions among plants and their consumers, pollinators and dispersers are central to evolutionary theory, but interactions among plants themselves have received much less attention. Thus focusing more attention on the evolutionary role of plant–plant interactions may provide greater insight into the processes that organize communities.

2. Here, we integrate divergent themes in the literature in an effort to provide a synthesis of empirical evidence and ideas about how plant interactions may affect evolution and how evolution may affect plant interactions.

3. First, we discuss the idea of niche partitioning evolving through competitive interactions among plants, the idea of niche construction evolving through facilitative interactions, and the connections between these ideas and more recent research on diversity and ecosystem function and trait-based community organization.

4. We then review how a history of coexistence within a region might affect competitive outcomes and explore the mechanisms by which plants exert selective forces on each other. Next, we consider recent research on invasions suggesting that plant interactions can reflect regional evolutionary trajectories. Finally, we place these lines of research into the context of extended phenotypes and the geographic mosaic of co-evolution.

5. *Synthesis.* Our synthesis of separate lines of inquiry is a step towards understanding the evolutionary importance of interactions among plants, and suggests that the evolutionary consequences of interactions contribute to communities that are more than assemblages of independent populations.

Key-words: co-evolution, competition, evolution, extended phenotype, facilitation, niche, plant–plant interactions, selection

…it may be argued, therefore, that the essential qualities that determine the ecology of a species may only be detected by studying the reaction of its individuals to their neighbours.

John Harper, 1964

Introduction

Understanding the nature of interactions among plants and their consumers, pollinators and dispersers has been vital to evolutionary theory, but interactions among plants themselves have received much less attention. Here, we integrate divergent themes in the literature including experiments testing evolution, niche theory, exotic invasions, extended phenotypes and the nature of geographic mosaics in a synthesis of how plant interactions might affect evolution and how evolution may affect plant interactions. Ecologists have extensively 'studied the reaction of individuals to their neighbours' (Harper 1964), arguably more than most other aspects of plant ecology, but there have been minimal efforts to tie these 'reactions' to evolution, and even fewer efforts to understand interactions that might lead to evolution and thus a rethinking of fundamental community theory (e.g. Lortie *et al.* 2004). For example, it can be argued that the 'the local community is an epiphenomenon [of populations] that has relatively little explanatory power in ecology and evolutionary biology' (Ricklefs 2008). However, this epiphenomenon perspective must be reconciled with the ubiquitous viewpoint that species interacting at the scale of local communities drives selection and thus speciation, and the very existence of the species pools on which regional and global analyses are based (Brooker *et al.* 2009; Kursar *et al.* 2009). Here, our fundamental goal is to explore the potential of community-scale interactions *among plant species* to result in evolution.

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Between 1979 and 1991, Roy Turkington, Lonnie Aarssen and their colleagues experimentally demonstrated that interactions between grass and legume species were affected by the community history of the populations from which individual plants were collected (Turkington, Cavers & Aarssen 1977; Aarssen, Turkington & Cavers 1979; Turkington 1979; Turkington & Cavers 1979; Turkington & Harper 1979; Turkington & Mehrhoff 1991). Their work raised the possibility that interactions among plant species generate 'continuous co-evolution maintaining balanced competitive abilities' (Aarssen & Turkington 1985b), that has the potential to 'result in a balanced, harmonious and dynamic stability within that community' (Turkington 1979). If co-evolution among plant competitors contributes to harmonious community stability, then plant communities are certainly more than just overlapping populations of species (Gleason 1926). Research on plant–consumer, plant–pollinator and plant–disperser interactions has been central to understanding the complex mutualistic and co-dependent interactions among species that structure communities. However, with some notable exceptions, interactions *among* plants have not been emphasized as processes that contribute to selection and evolution (Bronstein 2009).

Why have plant interactions attracted so little interest from evolutionary biologists? Or put another way, why have ecologists interested in plant interactions so seldom emphasized how these interactions might drive evolution? We can think of three inter-related possibilities. First, in natural communities, individual plants interact with many other species at the same time, and even a single individual may be interacting with multiple other species at any given moment. This creates dilute or 'diffuse' (Wilson & Keddy 1986) interactions which may strongly modify interactions among any two species (Callaway & Pennings 2000; Metlen 2010), thus making it difficult to envision interactions that are consistent enough among the same taxa to allow evolution. The problem of 'diffuseness' may be exacerbated by inconsistent spatial relationships among interacting plant species. For example, a plant species may interact with 10 different neighbours (very diffuse) or two different neighbours (not very diffuse) depending on conditions. The same plant species may always interact with the same 10 neighbours (highly spatially consistent) or a different set of 10 neighbours (highly spatially inconsistent) in each community in which it is found. We present a hypothetical gradient of selection intensity depending on the diffuseness and spatial consistency of interactions in Fig. 1.

A second possibility related to, and perhaps derived from, the logistical problems of quantifying interactions among plant species in groups, is theory for how plant communities 'assemble' in the absence of disturbance and in a homogeneous environment. One theory poses that plant communities are competitively transitive in nature (Keddy, Twolan-Strutt & Wisheu 1994). In other words, all species in a given pool, or community, can be ranked in a simple linear competitive hierarchy. This strict 'pecking order' that results from hierarchical competitive abilities provides a predictive tool for community organization, but produces a model that does not possess asymmetric (i.e. 'rock–paper–scissors') interactions and there-
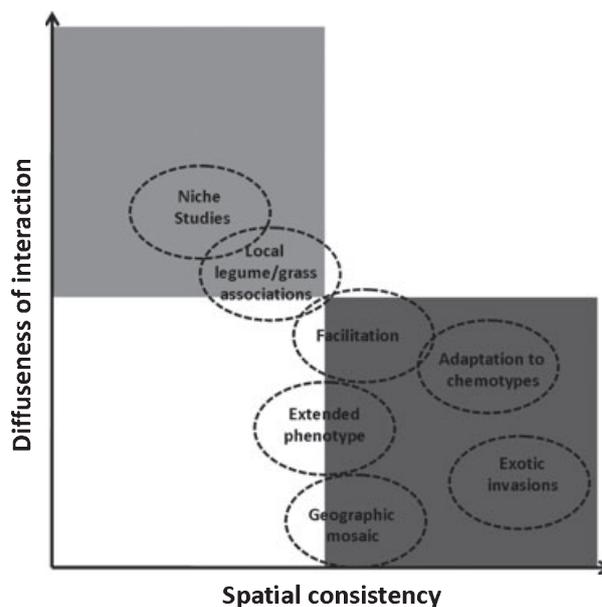

Fig. 1. Conceptual diagram for where selection derived from plant–plant interactions might be expected to be intense or weak. The darker the shade, the more intense natural selection is hypothesized to be. We have also speculated on where key conceptual ideas or key studies might be located along the gradient of selection intensity.

fore leaves little room for strong reciprocal selective forces. Much of the empirical evidence supporting the dominance of competitive hierarchies is derived from experiments in which each member of a community is grown in competition with a 'phytometer' species in the glasshouse (Keddy, Gaudet & Fraser 2000; Fraser & Keddy 2005; Storkey, Moss & Cussans 2010). The problems with this approach are numerous. As community members are not grown in competition with one another (only with the phytometer species), it is impossible to assess whether a highly ranked competitor could be outcompeted by a lower-ranked competitor. Thus, this approach eliminates any potential for spatial niche partitioning, a fundamental determinant of coexistence (Parrish & Bazzaz 1976). The phytometer approach also assumes that facilitative (Callaway 2007) or indirect interactions (Miller 1994; Levine 1999; Callaway & Pennings 2000) do not influence community structure. Lastly, this approach relies on the competitive *response* of community members to a phytometer species, a component of competition that may be poorly understood (Wang *et al.* 2010).

A third barrier may be the general 'individualistic' paradigm for the nature of plant communities. As Lortie *et al.* (2004) discuss in detail, plant interactions as drivers of evolution do not mesh seamlessly with individualistic community theory. In other words, if local interactions can affect the genotypes of interacting plant species, then communities cannot be organized only by 'the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment' (Gleason 1926). Although many plant ecologists now agree that communities are not wholly individualistic (e.g. Lortie *et al.* 2004), the underlying assumptions implicit in this theory

may have contributed to an historical under-emphasis of the importance of plant–plant interactions as drivers of evolution.

Here, we re-examine ideas that arose with Turkington and Aarssen and build on these ideas by synthesizing several lines of current research that shed new light on plant interactions, communities and evolution. These lines are not focused only on studies of direct plant–plant interactions but also include niche theory, biogeographical studies of invasive plants, extended phenotypes (e.g. Whitham *et al.* 2006) and the geographic mosaic of co-evolution (e.g. Thompson 2005). We present these conceptually overlapping lines of thought in separate sections, but with the hope of synthesizing these contributions to understanding the evolutionary consequences of interactions among plants.

THE IMPORTANCE OF LONG-TERM RELATIONSHIPS

As noted above, Turkington and colleagues conducted a series of innovative experiments indicating that a history (sometimes a very short history) of coexistence among plant species affected the outcome of interactions among the same species. Their results have strong implications for how rapid evolution may lead to greater niche partitioning among coexisting species. First, old field plant communities demonstrated species-specific positive and negative associations between grasses and legumes that often persisted over several seasons (Turkington, Cavers & Aarssen 1977; also see Aarssen, Turkington & Cavers 1979; Turkington & Cavers 1979). Other authors had previously observed relationships between grass and legumes and attributed them to differences in nutritional requirements, but plants in Turkington's old fields showed highly *species-specific* interaction outcomes. Each legume species was positively associated with at least one grass species and no two legumes had the same grass–neighbour relationship. Such disproportionate spatial arrangements among particular species may partially overcome the problem of diffuse interactions described above (i.e. the interactions between taxa may be consistent enough to allow evolution; Fig. 1). Survival (Turkington 1979) and biomass (Evans *et al.* 1985) were both higher when legumes were transplanted back into swards of the grass species from which they had been sampled. Different grass neighbours have also been shown to cause local selection on the genetic structure of *Trifolium repens* (Turkington & Harper 1979) and different strains of a grass elicited different growth responses and phenotypes from a single clone of *T. repens* (Hill 1977, in Aarssen, Turkington & Cavers 1979; see also Turkington & Mehrhoff 1991). This effect strengthened as the time of coexistence increased (Turkington 1979). Trends in species interactions could be detected after 1–3 years and clear differentiation into species-specific pairs occurred within 10 years.

Turkington and his colleagues' work may be the most complete exploration of how interactions among plants might affect their evolution, but similar research supports the general notion that plants may evolve in response to their competitive neighbourhood, an idea that is developed further in Thompson's (2005) idea of the geographic mosaic of co-evolution. Martin & Harding (1981) collected seeds of *Erodium*

cicutarium (L.) L'Hér. ex Aiton (Geraniaceae) and *E. obtusiplicatum* (Godr.) Thell. from co-occurring and widely separated populations. When seeds from co-occurring populations were planted together, the total seed output and reproductive rates of the two species were higher than when individuals from distant populations were grown together. Many of these early studies preceded knowledge about the potential importance of maternal effects; incorporation of maternal effects in future research on interactions among 'familiar' and 'unfamiliar' genotypes would be an important step forward.

HOW MIGHT PLANTS EXERT A SELECTIVE FORCE ON EACH OTHER?

Plants in a community interact directly and indirectly via different mechanisms, and the results of these interactions have the potential to produce evolutionary responses in plants as well as in other community members. The simplest interactions among plants are direct interactions, such as facilitation, resource competition and allelopathy.

Resource competition has strong effects on community composition and thus may be an important component of the selective environment experienced by plants. Because resource requirements among species vary, the nature of the selective forces experienced by plants could vary with different neighbouring species. Parrish & Bazzaz (1976) found that resource partitioning, as estimated from spatial overlap among root systems, was higher in stable prairie communities with a long community history than in early successional old-field communities composed of species without a common history. Aarssen & Turkington (1985a) found that associations between species were less stable in younger than in older communities. They suggested that in communities where resources were limiting, plants with a history of coexistence may develop balanced competitive abilities for limiting resources, niche differentiation not related to horizontal space, or some combination of the two. Later, Turkington (1990) found that both the root architecture and site of origin of grass species had significant effects on the growth and form of *T. repens*, supporting the idea that selection for niche-based spatial partitioning may be important.

Recently, Leger (2008) found evidence for selection in the North American native perennial grass *Elymus multisetus* M.E. Jones (Poaceae) caused by competitive interactions with the invasive annual grass, *Bromus tectorum* L. (Poaceae). *Elymus multisetus* individuals that were collected from invaded sites ('experienced' individuals) experienced smaller decreases in growth when grown in competition with *B. tectorum* compared to individuals from uninvaded sites ('naïve' individuals). In addition, experienced *E. multisetus* responded more quickly to watering and grew more quickly than naïve individuals. One of the competitive advantages of *B. tectorum* is its ability to pre-empt resources by germinating early in the season. Leger suggested that this selected for earlier growth in *E. multisetus*, allowing it to compete against *B. tectorum*.

Facilitation may also drive evolutionary responses (Callaway 2007; Bronstein 2009). Verdú & Valiente-Banuet (2008)

found that generalist facilitators of other species in an arid environment created dense and highly connected interaction networks. These networks made facilitation-shaped communities strongly resistant to extinction events, suggesting that facilitation has substantial potential to affect the evolution of beneficiary species. Similarly, Valiente-Banuet *et al.* (2006) provided evidence that many plant species from the Tertiary appear to have been maintained in modern Mediterranean-climate communities by the facilitative effects of species that arose in the Quaternary. These interdependent interactions among plants provide a mechanism for stabilizing selection and the conservation of ecological traits over evolutionary time-scales.

There is evidence that indirect interactions, mediated by soil microbes, also play a role in local adaptive relationships among plants. Lüscher, Connolly & Jacquard (1992) found that root sterilization reduced the strength, but did not eliminate the specificity in interactions between *Lolium perenne* and *T. repens*. More specifically, Chanway, Holl & Turkington (1989) found that genotypes of *Rhizobium leguminosarum* that coexisted with both *L. perenne* and *T. repens* enhanced the yield increases observed in interactions between 'familiar' genotypes, as described above. Similarly, *Bacillus polymyxa*, a growth-promoting soil microbe, had stronger positive effects on species-specific interactions among *T. repens* and *L. perenne* if ecotypes of all species had originally coexisted together in the field (Chanway, Holl & Turkington 1988, also see Chanway, Holl & Turkington 1990). Therefore, both adaptation by plants and changes in the associated microbial communities appeared to be involved in the 'familiarization' of neighbours.

Chemicals produced by plants may also drive evolution in their neighbours. Ehlers & Thompson (2004) and Grøndahl & Ehlers (2008) examined the potential of species-specific biochemistry to drive adaptation among plant species. Ehlers and Thompson collected *Bromus erectus* Huds. (Poaceae) seeds from plants growing in close association with *Thymus vulgaris* L. (Lamiaceae) from three phenolic populations and three non-phenolic populations. In a reciprocal transplant experiment, *Bromus* originally from soils beneath non-phenolic chemotypes performed significantly better on their home soil than on soil beneath phenolic chemotypes. This response to local chemotypes was observed only for soil collected directly underneath *Thymus* plants and not for soil collected near *Thymus* plants, but away from the effect of *Thymus* canopies. In contrast to *Bromus* of non-phenolic origin, seeds collected from *Bromus* associated with phenolic *Thymus* chemotypes showed no pattern in response to soil type. These differences in selective pressure have the potential to create different genetic strains in *Bromus*, similar to the selective forces seen in some edaphic communities, such as the evolution of serpentine-tolerant and intolerant ecotypes (e.g. Kruckeberg 1984).

Grøndahl & Ehlers (2008) found that some of the neighbours of *Thymus pulegioides* L. (Lamiaceae) and *T. serpyllum* auct. non L. appeared to be adapting to specific terpenes produced by *Thymus*. Plants that came from sites where they co-occurred naturally with carvacrol (a terpene)-producing *Thymus* also performed better on soil treated with carvacrol.

Jensen & Ehlers (2010) found the genetic variation in both *Thymus*-naïve and *Thymus*-experienced populations for responses to carvacrol, but importantly, the response varied among naïve and experienced individuals within a species. As shown before, plants from experienced populations performed better than naïve plants on carvacrol soil, but also produced more seed families possessing an adaptive response to carvacrol than naïve populations. Apparently *Thymus* can act as a selective agent on other species, by favouring genotypes which respond best to its allelopathic effects. Similar results have been found with the effects of chemicals produced by *Pinus sylvestris* L. (Pinaceae) on the neighbouring plant community (Iason *et al.* 2005).

In the following sections, we further explore current themes in the study of plant community ecology, including the niche, the importance of biogeography, the extended phenotype and the geographic mosaic of co-evolution. We synthesize these themes and discuss how each contributes a unique perspective to our understanding of how interactions among plants may lead to evolution.

The niche

The exceptionally rich body of ecological literature on the niche is based in part on the idea that competition can drive the evolution of niche differentiation, thus allowing species to coexist (Silvertown 2004; Vellend 2006; Levine & HilleRis-Lambers 2009). This literature is too large to review here, but decades ago, niche divergence among coexisting animals, plants and their pollinators, and within plant communities, was attributed to evolution (MacArthur 1958; MacArthur & Levins 1967; Levin & Anderson 1970; Putwain & Harper 1972; Pickett & Bazzaz 1976). Whether niche partitioning is the result of competition-driven evolution or an ecological sorting process of species that derive their different niches from other selective pressures is hard to know (see Ackerly 2003), but 'the fundamental niche is a mean phenotype of a population, a trait that can evolve by natural selection' (Holt & Gaines 1992). If niche evolution occurs through competition among neighbours, this must be despite highly diffuse and spatially inconsistent interactions (Fig. 1). The potential for niche partitioning to be derived, at least in part, from the effects of competition on evolution is fundamental to general niche theory, and an evolutionary perspective on niche partitioning has contributed tremendously to some of the most important developments in plant ecology.

The positive correlation between community diversity and ecosystem functioning is one such development. Tilman & Downing (1995) conducted a long-term study of grasslands showing that plant primary productivity was more stable during and after drought in communities with high species richness than in communities with low species richness. Tilman, Wedin & Knops (1996), Tilman *et al.* (1997) further tested the idea that more diverse ecosystems are more stable (see Elton 1958), more productive and more fully utilize available resources by experimentally manipulating plant species diversity in plots. They found that 'functional composition' and

'functional diversity' in experimental plots were the primary factors that explained productivity and nitrogen content in plants. Similar relationships between diversity and ecosystem function have been found in subsequent experiments (Hector *et al.* 2001; Cardinale *et al.* 2007; Hooper *et al.* 2005; Marquard *et al.* 2009). The strong implication of these results is that different species used different subsets of the total resource pool – i.e. different species occupied different niches.

Soon after the positive diversity–ecosystem function relationships were shown for productivity and stability, others found that new species colonized species-rich communities far less easily than species-poor communities. For example, Fargione, Brown & Tilman (2003) added seeds of 27 grassland species (previously not in the experimental system) to plots in grassland and found that the strongest inhibitory effect of the functional group previously occupying the plots was on new colonizers in the same functional group. This supported the prediction of niche theory that established species should more strongly inhibit colonizers that are more similar to themselves (also see Fargione & Tilman 2005). Crutsinger, Souza & Sanders (2007) found that experimentally determined high intraspecific diversity of *Solidago altissima* was negatively correlated with the biomass of colonizing species. Others have found that species and functional diversity resist exotic invasions and their impacts (Zavaleta & Hulvey 2004; Maron & Marler 2007, 2008).

At scales much larger than communities of interacting species, positive diversity–ecosystem function relationships may not hold (Stohlgren, Barnett & Kartesz 2003; Gilbert & Lechowicz 2005). However, at the scale of communities of interacting species there are a number of non-mutually exclusive hypotheses for the mechanisms driving the general relationship (Knops *et al.* 1999; Huston *et al.* 2001; Cardinale *et al.* 2007). The primary hypothesis for positive diversity–ecosystem function relationships has been niche 'complementarity', the idea that different species or functional groups occupy niches different enough from each other to more fully utilize resources or space, increasing and stabilizing productivity, and making it more difficult for other species to enter the community (Fargione *et al.* 2007). Facilitation is sometimes included within ideas about complementarity (Cardinale *et al.* 2007), but more importantly, we do not yet know whether complementarity is produced by interactions causing evolutionary shifts in niche space (and thus coexistence and more complete resource use) or by sorting of the existing species pool.

A second key development in ecology related to niche theory is the use of functional trait and phylogenetic analyses to synthesize ecology and evolution in the context of communities (Ackerly, Schwilk & Webb 2006; McGill *et al.* 2006). Trait-based approaches to studying community organization are also rooted in the idea that niche differentiation can arise from 'adaptive evolution' through interactions among plants, and of course other organisms, although others have pointed out that some functional traits and aspects of the niche can be highly conserved and thus perhaps only weakly selected upon (Valiente-Banuet & Verdú 2007; Peterson, Soberón & Sanchez-Cordero 1999). A large number of studies have taken trait-based approaches to understanding how adaptation might shape plant niches (Mooney & Dunn 1970; Enquist, Brown & West 1998; Cavender-Barrs *et al.* 2004; Angert *et al.* 2009).

Most efforts by far have been directed at understanding niche partitioning in the context of competition. However, recent studies suggest that more newly evolved plant taxa have preserved the regeneration niches of species with ancient lineages through facilitation (Valiente-Banuet *et al.* 2006). Valiente-Banuet & Verdú (2007) also found that regeneration niches are strongly conserved across evolutionary history and that nurse species facilitated distantly related species and increased the phylogenetic diversity of communities. This 'niche construction' (Keller 2003) and the consistent pattern of stronger facilitative interactions among distantly related benefactors and beneficiaries (also see Valiente-Banuet & Verdú 2008) raise the idea that selection may act on beneficiaries so that their niche diverges from that of their nurses. Butterfield & Briggs (2011) also found that the functional traits of a large number of seedlings and mature plants in deserts corresponded with their roles as benefactors or beneficiaries. The evolutionary role of niche construction may be in part the product of reciprocal interacting processes of natural selection and niche construction (Day, Laland & Odling-Smee 2003).

Whether or not niche partitioning (complementarity) and niche construction derive from natural selection is a key aspect of this review. Whittaker (1965) argued that the 'evolution of both niche and habitat differentiation permits many species to exist together in communities as partial competitors', but the direct evidence for this is scant. The diversity–ecosystem function effects produced by genotypic diversity *within* a species, as described by Crutsinger, Souza & Sanders (2007), strongly suggests that niche differentiation is selected for. Parrish & Bazzaz (1976) measured niche overlap among the root zones of six species of successional old-field annuals to that among the roots of species in a 'mature prairie' community and found much greater niche overlap among the successional species. They noted that competition may be more important in determining the evolution of niche partitioning among the prairie species, perhaps because of a longer history of coexistence. Stinchcombe & Schmitt (2006) studied the potential for oak trees to affect natural selection of *Impatiens capensis* through leaf litter deposition. Using a quantitative genetic experimental approach, they found that leaf litter significantly affected selection on germination timing and hypocotyl length, demonstrating the potential for oaks to drive the ecological and evolutionary dynamics of other species. Johnson *et al.* (2008) demonstrated the potential for adaptive evolution in response to selection by competitors *in Oenothera biennis*, and thus the potential for competitors to evolve towards niche partitioning. Vellend (2006) used models of competition among genotypes and species to show a strong positive effect of intraspecific genotypic diversity on species diversity. These models indicated that directional selection on niches depended on the initial niche similarity between species, but that competition has a great deal of potential as a selective agent on the niche. These and other studies (e.g. Donohue 2003, 2004; Dudley & File

2007) provide evidence that interactions among co-occurring plant species may affect the evolution of their niches.

Other 'meta' approaches have demonstrated problems for the idea that niche differentiation at the scale of interacting plant species can explain coexistence. In classic niche theory, environmental heterogeneity and species diversity should be positively correlated – more niches should result in more species. If niche differentiation is crucial for minimizing competition (see Levine & HilleRisLambers 2009) or more fully utilizing resources, as is assumed for positive diversity-ecosystem function relationships and trait-based community organization, then the scale at which heterogeneity and species diversity correlate should be quite small; small enough to realistically incorporate interactions among the species. However, not all studies support this perspective. Tamme *et al.* (2010) conducted meta-regressions for 19 experimental and observational studies of the relationship between environmental heterogeneity and plant species diversity and found a strong relationship between spatial scale and heterogeneity–diversity correlations. However, at very small spatial scales (< 1.0 m^2) this relationship was neutral to *negative*. Thus, plant species clearly had niche preferences at the scale of forests, grasslands or wetlands, but there was no evidence that these preferences occurred at the small scales necessary for competition-driven niche partitioning among plant species.

Evolution driven by competition is fundamental to niche theory for all organisms, including plants. However, for plants there have been very few explicitly focused studies of interaction-driven evolution in the context of niche partitioning. Studies that link niche theory with experimental manipulation of selection will contribute a great deal to our understanding of plant communities.

The effect of biogeography on plant interactions

T.A. Rabotnov (1982), an ecologist at Moscow State University, proposed a decidedly non-individualistic 'evolutionary approach to the study of allelopathy' (see Callaway & Hierro 2005). He argued that plants could evolve in response to the chemicals exuded from the roots or washed from the leaves of their neighbours, and that some exotic species might have far stronger effects on plants encountered in new ranges because they lack adaptations to deal with such chemicals. Rabotnov speculated that 'allelopathically neutral' or 'allelopathically homeostatic' conditions are more likely in communities with long histories of coexistence. In other words, plants and microbes in communities that have coexisted for a long time (see Bascompte, Jordano & Olesen 2006) may adapt to the chemicals produced by their neighbours much like they rapidly adapt to herbicides and other chemicals. Rabotnov extrapolated from this speculation to the idea that 'disturbed homeostasis' may occur when interactions take place among species without an evolutionary history.

Invasion by exotic plant species has provided hundreds of natural experiments with which we can test the ideas that plant interactions can drive evolution, and that a co-evolutionary history may be important to the nature of communities. If interactions over long periods of time among plants within a community drive natural selection in the direction of coexistence (Rabotnov's homeostasis), and the arrival of new plants disrupt this homeostasis, then it is quite reasonable to think that interactions among plants may affect the evolution of plants. Importantly, because invaders can create near monocultures over large distances, these systems have the potential to represent very low diffuseness of interactions and low spatial inconsistency, a context in which intense selection might occur (Fig. 1).

Collectively, plants produce a diverse array of over 100 000 different secondary metabolites, many of which appear to be species- or genus-specific (Flores 1999). This diversity is likely due to selection for the acquisition of resources, herbivory, microbial interactions and interactions with other plants. Recent experiments raise the possibility that some invaders may exude allelochemicals that are relatively ineffective against neighbours in natural communities, but highly inhibitory to plants in invaded communities. This has been dubbed the 'novel weapons hypothesis' (Callaway & Aschehoug 2000; Callaway & Ridenour 2004).

In France, the natural regeneration of two spruces, the native, *Picea abies* (L.) Karst. (Pinaceae; old neighbour), and the exotic, *P. mariana* (Mill.) Britton, Sterns & Poggenb. (new neighbour) was inhibited in the presence of the dominant understorey plant, *Vaccinium myrtillus* L. (Ericaceae; Mallik & Pellissier 2000). In field plots, only 2% of the *P. abies* and none of the *P. mariana* seeds germinated when the humus of *V. myrtillus* was present. When the humus was removed, germination of *P. abies* improved to 27%, but that of *P. mariana* improved to only 15%. Fresh leaves, leaf leachate, humus and humus leachate all decreased the growth of roots of *P. mariana* more than that of *P. abies*. Thus, while *V. myrtillus* appeared to have an allelopathic effect on both *Picea* species, the negative effect was strongest on the species with which it did not share an evolutionary history.

Prati & Bosdorf (2004) tested the allelopathic effects of *Alliaria petiolata* (M. Bieb.) Cavara & Grande (Brassicaceae; garlic mustard), an aggressive invader of the understorey of forests in North America, on two congeneric species that co-occur with *Alliaria* in the field; the North American *Geum laciniatum* Murray (Rosaceae: new neighbour) and the European *G. urbanum* L. (old neighbour). North American populations of *Alliaria* significantly reduced the germination of North American *G. laciniatum* seeds, but they had no effect on European *G. urbanum* seeds. In contrast, native European *Alliaria* reduced seed germination of both North American *G. laciniatum* and European *G. urbanum* in similar proportions. Contrasting inhibitory effects between *Alliaria* populations from Europe and North America on European *G. urbanum* suggest that North American *Alliaria* had lost its negative effects on a former neighbour.

Callaway & Aschehoug (2000) compared the growth of the invasive *Centaurea diffusa* Lam. (Asteraceae) with three North American and three Eurasian bunchgrasses that had been matched for genus (or historically congeneric), morphology

and size. *Centaurea diffusa* had much stronger negative effects on the growth of the North American (new) neighbours compared to the Eurasian (old) neighbours. However, when activated carbon, (which adsorbs to and deactivates many organic chemicals) was added, the effect of *C. diffusa* on the three North American species was greatly reduced. Similar results were obtained in a microcosm experiment when North American and Eurasian plant communities were grown in either North American or Eurasian soils; Eurasian communities were much more resistant to invasion by *C. diffusa* than North American communities (Vivanco *et al.* 2004). These results are conceptually in line with Rabotnov's and Turkington' ideas, and suggest that a long history among plant species may allow chemical tolerance to evolve, promoting coexistence. In contrast, the lack of an evolutionary history may make species susceptible to the chemical signatures of neighbours.

Results similar to those with *C. diffusa* have also been demonstrated with *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek (nee *C. maculosa* Lam.), which exudes the allelochemical, (±)-catechin, from its roots (Blair *et al.* 2005, 2006; Tharayil & Triebwasser 2010). A number of early reports of high levels of catechin exudation from *C. stoebe* roots have not been repeatable (see Stermitz, Hufbauer & Vivanco 2009), and thus whether or not the invader consistently exudes enough of the chemical to be ecologically relevant is an open question (see Blair *et al.* 2006; Perry *et al.* 2007; Duke *et al.* 2009), but the phytotoxic effects of very low levels of forms of catechin have been demonstrated *in vitro*, in sand culture, in controlled experiments with field soils, and in the field (Perry *et al.* 2005; Simões *et al.* 2008; Inderjit *et al.* 2008a,b; Pollock *et al.* 2009 and citations within). In other experiments catechin has not demonstrated phytotoxic effects (Blair *et al.* 2005; Inderjit *et al.* 2008a; Duke *et al.* 2009). The inhibitory effect of (±)-catechin on other plants varies substantially among species native to the invaded range (Perry *et al.* 2005; Thelen *et al.* 2005), and several experiments have found that (±)-catechin has more inhibitory effects on North American species than on European species (Inderjit *et al.* 2008b; He *et al.* 2009; Thorpe *et al.* 2009). These patterns suggest that a history of coexistence, or lack thereof, may be important for structuring communities, which further supports the conclusions of Turkington and colleagues.

Biogeographical differences in the effects of allelopathic chemicals circumstantially suggest they have roles as drivers of evolution. However, direct evidence from invasive species research indicates that the allelochemicals of an invader can be a strong selective force on native plants. Specifically, populations of native grasses that have experienced invasion by *C. stoebe* appear to have evolved a degree of resistance to the allelopathic effects of *C. stoebe* (Callaway *et al.* 2005). *Centaurea stoebe* suppressed the growth of clones of 'naïve' grasses (from uninvaded grasslands) more than clones of 'experienced' grasses (from highly invaded grasslands). These effects were passed on to the next generation. When grown in competition with *C. stoebe*, *Festuca idahoensis* Elmer (Poaceae) and *Stipa occidentalis* Thurb. (Poaceae) that were grown from seed of naïve maternal plants were smaller than those grown from seed

of experienced maternal plants. Activated carbon eliminated these differences, suggesting that allelopathy might contribute to these effects. The difference in response between naïve and experienced grasses was also reflected in the effect of the grasses on the growth of *C. stoebe*. Plants grown from seed of experienced maternal lines decreased the growth of *C. stoebe* by 31% relative to controls, whereas plants grown from the seeds of naïve maternal lines had no effect on the growth of *C. stoebe*. These results suggest that in invaded populations, there has been selection for plants with traits that confer resistance to *C. stoebe*.

In a similar case, Mealor, Hild & Shaw (2004; also see Mealor & Hild 2006) investigated the potential of competition from *Acroptilon repens* (L.) DC to select on the genetic characteristics of *Hesperostipa comata* (Trin. & Rupr.) Barkworth and *Sporobolus airoides* (Torr.), two native grasses. They found that 'experienced' populations were genetically different from 'naïve populations. More recently, Mealor & Hild (2007) found that remnant *S. airoides* displayed a consistent positive response to long-term coexistence with the invader, suggesting that *A. repens* had a selective effect on *S. airoides*.

Biogeographical variation in the effects of novel plant chemistry has also been shown for arbuscular mycorrhizae. *Alliaria petiolata* has far stronger inhibitory effects on mycorrhizae in invaded North American soils than on mycorrhizae in European soils where *A. petiolata* is native (Callaway *et al.* 2008). This antifungal effect appears to be due to specific flavonoid fractions in *A. petiolata* extracts. Furthermore, suppression of North American mycorrhizal fungi by *A. petiolata* corresponded with inhibition of North American plant species that rely on these arbuscular mycorrhizal fungi, whereas congeneric European plants were only weakly affected.

Genes to ecosystems, the extended phenotype

In the previous sections, we have provided examples of how characteristics of dominant species can drive interactions leading to heritable change in neighbouring species. Here, we consider how these types of interactions may lead to associations that Whitham *et al.* (2003) called 'the extended phenotype' (also see Dawkins 1982). The extended phenotype of a species is the environment that is created by the species. It can vary within a species as the result of relatively small genotypic differences, but these small genetic differences can have strong effects on the way that genotypes interact with other organisms. Because of the large number of species involved in interactions determined by extended phenotypes, we hypothesize that such interactions will be diffuse, but because extended phenotype interactions are often determined by biochemistry, we propose that these interactions will be quite spatially consistent; e.g. among the same relatively large groups of species (Fig. 1).

The majority of studies of extended phenotypes have focused on the effects of genetic variation within a species on soil characteristics (Schweitzer *et al.* 2004) and/or the trophic structure of herbivore communities (e.g. Whitham *et al.* 1999; Bangert *et al.* 2005). For example, differences in soil chemistry

can provide a mechanism by which the extended phenotype of a dominant plant species alters plant communities; in other words the effects of plant-mediated variation in soil characteristics may result in differences in plant communities (e.g. Iason *et al.* 2005; Ehlers & Thompson 2004; Whitham *et al.* 2006 and references therein). Specific changes in soil microbial communities influenced by plants could also be seen as extended phenotypes. These changes can have predictable effects on the performance of other plants, generating feedback processes in the community (Petermann *et al.* 2008).

Genetically-based differences in the production of biochemicals and subsequent effects on different ecosystem components have been observed for several species. Treseder & Vitousek (2001) compared allozyme diversity of functional enzymes in *Metrosideros polymorpha* Gaudich. (Myrtaceae) along a fertility gradient and grew seedlings collected from each population in a common garden with reciprocal nutrient treatments. They found that small differences in allelic diversity led to differences in plant traits such as root and leaf litter chemistry, which, in turn resulted in positive feedbacks that may influence nutrient cycling and the surrounding plant community. As noted above, Ehlers & Thompson (2004) found that at least some of the patterns observed in *Thymus vulgaris* communities appeared to be due to differences in the production of biochemicals by different *Thymus* chemotypes. The chemical diversity of the mixture of the 11 monoterpenes within *Pinus* individuals explained one-fifth of the variation in the species richness of understorey plants (driven by vascular plants) underneath individual trees (Iason *et al.* 2005). Although the mechanism driving this relationship was not studied, it may act through locally variable (*between-tree variation*) inhibition of decomposition and nitrogen mineralization, by inhibiting germination, seedling growth, survival through allelopathy and/or a combination of these direct and indirect effects.

The mechanisms by which the extended phenotype of a dominant species alters ecosystem and community structure are the same kinds of indirect and direct interactions that drive evolution in neighbouring species and that play roles in community evolution and the geographic matrix of co-evolution. The kinds of interactions between plants that are the focus of this article fit within the definition of an extended phenotype – an individual's genotype affects ecosystem processes and community structure. Conversely, extended phenotypes provide examples of how interactions among plant species can drive evolution.

Co-evolution and the geographic mosaic

John Thompson (2005, 2006) developed a powerful synthesis of the literature by showing that particular environments (different abiotic conditions, densities of interaction partners, etc.) promote co-evolutionary interactions between species while others do not. As a result, spatial variation in the environment does not necessarily eliminate the potential for interactions among species to drive evolution, but instead may lead to predictable variation in evolution. Locations where conditions promote evolution are called 'co-evolutionary hotspots', and

'coldspots' are locations where conditions do not promote co-evolution. A major contribution of the geographic mosaic model is that it provides a framework for understanding how evolution might occur among organisms that vary substantially in their spatial distributions relative to each other, a major problem for understanding how interactions among plants affect their evolution. It is important to note than in this review we have not focused on co-evolution, but geographic mosaic ideas are also applicable to understanding selection on just one interaction partner, and not necessarily reciprocal evolution by the other. The kinds of interactions explored in the context of the geographic mosaic have been highly specialized, thus with very low diffuseness, but by definition, these interactions are spatially inconsistent (Fig. 1).

Because plants are sessile and most plant communities contain many species, the spatial arrangement among these species must play a key role in how interactions between plant species affect evolution. Therefore, the geographic mosaic model may be a particularly useful framework for understanding the evolutionary consequences of interactions among plants.

Hotspots and coldspots for plant evolution may be determined by the degree of spatial association between different species, and thus how 'diffuse' interactions are. If different interaction partners select for antagonistic traits, adaptation to neighbours will be difficult. However, if certain species cluster in space, or if different species elicit similar interaction effects, interactions have more potential to result in adaptation. For example, in the old-field community experiments of Turkington and colleagues, they found that in young communities where spatial association among particular plant species was low and competitive interactions were diffuse, adaptation was not observed. Instead, species in young communities displayed plastic responses mediated by changes in soil microbial communities (Chanway, Holl & Turkington 1989; Turkington 1996). However, in older fields consisting of larger and more uniform patches of grass species, adaptive responses by *Trifolium* occurred (see Turkington 1989, 1996). These more stable and uniform communities, in which adaptation by *Trifolium* could occur, could be considered hotspots for the evolution of *Trifolium* as it interacts with other plant species. The geographic mosaic provides a context in which we can explore evolutionary dynamics among particular species and genotypes present, but also in the context of variation in the distribution of these species and genotypes. Explicit integration of geographic mosaics into future studies of plant interactions has tremendous potential for expanding our understanding of communities.

Factors limiting adaptation to plant interactions

There are many conditions in which adaptation may not occur despite strong selective forces, and understanding factors that constrain adaptation are as important to consider as the factors that promote it. These factors include plasticity, spatial heterogeneity in selective forces, gene flow, lack of additive genetic variance and ecological factors.

Plants are highly plastic organisms. Whether adaptation in a plastic trait can occur depends on the nature of the selective force, the nature of the plasticity, and whether its effects on fitness are consistent among different genotypes (no G × E interaction). High levels of plasticity can mean that certain genotypes are selected only in specific conditions. For example, plants adapting to compete with one species or genotype may lose some ability to compete with other species or genotypes (e.g. Turkington 1979; Aarssen & Turkington 1985b; Ehlers & Thompson 2004). In this way, an evolutionary tug-of-war can ensue when plants are subjected to the multi-species competitive environment of communities. Lankau (2008) found that competitive interactions between *Brassica nigra* and other unrelated species in the community favoured a genotype of *B. nigra* that produced high levels of sinigrin, a putative allelopathic agent. However, high levels of sinigrin did not confer competitive advantage among conspecifics, but instead resulted in lower fitness (Lankau & Strauss 2008), setting the stage for strong trade-offs for a highly heritable trait that affects how *B. nigra* interacts within communities. This suggests that the evolutionary consequences of plant–plant interactions may be highly context- and competitor-specific and that diversity of genotype may be important for coexistence among competitors (Hughes *et al.* 2008).

Extremely strong competition may also reduce rates of adaptation in a spatially heterogeneous selective landscape by reducing the fitness of a particular neighbour effectively to zero. In this case, adaptive alleles may not increase in frequency. Gene flow between two populations of plants, one in sympatry with the strong competitor and the other not, may even result in the extinction of the sympatric population, rather than in adaptation (Case & Taper 2000). This process may be important in systems with invasive species forming dense monocultures and causing substantial losses in reproduction by native plants.

Finally, ecological factors may play an important role in the rate and direction of responses to selection caused by competing plants. For example, Lau (2006) found that adaptation by *Lotus wrangelianus* Fisch. & C.A. Mey. (Fabaceae; an annual herb) to *Medicago polymorpha* L. (an invasive annual herb) could only be observed when *Hypera brunneipennis* (an exotic, shared herbivore) was excluded from the experimental plots. The causes of this are unclear but the data suggest that ecological factors can change the consequences of the interaction between *Lotus* and *Medicago* in ways that could influence the ability of one to adapt to the presence of the other. As we progress in our exploration of how interactions among plants affect their evolution, we will gain insight into the factors that drive evolution and those that limit evolution.

Conclusion

Our goal for this synthesis of studies of interactions among plant species that generate 'continuous co-evolution maintaining balanced competitive abilities', niche theory, biogeographical studies of invasive plants, extended phenotypes, and concepts arising from the geographical mosaic of co-evolution,

is to take a step toward considering how interactions among plants might drive important evolutionary changes. If such evolution is common, plant communities are not random assemblages of species, and not all communities appear to be assembled following the same rules (see Lortie *et al.* 2006). In addition to challenging current perspectives on the nature of plant communities, emerging evidence for plant–plant interactions as drivers of evolution has important implications for applied ecology as we attempt to manage and restore systems that are both resistant and resilient to ongoing stresses, including invasive species and climate change. Our understanding of the importance of plant interactions and evolution can be greatly enhanced by addressing information gaps we have noted (e.g. Bronstein 2009) and by explicitly considering potential evolutionary outcomes within the context of traditional research on plant interactions. By looking for parallel themes within various research areas, we can greatly improve our understanding of the structure and long-term dynamics of plant communities.

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