

Special Issue: Specificity of plant–enemy interactions

# Community specificity: life and afterlife effects of genes

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**Community-level genetic specificity results when individual genotypes or populations of the same species support different communities. Our review of the literature shows that genetic specificity exhibits both life and afterlife effects; it is a widespread phenomenon occurring in diverse taxonomic groups, aquatic to terrestrial ecosystems, and species-poor to species-rich systems. Such specificity affects species interactions, evolution, ecosystem processes and leads to community feedbacks on the performance of the individuals expressing the traits. Thus, genetic specificity by communities appears to be fundamentally important, suggesting that specificity is a major driver of the biodiversity and stability of the world's ecosystems.**

## Genetic specificity by communities

Specificity is often defined as the number of different host species with which a plant enemy or mutualist associates. Researchers in diverse fields have expanded this definition to include factors such as phylogenetic relationships among hosts [1,2]. We propose that specificity should be broadened in two additional ways. First, we provide evidence that specificity by plant associates such as pathogens, herbivores or mutualists frequently occurs below the species level. Studies of this genetic specificity are important for understanding the process of speciation [3]. Second, we show that entire communities of organisms can exhibit specificity for plants below the species level, in which different genotypes of plants support different communities (see [Glossary](#)). In turn, these communities can feed back to affect the performance of the individual genotypes with which they interact. Studies of specificity at this level demonstrate novel links between ecology and evolution.

Figure 1 shows an example of specificity in which a diverse community of arthropods (103 species from 12 orders) exhibit specificity for individual tree genotypes [4]. Replicate clones of the same genotypes of narrowleaf cottonwood (*Populus angustifolia*) showed significant broad-sense heritability of the community phenotype. Similarly, repeated censuses across years showed high repeatability, demonstrating that the colonizing communities of arthropods responded similarly each year to individual tree genotypes. Specificity among species has long been

studied in the context of coevolution. At the community level, coevolutionary dynamics undoubtedly play a role; however, we predict that the effects of plant genetics on the associated community is highly asymmetric [5] in which only a few species are coevolved and the genetically based interactions of a few species (e.g. plant–enemy interactions) are likely to define much of the community. Many associated species may have no individual feedbacks to the plant, whereas the whole community of arthropods or soil microbes, acting together, does affect the fitness of individual genotypes.

Although several reviews have documented the extended community and ecosystem phenotypes of individual plant genotypes [6,7], this review emphasizes the breadth of model and non-model systems that have demonstrated genetic effects at the community level and is the first to place these within the context of specificity. Community specificity is largely an outgrowth of community heritability, which is the tendency for related individuals to support similar community members and ecosystem processes [6]. Thus, with low heritability, community specificity should be weak, but as heritability increases, specificity should also increase. Our review examines: (i) how subspecific levels of plant genetic variation (populations, genotypes) differentially affect community structure, ecosystem processes, diversity and stability across a range of organisms,

## Glossary

**Afterlife effects:** the phenotypic effects of a plant that extends beyond the life of the individual plant or plant part such as leaf litter.

**Broad-sense heritability:** the contribution of all genetic factors (additive, dominant, epistatic) to the total variance in phenotype.  $H^2$  is the broad-sense heritability of a traditional phenotype and  $H^2_C$  is the broad-sense heritability of a community or ecosystem phenotype [35].

**Community and ecosystem phenotypes:** the effects of genes at levels higher than the population [6].

**Community genetics:** the study of the genetic interactions that occur between species and their abiotic environment in complex communities [6].

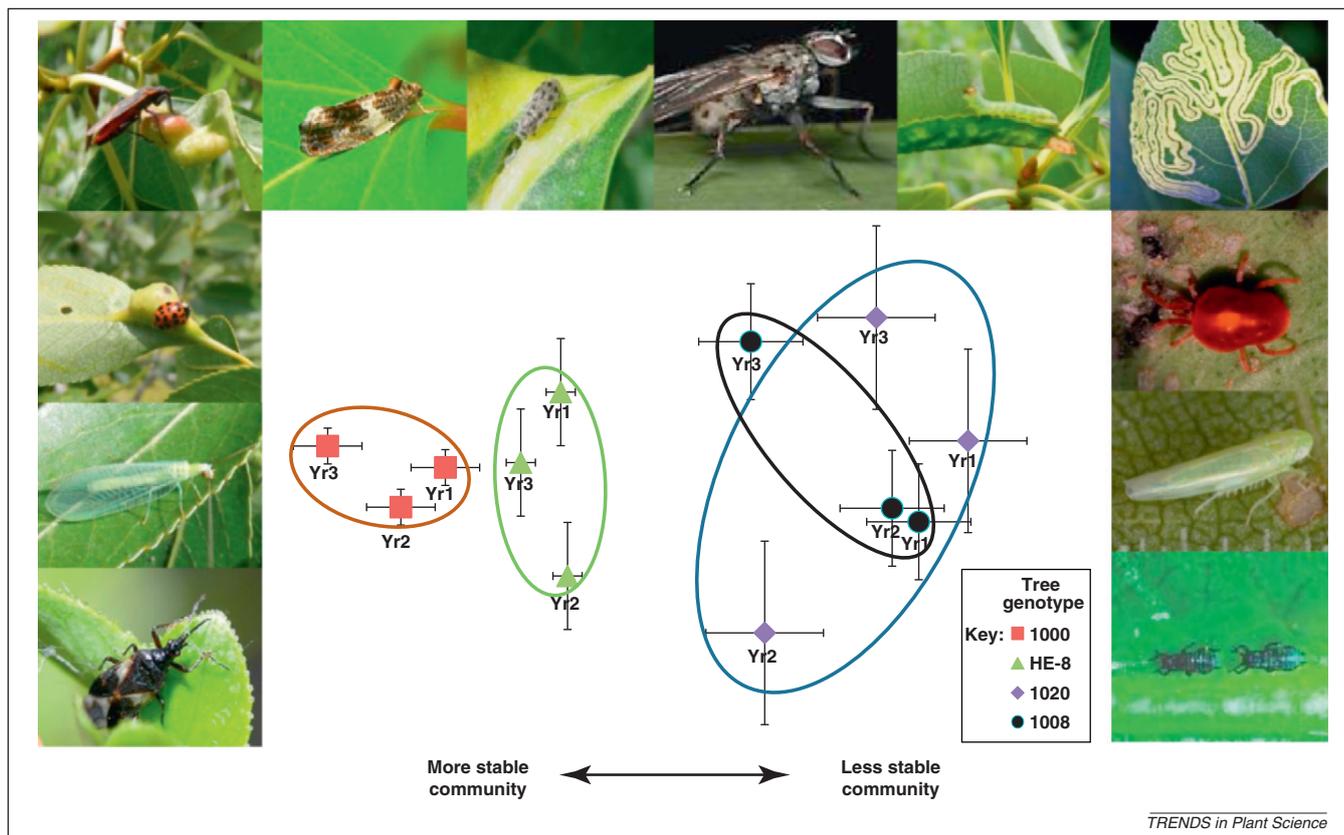
**Community specificity:** the genetically based tendency for individual populations or individual genotypes within a species to support different communities of organisms and ecosystem processes.

**Community stability:** the similarity in the community composition of associated species across years for individual plant genotypes or populations [4].

**Deme:** genetically distinct populations that form despite close proximity to one another [3].

**Foundation species:** 'a single species that defines much of the structure of a community by creating locally stable conditions for other species. ...' [72]. Other terms such as keystone, ecosystem engineers or dominant species have similar meanings and overlap in their definitions.

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**Figure 1.** Non-metric multidimensional scaling (NMDS) analysis showing replicated genotypes of narrowleaf cottonwood (*Populus angustifolia*) vary in arthropod community composition and stability. Points represent the mean arthropod communities on replicate clones of an individual tree genotype and bars represent 95% confidence limits. These censuses were repeated each year for 3 years, so the mean community of each tree genotype is represented three times, once for each year (circles encompass the three years of each genotype). Because the within genotype variance is much less than the between genotype variance, individual genotypes differed significantly in arthropod community composition (Analysis of similarity (ANOSIM)  $R$  for community composition = 0.21,  $P < 0.0001$ ). Furthermore, because the communities of some genotypes changed significantly less over the 3 years of study than other genotypes (see size of encompassing circles), there is also a significant genetic component to community stability (Restricted estimated maximum likelihood (REML) for community stability  $P < 0.0001$ ). Replicate clones also showed significant broad-sense heritability of the community phenotype (species composition;  $H^2_c = 0.65$ ). Images of the 11 most common arthropods from the study are shown clockwise from bottom left: *Anthracoris antevolens*, *Chrysopa* sp. 1, *Harmonia axyridis*, *Boisea trivittata*, *Tortricidae* sp. 2, *Listrus* sp. 1, *Ceratopogonidae* sp. 1, *Dasyhelia* sp. 1, *Thecabius populomonilus*, *Tortricidae* sp. 1, *Trombiculidae* sp. 1, *Gypona* sp. 1, *Pemphigus betae*. We know that at least one member of the community, the bud-galling mite, *Aceria parapopuli* has evolved and adapted to individual tree genotypes indicating that specificity has both ecological and evolutionary implications. Photos courtesy of A. Keith, J. Dombroskie and K. Matz. Reproduced, with permission, from [4].

both in the context of the living organism and effects that endure after the organism has died; (ii) the effect of specificity on the evolution of dependent organisms and how genetically based species interactions among relatively few species can define a larger community; (iii) how the community can feed back to affect the genotypes expressing specific community and ecosystem phenotypes; and (iv) the key postulates that are necessary to demonstrate that specific genes are responsible for community and ecosystem phenotypes. Because community and ecosystem ecology have been largely genetics free, while molecular ecology has been largely community and ecosystem free, the demonstration of genetic specificity across these levels represents an important merger of disciplines.

### Community specificity to plant genotype

Community genetics studies have revealed a diverse suite of plant-associated communities that exhibit specificity below the level of plant species. Initially, studies that focused on specificity of communities had a strong emphasis on arthropod herbivores, reflecting the field's roots in plant–enemy interactions. However, this research has expanded to

include organisms such as fungal endophytes [8], mycorrhizal fungi [9], epiphytic and terrestrial plants [10,11], soil microbes [12] and terrestrial invertebrates [13]. Table 1 highlights the diversity of study systems where community specificity has been examined. Because studies based on whole communities within a genetics context are rare, to reflect more complex communities only studies with five or more species were included. Of the 75 communities shown in Table 1, 85% responded to genetic variation in focal plant species from 28 genera within 15 plant families, including angiosperms and gymnosperms. Aboveground arthropod and plant communities seemed particularly responsive, with 93.5% and 88.9%, respectively, showing a significant effect, whereas litter/soil invertebrates and microbial communities responded to plant genetics approximately 75% of the time. In addition to their phylogenetic diversity, organisms exhibiting community specificity represent a range of relationships with the focal plant, including mutualism, parasitism, commensalism, facilitation and competition.

Evidence of community specificity comes from ecosystems around the world. Genetic variation in plants as varied as neotropical canopy trees, Tasmanian eucalypts,

**Table 1. Plant genera within which at least one focal plant species has been examined for community specificity<sup>a</sup>**

Focal plant taxa	Growth form	Genetic scale	Biome and habitat	Study region	Study method <sup>b</sup>	Communities responding	Refs
<b>Asteraceae</b>							
<i>Artemisia</i> <sup>c</sup>	Shrub	Intraspecific hybridization; population; subspecies	Temperate semi-arid shrubland	North America	CG; F	Herbivores (stem, bud and leaf arthropods, deer); soil bacteria <sup>d</sup> ; fungal endophytes (root, shoot and leaf) <sup>d</sup>	[73–75]
<i>Baccharis</i>	Shrub	Genetically based phenotype	Temperate coastal dune	North America	CG; F	Leaf, bud and stem arthropods; herbaceous and woody plants	[17,76]
<i>Borrchia</i>	Forb <sup>e</sup>	Genotype	Temperate coastal	North America	CG	Leaf and stem arthropods	[77]
<i>Chrysothamnus</i>	Shrub	Subspecies	Temperate conifer forest	North America	F	Leaf, stem and bud arthropods	[78]
<i>Helianthus</i>	Forb	Subspecies	Temperate grassland and savannah	North America	CG	Leaf, stem and seed arthropods	[79]
<i>Iva</i>	Shrub	Genotype	Temperate coastal	North America	CG	Leaf and stem arthropods <sup>d</sup>	[77]
<i>Solidago</i> <sup>c</sup>	Forb	Genotype; ploidy; half-sibs	Temperate old-field <sup>f</sup>	North America	CG; F	Herbaceous plants; leaf, bud and stem arthropods; litter arthropods; arthropod pollinators	[16,25,33,80,81]
<b>Apocynaceae</b>							
<i>Asclepias</i>	Forb	Full-sibs	Temperate old-field	North America	CG	Leaf, flower and stem arthropods	[82]
<b>Betulaceae</b>							
<i>Betula</i>	Tree; shrub	Genotype; half-sibs	Subarctic birch forest; boreal forest	Northern Europe	CG; L	Fungal leaf endophytes; leaf and stem herbivores (arthropods and small mammals)	[8,83]
<b>Brassicaceae</b>							
<i>Alliaria</i>	Forb	Genetically based phenotype	Temperate forest	North America	G	Mycorrhizal fungi; soil bacteria; soil fungi	[84]
<i>Brassica</i>	Forb	Genetically based phenotype	Temperate grassland/old-field; temperate coastal cliffs	North America; Europe	CG; F; G	Herbaceous plants; mycorrhizal fungi; soil bacteria; soil fungi; foliar and inflorescence herbivores (arthropods and mollusks)	[14,85,86]
<b>Fabaceae</b>							
<i>Acacia</i> <sup>c</sup>	Tree; shrub	Population	Arid tropical savanna; temperate forest	Western Africa; Australia	CG; G	Soil nematodes; foliar arthropods <sup>d</sup>	[87,88]
<b>Fagaceae</b>							
<i>Nothofagus</i> <sup>c</sup>	Tree	Population	Temperate deciduous forest	South America	CG	Foliar arthropods	[89]
<i>Quercus</i> <sup>c</sup>	Tree; shrub	Genotype; half-sibs; genetically based phenotype	Temperate forest	North America; Japan; Europe	CG; F	Herbivores (leaf and stem arthropods, deer); litter microarthropods <sup>d</sup> ; soil bacteria <sup>d</sup>	[21,90–92]
<b>Moraceae</b>							
<i>Brosimum</i>	Tree	Genotype	Tropical rainforest	Central America	F	Litter and trunk arthropods, epiphytic plants	[10]
<b>Myrtaceae</b>							
<i>Eucalyptus</i> <sup>c</sup>	Tree	Sib-families; population	Temperate forest	Australia	CG	Trunk, litter and foliar arthropods; foliar pathogens; decomposer macro fungi <sup>d</sup>	[13,15,24,93]
<i>Metrosideros</i> <sup>c</sup>	Tree	Genetically based phenotype	Tropical rainforest	Polynesia	CG	Foliar arthropods	[94]
<b>Onagraceae</b>							
<i>Oenothera</i>	Forb <sup>e</sup>	Full-sibs	Temperate meadow and old-field	North America	CG	Leaf and inflorescence arthropods; herbaceous plants <sup>d</sup>	[19,55,95]
<b>Pinaceae</b>							
<i>Picea</i> <sup>c</sup>	Tree	Genotype; genetically based phenotype	Boreal forest	Europe	CG	Mycorrhizal fungi; soil microbes (bacteria and fungi); needle endophytic fungi <sup>d</sup> ; litter decay fungi <sup>d</sup> ; understory plants	[9,96,97]
<i>Pinus</i> <sup>c</sup>	Tree	Population; genetically based phenotype	Temperate semi-arid woodland; temperate forest; boreal forest	North America; Europe	CG; F	Mycorrhizal fungi; litter arthropods; soil bacteria; soil fungi; understory plants	[12,31,98,99]

Table 1 (Continued)

Focal plant taxa	Growth form	Genetic scale	Biome and habitat	Study region	Study method <sup>b</sup>	Communities responding	Refs
<b>Piperaceae</b>							
<i>Piper</i>	Shrub	Genotype	Tropical rainforest	Central America	CG	Leaf arthropods	[18]
<b>Poaceae</b>							
<i>Ammophila</i>	Grass	Population	Temperate coastal dune	Europe	CG	Root nematodes; foliar arthropods and mollusks	[100]
<i>Festuca</i>	Grass	Genotype	Temperate meadow	North America	CG	Foliar arthropods	[101]
<i>Spartina</i> <sup>c</sup>	Grass	Genotype	Temperate coastal wetland	North America	CG	Herbaceous plants	[102]
<b>Rosaceae</b>							
<i>Geum</i> <sup>c</sup>	Forb	Genetically based phenotype	Temperate alpine tundra	North America	F	Herbaceous plants	[11]
<b>Salicaceae</b>							
<i>Populus</i> <sup>c</sup>	Tree	Genotype; genetically based phenotype	Temperate forest; temperate riparian forest	North America, Europe	CG; F	Leaf, bud and stem arthropods; root fungal endophytes; soil bacteria; soil fungi; mycorrhizal fungi; aquatic invertebrates <sup>d</sup> ; aquatic fungi	[4,22,23,26,35,36,103]
<i>Salix</i> <sup>c</sup>	Tree, shrub	Half-sibs	Temperate swamp	North America	CG	Leaf and stem arthropods	[104]
<b>Solanaceae</b>							
<i>Datura</i>	Forb	Genetically based phenotype	Temperate semi-arid canyons and dry stream channels	North America	CG	Foliar arthropods	[105]
<i>Solanum</i>	Forb	Genotype; population	Temperate old-field	North America	CG	Herbivores (stem, flower, leaf and fruit arthropods, voles)	[20]

<sup>a</sup>Studies focus on non-agricultural systems where the response of at least five community members were measured. Additionally, studies were chosen to represent the diversity of plant genera that have been examined.

<sup>b</sup>Study method codes: CG = common garden, F = field, L = laboratory, G = greenhouse or nursery (communities in soils only).

<sup>c</sup>Taxa where status as a foundation species is established.

<sup>d</sup>A community that has not shown a significant response in any study for a particular focal plant taxa.

<sup>e</sup>Broad-leaved, non-woody flowering plants as distinguished from grasses and sedges.

<sup>f</sup>Abandoned agricultural fields in various stages of recovery.

coastal dune shrubs, boreal conifers, alpine cushions and old-field (i.e. abandoned agricultural fields) forbs influences associated communities (Table 1). The scale of focal plant genetics varies among studies, including subspecies, populations, genotypes and sib-families. Although community specificity to each of these genetic levels has different ecological and evolutionary implications, these studies emphasize that genetic effects on diverse communities are common. In some systems, quantitative traits of the focal plant, including chemistry [14], bark characteristics [15], productivity [16] and architecture [17], are identified as potential mechanisms linking communities to plant genetics. Focal plants examined in this research are often foundation species (Table 1). Because of their strong influences on communities and ecosystems, genetic variation in the traits of foundation species is most likely to have a large impact on associated communities [6].

The extended effects of genes on community specificity also occur within plant species that do not define habitats. In a hyperdiverse tropical forest, the communities of trunk and litter arthropods, as well as epiphytic bromeliads and orchids, were more similar on genetically similar breadnut trees (*Brosimum alicastrum*) relative to genetically dissimilar individuals [10]. In addition, in a Costa Rican rainforest, communities of arthropod herbivores were found to

vary among genotypes of the understory shrub *Piper arieianum* [18]. Even non-foundation species such as evening primrose (*Oenothera biennis*) and horsenettle (*Solanum carolinense*) exhibit genetically variable effects on associated arthropod communities [19,20]. These examples illustrate two important points: intraspecific genetic variation in non-foundation plant species can exhibit community specificity, and these effects can occur in diverse systems, including species-rich rainforests.

### Specificity of afterlife effects

Some of the longest lasting effects of plant genetic identity on communities and processes may occur after the death of either the whole plant or its components (e.g. litter, Table 1). All seven plant genera and families referenced in this section showed some afterlife response by biota or processes to subspecific genetic variation in plants. The afterlife effects of genetically based differences in leaf litter properties, in particular chemistry, are well documented [17,21–23], although the afterlife effects of bark and dead wood have also been examined [15,24]. Subspecific genetic variation in plants can influence soil and litter microbial biomass, microbial biomass nitrogen, microbial communities and litter arthropod communities [10,13,22,23,25,26]; however, soil and litter biota are not always sensitive to the

afterlife effects of fine-scale plant genetic variation [21]. These biotic responses may influence decomposition and nutrient dynamics, extending the effects of specificity to ecosystem processes [21,22].

The response of soil organisms and soil processes to genetically based differences in litter expands the temporal footprint of plant genetic identity beyond that of living tissue. Researchers have documented afterlife effects of litter lasting for days to years [21,22]. Genotypic variation in turkey oak (*Quercus laevis*) litter chemistry altered soil and litter nutrient dynamics during an 18–36 month sampling period [21]. We hypothesize that afterlife effects may last longer than have been reported to date, particularly if recalcitrant compounds such as lignin and polyphenols vary by genotype or population, as is often the case [21–23], or if soil processes are influenced by repeated litter deposition by long-lived plants.

Genetic specificity by plant enemies can also result in afterlife effects in litter and soil. Genetically based susceptibility to herbivores [3,27,28] results in damage to living leaves that translates to altered litter chemistry, which then influences litter and soil nutrient dynamics, soil microbial communities, microarthropod abundance and decomposition rates [29–32]. For example, the abundance of galls made by the rosette gall midge (*Rhopalomyia solidaginis*) on tall goldenrod (*Solidago altissima*) is dependent upon plant genotype and ploidy [27,33]. Leaf litter associated with galls contains higher initial carbon concentration, exhibits short-term lower mass loss and retains more nitrogen than litter not associated with galls [32]. These studies provide evidence that life and afterlife effects of genetic specificity do not operate independently of each other. They can be linked by other organisms, and plant enemies may be particularly important in this context.

### Specificity of species interactions

The community phenotypes described above result from interactions among species that can lead to greater specificity. It is important to distinguish between ecological [34] and genetic interactions [35] among species in which ecologists and geneticists define interactions differently for their purposes. In the ecological sense, two general types of indirect interactions have been described: interaction chains and interaction modifications [34]. These 'indirect ecological interactions' are distinct from 'indirect genetic interactions' in that they require more than two species, and do not consider the particular effect plant genotype may have on affected species. Yet indirect ecological interactions [34] can be linked to indirect genetic interactions [35] as follows. First, as an example of an interaction chain, plant genotypes can influence communities through another species [14]. With cottonwood (*P. angustifolia*), genetically based resistance and susceptibility to the galling aphid (*Pemphigus betae*) differentially shape the surrounding community and ecosystem [4,28,30,36]. Using experiments with naturally occurring tree genotypes, aphid-susceptible trees supported a different community of foliar arthropods, different rates of litter decomposition and more stable communities through time than resistant trees. Furthermore, the experimental removal of aphids from susceptible trees showed that the genotypic effects on

the community were mediated by the aphids [36]. This example shows that plant–enemy interactions, specific to particular plant genotypes, can shape a much larger community. In particular, it shows the importance that plant genotype, environment and selection in a community context can have on community organization. Second, in what has been termed interaction modification [34], plant genotype may mediate the interaction between two other species. For example, interactions between aphids and tending ants on common milkweed (*Asclepias syriaca*) ranged from antagonistic to mutualistic depending on plant genotype [37]. Thus, not only did the quantity of species change but the type of species interactions changed across plant genotypes, a result that has also been observed in other systems [19,28]. Here too, plant genotype, environment and selection in a community context significantly define community organization.

In contrast to the ecological requirement that indirect effects are mediated by a third species, for geneticists, two classes of indirect genetic effects are identified. Indirect genetic effects (IGEs) refer to the influence that an individual genotype has on the expression of phenotype in other individuals within the same species, whereas interspecific indirect genetic effects (IIGEs) refer to the influence that an individual genotype in one species has on phenotypic expression among individuals in another species, with consequent effects on fitness [35]. Thus, in an evolutionary sense, IIGE theory shows that genetic variation in one species can influence the fitness and distribution of other species. Again, using the cottonwood (*P. angustifolia*), species interaction models showed that plant genotype can affect the fitness of other community members and that the accumulation of these fitness effects on multiple species can shape the unique communities that individual plant genotypes support [35]. This represents an important step towards incorporating genetics into community analyses and better understanding the genetic basis of 'indirect effects' in ecology.

Although the extended consequences of these differing interactions on the rest of the community have not yet been shown in the wild, it is noteworthy that simply quantifying the abundances of species in a community is not sufficient to characterize the differing community dynamics among plant genotypes. Furthermore, most studies have focused on just a few species; considering the community in its entirety could reveal a larger and more realistic suite of genetically based interactions. For example, network theory may be a powerful tool to explore genetically based interactions in whole communities [38]. Network analysis revealed that communities were generally resilient to random elimination of species, but communities collapsed with the removal of well-connected species [39], suggesting that community stability is tied to the fate of a few, well-connected foundation species.

### Specificity affects the evolution of dependent organisms

The community context of the evolution between plants and their enemies can shape specificity as well as be a product of it. Specialization occurs in microbes, arthropods and vertebrates to plant populations and genotypes [3,40–42],

which can be influenced by the community context [43]. This community-driven evolution and specificity at the population level is evident in the interactions between lodgepole pine (*Pinus contorta*) and its seed predators. Red squirrels (*Tamiasciurus hudsonicus*) are dominant seed predators and independently drive the evolution of cone shape; however, in their absence crossbill (*Loxia curvirostra* complex) bill size and cone shape show evidence of a coevolutionary arms race [41]. Where squirrels are absent, a moth seed predator (*Eucosma recissoriana*) also influences cone evolution, underscoring the importance of a community context in specialization [44]. Selection on cones from squirrels influences serotiny (i.e. cones that release their seeds after fire) so extensively that it may shape fire dependency of seedling establishment and stand dynamics, resulting in community and ecosystem consequences [45].

Community context can also influence the evolution of dependent species in response to genetic variation at a finer scale than populations. The adaptive deme hypothesis [3] posits that individual host plants within a single population represent heterogeneous environments, which can lead to the formation of adapted demes of dependent herbivores and microbes. Reciprocal transfer experiments have demonstrated adaptation to individual plant genotypes across a broad range of arthropod and microbial taxa [3,46–48]. Where genetic interactions between species are affected by a third species [49], they indicate that community context drives genetic specificity [50]. When these interactions involve foundation species, for example, narrowleaf cottonwood (*P. angustifolia*) and the galling aphid (*P. betae*) [4,28], adaptive deme formation may influence the specificity of entire communities at the subspecies level.

The community context in which differentiation of host-associated herbivore lineages occurs may lead to differentiation of taxa outside the direct interaction between plants and their enemies. For example, parasitoids of two herbivores, each consisting of genetically divergent lineages on different *Solidago* species, have themselves differentiated in response to herbivore evolution, demonstrating evolutionary consequences at the community level driven by plant genetic variation [51]. Similar interactions are likely in response to herbivore specificity at finer levels of plant genetic variation, and a test of this would represent a major step forward in community genetics. Although most studies have examined species pairs when investigating the evolutionary consequences of plant genetic variation, it is clear that the community context of evolution is a frontier of community genetics research.

### Specificity affects community diversity and stability

Specificity to genotypes can extend beyond community and ecosystem phenotypes to affect biodiversity and community stability. Often considered emergent properties, community diversity and stability can result from the sum of communities over all individual host genotypes (i.e. additive) or as a result of complex interactions of multiple communities and many genotypes that cannot be predicted by simple summation (i.e. non-additive) [52]. A clearer understanding of how genetically based traits may promote biodiversity has conservation value and could help prevent the loss of biodiversity.

Plant genetic diversity at both the individual and population levels can alter associated species diversity. Although some studies have found negative or no effects of plant genotypic diversity on associated community biodiversity [25,53,54], a greater number show that increased plant genetic diversity positively affects species richness and diversity (Table 1). With these patterns becoming more apparent, research is now focusing on potential mechanisms. For example, in tall goldenrod (*S. altissima*), increases in genotypic diversity led to greater above-ground net primary productivity, resulting in non-additive increases in arthropod community diversity [55]. A similar focus on the potential mechanisms by which genetic diversity can affect associated communities is necessary to predict when effects will be absent, additive or non-additive.

Community specificity can also result in variation in community stability among genotypes and populations. A recent study showed that individual plant genotypes differed significantly in the stability of their associated arthropod communities across multiple years of study. They also showed that stability could be considered a heritable plant trait and that differences were likely to be the result of an indirect interaction with the galling aphid (*P. betae*), a foundation herbivore [4]. These results emphasize that although the composition of a large community can be structured by host genetic differences, there may be one or a few species that respond to those differences, which in turn define much of the remaining community. Genotypes of the biennial evening primrose (*O. biennis*) also varied in arthropod community structure, but the effects of particular genotypes changed across years, potentially due to large changes in phenotype [56]. Expanded to the stand or patch scale, variation among plant genotypes in diversity and stability could provide an additional mechanism linking diversity and stability. Furthermore, just as plant diversity has been shown to affect the stability of plant communities [57], it seems probable that genotypic diversity within a species will affect the stability of associated communities such as arthropods across multiple scales.

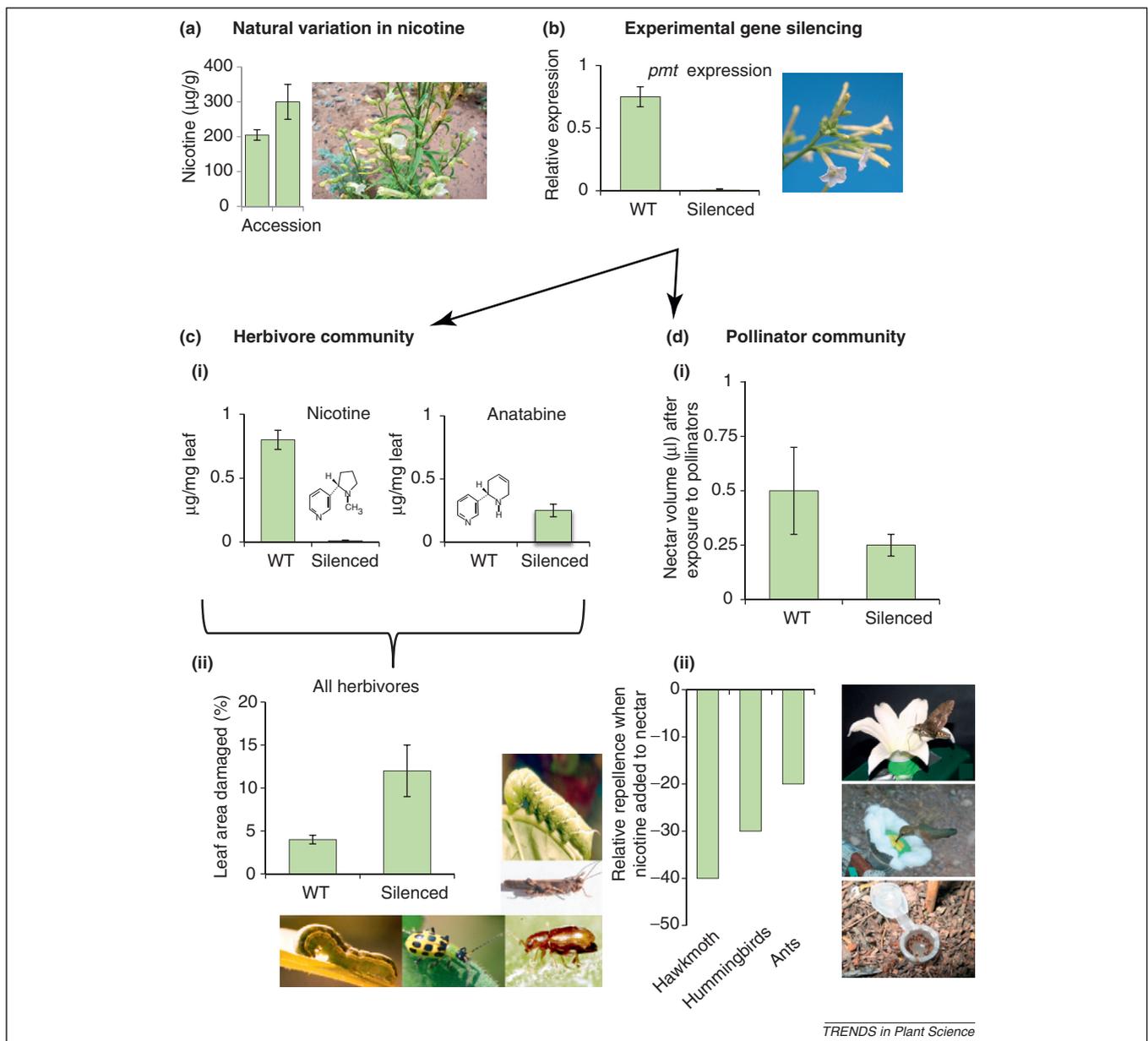
Although studies are limited, it appears that plant genetic differences influence biodiversity and stability [4,56,58]. They suggest that complex community properties may be understood by considering the potential specificity of entire communities to host genetic variation. Because natural selection acting on individual tree genotypes can affect the associated community properties of diversity and stability, the diversity–stability hypothesis itself [59] may be genetically based and subject to natural selection. The conservation consequences of specificity are important because the choice of genotypes used in restoration could stabilize or destabilize a community as well as determine overall biodiversity.

### Genetic specificity and community feedbacks

The community and ecosystem phenotypes that result from genetic specificity may feed back to affect the fitness of the individuals generating those phenotypes, resulting in an eco-evolutionary feedback, or ‘bidirectional interaction that unifies ecology and evolution’ [7,60]. For example, genotypes of *P. angustifolia* differentially affect soil microbial

communities and the nitrogen transformations they mediate [26,30]. A reciprocal transplant experiment showed that *P. angustifolia* seedlings survived twice as well and were larger when grown in their local (maternal) soils, providing evidence of a positive feedback [61]. Similarly, research in plant–pollinator systems has demonstrated selection by the pollinator community on flowering phenology [62] and a gene associated with such changes [63], suggests that a mechanistic understanding of these relationships is attainable.

Community–genotype feedbacks can be positive or negative, with fundamentally different consequences for community specificity. If feedbacks are positive between individual plant genotypes and their associated community, and of similar strength among plant genotypes, both genotypic and community diversity will be maintained. However, if some genotype–community associations have higher fitness than others, the former will be selected for, ultimately reducing genotypic variation and species diversity. For example, *P. angustifolia* seedling genotypes varied more



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**Figure 2.** Genetic variation in the nicotine defenses of tobacco (*Nicotiana attenuata*) affects entire communities. **(a)** Different tobacco accessions exhibit natural variation in the production of nicotine. Photograph of *N. attenuata* in the wild (courtesy of USDA-NRCS PLANTS Database). **(b)** Silencing the *putrescine N-methyl transferase* (*pmt*) genes responsible for this variation in the laboratory leads to altered production of the pyridine alkaloids, nicotine and anatabine (photo of silenced *pmt* plant courtesy of Anke Steppuhn). **(c)** Silenced *pmt* plants produce lower foliar nicotine levels **(i)**, leading to higher levels of herbivory by a large suite of herbivores **(ii)**. Herbivore examples include, clockwise from top in **(c) (ii)**, *Manduca sexta* (Clemson University – USDA Cooperative Extension Slide Series, Bugwood.org), *Timeroptropis* sp. (courtesy of David J. Ferguson), *Diabrotica undecimpunctata* (Creative Commons Attribution License), *Epitrix hirtipennis* (Clemson University – USDA Cooperative Extension Slide Series, Bugwood.org), *Spodoptera exigua* (courtesy of Anke Steppuhn). **(d) (i)** Nicotine also alters pollinator preference, with *pmt* silenced plants preferred over wild type because of the lower level of nicotine in the nectar. **(d) (ii)** Nicotine is a deterrent for common pollinators of *N. attenuata*, such as the hawkmoth, hummingbirds and ants, as demonstrated by the experimental addition of nicotine to the nectar of *pmt* silenced plants. Data and images modified, with permission, from [66–68].

than twofold in the survival advantage they gained by associating with their local versus foreign soil community [61], setting the stage for selection against the less favorable genotype–community combinations. By contrast, negative feedback is unlikely to result in community specificity, but instead may result in strong selection against some genotypes. The cushion plant (*Geum rossii*) has two distinct architectural phenotypes. Common garden studies indicate that there is a genetic basis to these architectures and they are associated with distinct associated plant community phenotypes in the field. The more species-rich plant community associated with cushions with an open architecture significantly reduces their fitness, potentially leading to directional selection against open cushions and the plant community associated with them [11].

The interactions between genotypes and their associated communities vary with environmental context, leading to complex spatial and temporal dynamics. In *G. rossii*, open architecture cushions persist because they are favored in locations where environmental disturbance is high, showing the importance of spatial variation to feedback dynamics [11]. Studies of garlic mustard (*Alliaria petiolata*) across its introduced range provide an example of the importance of temporal variation. Genotypes of *A. petiolata* vary in their production of a family of allelochemicals, the glucosinolates. Glucosinolates alter the soil microbial community, particularly the arbuscular mycorrhizal fungi upon which many native plants depend for resource uptake [64]. Early in the invasion of a site, genotypes with high glucosinolate production are favored because they make *A. petiolata* more competitive against native plants. However, later in the invasion when *A. petiolata* interacts mostly with conspecifics, genotypes that invest less in the costly production of glucosinolate are favored [64]. Variation in the selection pressures associated with plant–plant interactions through time results in altered geographic patterns of genotype–microbial community feedbacks. These studies, along with similar research in other plant–soil systems [23] suggest that community and ecosystem feedbacks can influence our understanding of the evolution of specificity and its ecological impacts.

#### Postulates of genetic specificity at higher levels

Four postulates (analogous to Koch's postulates for demonstrating the causal relationship between a microbe and a disease) have been proposed for testing the hypothesis that specific genes have community and ecosystem phenotypes [65]. These include: (i) the demonstration that a target organism affects other community members and/or ecosystem processes; (ii) the demonstration of key traits in the target organisms that are heritable; (iii) the demonstration of genotypic variation in these traits that result in different communities and/or ecosystem processes; and (iv) the identification of target gene(s) or their expression to evaluate a community and ecosystem effect experimentally. The fourth postulate could involve the use of quantitative trait loci mapping, genome-wide and fine-scale association mapping, knockouts, knockins, or other technologies tailored to the practical and ethical concerns of a given study.

Although evidence in support of two or more of these postulates has been found in numerous systems, only a few studies have tested all four. Using transformed native tobacco (*Nicotiana attenuata*) with silenced *putrescine N-methyl transferase* (*pmt*) genes, the production of nicotine defenses was reduced by 95% relative to the wild type (Figure 2) [66,67]. When planted in their native habitat and exposed to their natural community of herbivores, transformed plants suffered three times greater defoliation than wild-type plants. The silencing of nicotine genes also affected native insect and avian pollinators as well as nectar robbers [68], supporting all four postulates. Similar connections between plant genes and diverse community members have been observed in native populations of *Arabidopsis thaliana* [69]. With the increased use of transgenic plants on a global scale, the fourth postulate will receive widespread testing. For example, genetically modified aspen (*Populus tremula* × *P. tremuloides*) expressing *Bacillus thuringiensis* (Bt) toxins that affect insect herbivores have unintended effects on the non-target aquatic insect community [70]. Such multidisciplinary research and experimental confirmation is likely to become common and should allow us to expand specificity studies to new levels.

#### Concluding remarks

Several major findings and future directions have emerged. (i) Genetic specificity at the community and ecosystem level has been demonstrated in diverse taxonomic groups, aquatic to terrestrial ecosystems, and from species-poor to species-rich systems (Table 1). Future work should assess how common this type of specificity is in different environments and investigate the cause(s) of significant differences. (ii) The effects of plant genetics can extend after the death of living plant tissue, but the breadth of the temporal and spatial footprints of these effects remains unknown. (iii) The genetically based interactions of relatively few species (e.g. foundation species) appear to drive the structure of a much larger community. For most systems, particularly species-rich systems, we have yet to characterize the highly interactive species, particularly those that might be 'hidden' players such as microbes. Network analysis at the population and genotype levels could provide a powerful tool for identifying key interactions. (iv) Specificity in one species for individual host genotypes or populations can affect the evolution of other species, which in turn can affect a larger community. Importantly, these genetically based interactions can change across the landscape to result in a geographic mosaic of evolution. The community context of evolution remains a frontier of ecology and evolutionary biology. (v) Because different genotypes support different communities, even emergent properties such as community stability are, in part, defined by genetic specificity. Understanding the links between biodiversity and genetic diversity is an important challenge. (vi) Because communities can differentially affect the performance of the individual genotypes they are associated with, feedbacks provide a major mechanism for evolution. In combination, it appears that genetic specificity is a fundamental feature of most ecosystems that has important ecological, evolu-

tionary and applied consequences. For example, if individual genotypes or populations differ in their response to climate change [71], such interactions could alter community structure, biodiversity, stability and specificity. Because of community specificity, losses of plant genetic diversity, even in common species, may cascade to affect whole communities.

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