Intraspecific genetic variation and species coexistence in plant communities

Bodil K. Ehlers1, Christian F. Damgaard1 and Fabien Laroche2,3,4

1Department of Bioscience, Aarhus University, Vejlsøvej 25, Silkeborg 8600, Denmark
2CEFE UMR 5175, CNRS-Université de Montpellier-Université Paul Valéry Montpellier-EPHE, 1919 route de Mende, Montpellier 34293, France
3IRSTEA, U.R. Ecosystèmes Forestiers, Domaine des Barres, Nogent-sur-Vernisson 45290, France
4Sveriges Lantbruksuniversitet, Ekologicentrum, Ulls väg 16, Ultuna, Uppsala, Sweden

Many studies report that intraspecific genetic variation in plants can affect community composition and coexistence. However, less is known about which traits are responsible and the mechanisms by which variation in these traits affect the associated community. Focusing on plant–plant interactions, we review empirical studies exemplifying how intraspecific genetic variation in functional traits impacts plant coexistence. Intraspecific variation in chemical and architectural traits promotes species coexistence, by both increasing habitat heterogeneity and altering competitive hierarchies. Decomposing species interactions into interactions between genotypes shows that genotype × genotype interactions are often intransitive. The outcome of plant–plant interactions varies with local adaptation to the environment and with dominant neighbour genotypes, and some plants can recognize the genetic identity of neighbour plants if they have a common history of coexistence. Taken together, this reveals a very dynamic nature of coexistence. We outline how more traits mediating plant–plant interactions may be identified, and how future studies could use population genetic surveys of genotype distribution in nature and methods from trait-based ecology to better quantify the impact of intraspecific genetic variation on plant coexistence.

1. Introduction

The question of what maintains species coexistence is central to ecology and evolution. Numerous studies document that intraspecific genetic variation in plants affects both ecological structure and species diversity of communities at different trophic levels (arthropods, soil fungi and epiphytes [1–3]). However, intraspecific genetic variation in plants can also affect community structure and coexistence at the same trophic level. A recent meta-analysis [4] found that the impact of intraspecific genetic variation in plants on the associated plant communities depends on whether the estimates of genetic diversity depict neutral or non-neutral variation, with a positive relation between genetic diversity and species diversity for non-neutral genetic variation. Recent reviews [5,6] also stress that the effect of genetic variation on ecological interactions depends on the genetic variation that underlies adaptive phenotypic variation. However, so far little emphasis has been given to documenting which adaptive traits specifically impact plant–plant interaction, and the mechanisms by which these traits affect plant coexistence. Here, to fill that gap, we review studies explicitly focusing on the effects of intraspecific genetic variation in known phenotypic traits, and when possible emphasize the mechanism by which variation in these traits affects coexistence with other plant species.

First, we briefly summarize the theory for coexistence mechanisms. Given the vast literature on this topic, we do not review the theory comprehensively but rather we sketch the major mechanisms promoting coexistence and how they can be affected by intraspecific genetic variation. Second, we review...
empirical studies documenting how genetic variation in plants for known adaptive traits impacts their interaction and coexistence with other plant species. Finally, we outline how future empirical research can add more insights into the role that intraspecific genetic variation plays in determining among-species coexistence.

2. Plant species coexistence: insight from theory

The ecological success of plant species and the means by which they coexist in a community can be seen as ultimately determined by four main processes: speciation, migration, demographic stochasticity and ecological differences between species [7]. Various coexistence paradigms have been proposed that attribute different weights to these four pillars. The neutral theory of biodiversity [8] suggests that migration, stochasticity and speciation can explain species abundance distributions in speciose communities without need of considering ecological differences among species. However, patterns predicted by the neutral theory could also readily emerge with mechanisms involving ecological differences [9]. Therefore, understanding the causes of coexistence cannot be based on inferences of mechanisms from patterns only and should also directly address the interaction mechanisms among species.

A paradigm well-suited for such direct inquiry is the stabilizing–equalizing framework introduced by Chesson [10]. This framework focuses on ecological differences among competing species and how these differences enable coexistence—or not. Here, species interactions are conceptually understood by their amount of overlap in a multidimensional niche space made up of resources, natural enemies, time and space. When species show large niche overlap, their coexistence is challenged by the competitive exclusion principle, which predicts the extinction of the inferior competitor. The mechanisms promoting coexistence between species that overlap in their fundamental niche can be divided between equalizing and stabilizing mechanisms [10]. Equalizing mechanisms are those that reduce the mean fitness differences between interacting species, thereby delaying a competitively deterministic winner and promoting long-term coexistence. Stabilizing mechanisms are those that favour species when they become rare and increase intransitive competition relative to interspecific competition. Niche differences will act as a stabilizing mechanism between two competing species because species will ultimately limit their own population growth more than others.

When species interactions involve more than two plant species, intransitive competitive hierarchies promote coexistence even when species show large overlap in their niche requirements [11,12]. Intransitive dynamics can be understood as the well-known rock–scissors–paper game, where species A outcompetes species B, species B outcompetes species C, and species C outcompetes species A. Such dynamics act as a stabilizing mechanism as they will disfavour the most common species by favouring rapid population growth of the species that outcompetes it.

To date, most theory on plant species coexistence focuses exclusively on competitive interactions. However, a few theoretical studies also include facilitative interactions [13–16]. These models predict that, under some conditions, facilitation can maintain species-rich communities. For instance, facilitation increases coexistence, even for species competing for the same limiting resource, when superior resource competitors also act as benefactors for inferior resource competitors [13]. Thus asymmetric facilitation maintains species diversity when the superior competitors reduce the mortality rate of inferior competitors [13,14]. Facilitation can act as a stabilizing mechanism—especially in harsh environments—because the overall increased species abundance around benefactors favours rare species by reducing their risk of stochastic extinction [15]. However, facilitation may indirectly decrease local coexistence when plant density increases around the benefactor, causing the beneficiary species to experience more intense competition from other species [16].

(a) Adding intraspecific genetic variation to coexistence theory

Intraspecific genetic variation can impact species coexistence in several ways. First, genotypic diversity of a species determines its fundamental niche, and a species’ fundamental niche can be understood as the union of niches of the different genotypes ([17], figure 1). Decomposing species interactions into interactions between genotypes illustrates how the outcome of an interaction may depend on the genotype identity rather than species identity (figure 2). Because genetic variation for resource optima allows species to diversify into different niches, coexistence can occur if at least one genotype of each species can be stably maintained locally. Variation in competitive ability among genotypes can lead to intransitive competitive hierarchies at a local scale allowing coexistence of competitors at larger scales [18,19]. Second, genetic variation can affect species interactions differently depending on the ecological role that individual plant species play in the community. For numerically dominant or so-called foundation species (i.e. species instrumental in shaping their habitat), the impact of intraspecific genetic variation may affect a larger number of subordinate species. Genotype diversity in dominant species generates spatial heterogeneity [18], which can promote species coexistence at a larger spatial scale by favouring different plant species in different micro-environments. Lastly, presence of intraspecific genetic variation is a prerequisite for evolutionary adaptation. Local adaptation increases species coexistence if competitively inferior species benefit most from this adaptation,

Figure 1. Niche variation hypothesis. Axes represent niche axes (amount of resources, climatic factors, etc.). Continuous shapes: fundamental niche of a species with low (black) or high (grey) genotype richness. Dotted shapes: fundamental niche of individual genotypes. Niche expansion arises via increased variation among individual genotypes rather than via increased niche breadth within individual genotypes.
thereby equalizing fitness differences between species. However, local adaptation can decrease coexistence if adaptation increases the fitness of the competitively superior species [6].

3. Impact of intraspecific genetic variation on plant species coexistence: insight from empirical studies

(a) Intraspecific genetic variation in dominant species as a source of micro-environmental variation

Genetic variation for the production of chemical compounds that are leached to the local environment by some foundation species can affect species coexistence by creating small-scale differences in local environments among different chemical types. For instance, genetic variation in Scots pine for chemical diversity of terpenes correlates with species richness and composition of the vegetation under the pine trees [20,21]. Genetic variation in monoterpene composition of the essential oils produced by the dominant wild thyme also impacts species richness and composition of the local vegetation around thyme plants [22]. The possible mechanisms for how variation in chemical phenotypes impacts the community of associated species include variation in the allelopathic effects of the different chemicals combined with different sensitivity to these allelochemicals of associated plant species [23,24] and, as found for soil under Populus, via differences in litter composition and soil nutrition under chemically different tree genotypes [25].

Phenotypic variation in plant architecture also impacts species coexistence. For instance, intraspecific variation in the cushion morphology among nurse plants differs in their effects on associated plants [26]. The coyote bush, *Baccharis*, is a dominant species in the coastal dunes of California. It has a genetic dimorphism for plant architecture, with co-occurrence of plants having either a prostrate or an erect morphology. Species richness and plant cover differ between the two morphs, with the erect form supporting more species [27]. Differences in light availability, and soil properties underneath these two morphs were suggested to explain the difference in their ability to support colonizing species.

(b) Intraspecific genetic variation can promote both stabilizing and equalizing coexistence mechanisms

Experiments performed at Sheffield University by Booth and Grime have contributed extensively to unravelling how intraspecific genetic variation impacts species coexistence in grassland vegetation. They created 36 experimental communities, each consisting of the same number of species but varying in the level of genotypic diversity within species. After five growing seasons, more species were retained in the communities with multiple genotypes [28]. Pairwise interactions between two abundant species from these communities (a grass and a sedge) showed that the outcome varied with genetic identity of the plant neighbour and that the competitively dominant genotype varied between high and low fertility environments [29]. In a different set of experimental communities but using the same site and species and a subset of the genotypes, it was found that the outcome varied with genetic identity of the plant neighbour and that the competitively dominant genotype varied between high and low fertility environments [29]. In a different set of experimental communities but using the same site and species and a subset of the genotypes, it was found that the outcome varied with genetic identity of the plant neighbour and that the competitively dominant genotype varied between high and low fertility environments [29].

Figure 2. Decomposing competition between two species (species 1 and 2) to the genotypic scale. Abiotic niche space is represented as a two-dimensional space. Each species has two genotypes, X and Y, and genotypes have different fundamental niches (dotted shapes). (a) Grey zone represents fundamental niche overlap too prominent to allow stable coexistence. Overlaps in white are narrow enough to allow coexistence. (b) Coexistence depends on fitness of individual genotypes. 1X is assumed to be always fitter than 2X. Upper graph: 1Y excludes 2Y, leading to exclusion of species 2. Lower graph: 2Y excludes 1Y, leading to stable coexistence of both species.
Lankau and co-workers also found that genetic variation impacts species coexistence. However, rather than equalizing fitness differences among competing species, they found evidence for a stabilizing mechanism driven by intraspecific genetic variation in communities containing *Brassica nigra*. *Brassica nigra* show a genetic variation for the concentrations of sinigrin in leaves. Sinigrin acts as an allelochemical against heterospecific species. *Brassica* genotypes of high sinigrin concentration are strong competitors against heterospecific, but poor against conspecific genotypes. The reason for the negative impact of sinigrin on heterospecific plants can, at least partly, be explained by the toxic effects of sinigrin on mycorrhizal fungi in the soil. Most heterospecifics benefit from mycorrhiza association, whereas *Brassica* is non-mycorrhizal and hence not affected by reduced mycorrhizae in the soil [31]. High concentration genotypes are favoured when *B. nigra* is rare and most often competes against heterospecifics but are disfavoured as *B. nigra* becomes more abundant and increasingly competes against conspecifics. This negative genetic correlation between intra- and interspecific competition creates cyclic dynamics across generations, maintaining both species coexistence and genetic variation for sinigrin concentration [32].

Clark and co-workers studied fecundity and growth response to environmental variation over a decade in more than 25,000 individuals belonging to 33 co-occurring tree species in 11 forest stands in North America. Overall, the different species responded similarly to environmental variation, suggesting that they were in strong competition. However, neighbour trees of the same species responded more similarly to local environmental variation than heterospecific neighbour trees. This suggests that, at the local scale, intraspecific competition was stronger than interspecific competition. Intraspecific genetic variation was not assessed, but the phenotypic variation in environmental response within and among species was spatially structured such that it contributed to stabilizing species coexistence [33,34].

(c) Plant recognition impacts coexistence

Mounting empirical evidence shows that some plant species can recognize the identity of a neighbour plant and alter their root growth depending on either previous encounter with heterospecifics or genetic relatedness of conspecifics [35]. Root exudates may be one mechanism by which plants recognize their neighbour. In *Deschampsia caespitosa* plants, growing with root exudates from unrelated individuals increased their root length compared with plants growing with root exudates from genetically related individuals. Moreover, plants grown with root exudates from unrelated individuals originating from the same populations grew longer roots than those grown with root exudates from individuals originating from a different population [36]. This suggests that response to a plant neighbour depends on the coevolutionary history of the interacting genotypes rather than fixed species-specific responses [37]. Genetically similar plants are expected to also be similar in resource requirements, and competition with kin should therefore be stronger than with non-kin. However, some species exhibit a kind of kin-facilitation where plants reduce their competitive effects towards kin relative to unrelated conspecifics [38,39]. With kin-facilitation, individuals perform better when interacting with kin compared with a non-related conspecific. Depending on how frequently kin interactions occur, kin-facilitation may switch the relative intensity of intraspecific competition, thereby altering predictions for coexistence. For plant species with limited dispersal, the nearest neighbour is often a genetic relative, making the distinction between kin and non-kin interactions relevant.

(d) Local adaptation impacts species coexistence

Populations can adapt evolutionarily to their local environment on a time scale equivalent to that of ecological processes [40], thereby affecting present day species interactions. For instance, facultative plant–plant interactions prevail in stressful habitats, where the presence of a benefactor plant ameliorates local growing conditions, allowing the establishment and growth of other plants. However, whether or not an environment is perceived as stressful depends on the local scale of adaptation in the beneficiary plants. The facilitative effect of the shrub *Gymnocarpos decander* varied between two ecotypes of the annual grass *Brachypodium distachyon*. One ecotype was adapted to the arid study site, whereas the other was not. Unlike the locally adapted ecotype, the maladapted ecotype could only survive and reproduce under the canopy of the benefactor shrub [41]. A similar result was found for *Plantago* ecotypes that varied in their adaptation to serpentine soil [42]. The importance of facilitation for beneficiary plants varies with their level of adaptation to the local abiotic conditions, and importantly facilitation may account for the coexistence with maladapted species.

In the species-rich Mediterranean garrigue, the aromatic shrub wild thyme (*Thymus vulgaris*) is a dominant component of the vegetation. Wild thyme has a genetic polymorphism for the production of dominant monoterpenes in its essential oil. Some monoterpenes are of a phenolic type and others of a non-phenolic type. The competitively strong perennial grass *Bromus erectus* shows adaptation to growing with local non-phenolic thymes, but not with its phenolic type [43]. In a large vegetation survey [22] comprising several communities dominated by thyme that varied in chemical phenotype, the presence and abundance of *B. erectus* was significantly lower around phenolic thyme, i.e. the chemical type that it was not adapted to. Moreover, plant species richness around phenolic thyme was relatively higher than around non-phenolic thyme. The lower abundance of brome—a strong competitor—around phenolic thyme plants may be one reason why species richness, particularly small annual herbs, is higher. The differences in adaptation of brome to thyme chemical types may explain why brome abundance is only reduced in phenolic thyme sites and suggests that a ‘competitor release’ effect varies among thyme plants producing different monoterpenes.

Variation in adaptation to metal-rich soils also creates variation in competitive and facilitative interactions among metal-accumulating plants and their surrounding neighbours. Some plants are known to extract metals from soil (i.e. phytoextraction). In metal-rich soils, these metal-accumulating plants can facilitate the presence of non-metal-tolerant species by locally alleviating the toxic effects of metals by reducing their concentration in the soil [44]. However, metal-accumulating plants also accumulate these metals in non-contaminated soils (where the concentration is much lower) and via leaching create a higher concentration of metals in the soil around these plants than away from them. For instance, the soil around the selenium-accumulating plants *Astragalus bisulcatus* and *Stanleya pinata* is enriched in
selenium, and the selenium concentration in plants growing in the vicinity of these hyper-accumulators is increased by 10–20-fold relative to the concentration in plants grown away from these plants [45]. Plants that are adapted to this element are facilitated by the selenium-accumulators as the increased concentration of selenium in their plant tissue reduces herbivory, whereas plants that are not adapted to selenium show impaired growth on soil near selenium-accumulators, possibly due to the negative allelopathic effects of increased selenium [46]. Hyper-accumulators may show genetic variation for metal accumulation [47] and non-accumulators show genetic variation for metal tolerance. Hence, the plant interactions between accumulators and non-accumulators can shift from negative to positive depending on the level of adaptation and whether or not the soil is contaminated with metals.

4. Gaining further insight into plant species coexistence

The studies reviewed here show examples of how intraspecific genetic variation impacts species coexistence on a local scale via both stabilizing and equalizing mechanisms. Intraspecific genetic variation could also impact coexistence at larger spatial scale when the variation in dominant species increases environmental heterogeneity, allowing more species to co-occur by favouring different species in different micro-environments. Maintenance of genetic variation then becomes essential for the long-term positive effects on plant species richness. If intraspecific genetic variation in foundation species is eventually lost due to intraspecific competition between genetic variants [48], or other processes reducing genetic variation in foundation species, the positive effects on species coexistence may be short lived.

Because plants are sessile, genetic variation within a given species can be conceptually viewed as a form of environmental variation for neighbour plants. One route to further understand how variation in traits impacts coexistence is, then, to explore how these traits affect local abiotic (such as concentration and composition of phytochemicals in soil, nutrient and light availability) and biotic (abundance and composition of competitors and mutualist partners) environments (i.e. their interspecific indirect genetic effects [49]). Viewing intraspecific genetic variation as a source of environmental variation emphasizes the dynamic nature of plant coexistence as neighbour species may—depending on their own genetic variation—progressively adapt to dominant neighbour genotypes (or the environment they create).

Although many studies document genotype-dependent outcomes of plant—plant interactions, fewer have identified the trait mediating these interactions. Depending on the species, genome-wide molecular polymorphisms might be available but this still requires the hard task of assessing what polymorphism underlies the relevant phenotype variation. Though advancement in eco-genomics makes this gradually more feasible [50], we believe an approach starting from a candidate ecological trait and revealing its genetic basis by quantitative trait locus (QTL) analysis or classical quantitative genetics designs still remains a fruitful strategy. This review found mostly examples showing that genetic variation in chemical and architectural traits influence plant—plant interactions (electronic supplementary material, table). These traits may therefore be promising candidates for adaptive traits mediating genotype-specific interactions. Plants produce a vast amount of secondary compounds with known phytochemical properties (e.g. terpenoids, glucosinolates, phenolic acids and flavonoids). Variation in production of these compounds can be studied using gas chromatography–mass spectroscopy and combined with studies estimating how heritable this variation is. Experimental studies using genotypes that vary in the production of phytochemicals can inform how variation in these compounds impacts plant interaction: do they contribute to increase habitat heterogeneity—thereby producing more niche space? Can phytotoxic effects alter local competition hierarchies? Or are negative frequency-dependent interactions—as demonstrated for sinigrin production in *Brassica*—common and generally instrumental for species coexistence?

Future studies on genotype-dependent interactions should include information from surveys of the natural frequency and spatial distribution of genotypes. This can determine how likely it is that a given species encounter the different genotypes that show trait variation and allow design of realistic experiments that manipulate genotype identity and frequency to match those found in natural plant communities. This is important as a mismatch between genetic and environmental variation in experimental studies may artificially boost the importance of either one. Moreover, it allows results from controlled experiments to be convincingly validated by ‘in natura’ observations of covariation in species richness and composition associated with specific genotypes.

By stressing the importance of specific traits for species coexistence, our approach echoes ‘trait-based’ community ecology [51], which in line with classic niche theory, envisions a strict competitive hierarchy among phenotypes in a given environment. Species coexistence is ultimately explained by fine-scale environmental heterogeneity that allows different phenotypes belonging to different species to be maintained. However, most of the adaptive traits discussed in this review are not the functional traits typically used to quantify community structure (e.g. specific leaf area, plant height, root depth, drought and shade tolerance). The plant traits more typically studied in functional ecology could be further candidates for traits for which variation within species could impact among-species coexistence.

The studies reviewed here illustrate that competition is often intransitive instead of hierarchical and emphasize the importance of both facilitation and genotype-dependent interactions—aspects that extend the classic trait-based ecology. Including these aspects may significantly improve the predictive power of trait-based community ecology. Reciprocally, studies on genotype-dependent interactions demonstrate effects on coexistence at a very local scale but the relative impact of such interactions on large-scale coexistence needs to be explored. Although non-neutral processes shaped by intraspecific variation may determine local-scale coexistence, it is still not known if these local processes will scale up to the level of meta-community, or if stochastic processes override their importance. Future studies could apply methods of trait-based community ecology (like partitioning of trait variance within and among communities [52]) to the adaptive traits identified and use the spatial genotypic composition as environmental gradient. This may help quantify how much variation in community structure is explained by intraspecific variation and if variation in specific traits has similar effects across communities.

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