

A framework for community and ecosystem genetics: from genes to ecosystems

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Abstract | Can heritable traits in a single species affect an entire ecosystem? Recent studies show that such traits in a common tree have predictable effects on community structure and ecosystem processes. Because these ‘community and ecosystem phenotypes’ have a genetic basis and are heritable, we can begin to apply the principles of population and quantitative genetics to place the study of complex communities and ecosystems within an evolutionary framework. This framework could allow us to understand, for the first time, the genetic basis of ecosystem processes, and the effect of such phenomena as climate change and introduced transgenic organisms on entire communities.

Community and ecosystem genetics

The study of the genetic interactions that occur between species and their abiotic environment in complex communities.

Community

An association of interacting species that live in a particular area.

Ecosystem

A biotic community and its abiotic environment.

Jeffrey Mitton¹ asserted that the elaboration of community and ecosystem genetics could “herald a new era in evolutionary biology” and that “if this comes about, evolutionary biology and ecology will be more tightly linked than ever before.” Although great strides have been made in understanding the ecology and evolution of two-species interactions since Ehrlich and Raven², only recently have scientists begun to consider evolution in a broader community^{3–22} and ecosystem^{23–32} context. Furthermore, although multi-level selection theory has advanced^{33–37}, it has not been incorporated into the prevailing models of community organization and ecosystem dynamics^{38–40}.

A major deterrent to advancing community and ecosystem genetics is the overwhelming number of species that comprise even simple communities, and the complexity of the interactions that involve diverse taxa. However, it is important that we make this conceptual leap because species do not evolve in a vacuum. Rather, they are embedded within matrices of hundreds of species that coexist in variable environments. Understanding this frontier requires placing the community and ecosystem within an evolutionary framework that is defined by the genetic interactions that exist among their component species (BOX 1). From an ecosystem science perspective, this is an especially important advance as this field has not previously incorporated genetics into studies of

fundamental processes such as energy flow or nutrient cycling. Examination of the role of genetic interactions at the ecosystem level begins a new era of evaluating ecosystems within an evolutionary framework.

Although the genetic analysis of a complex community or ecosystem might seem to be a hopeless quagmire, recent advances have made it possible to develop a model system that is centred on the *Populus* species. *Populus* is the only system with documented links between a phytochemical quantitative trait locus, a community of diverse organisms and important ecosystem processes^{19,21,27–30,41–43}. It is also the first tree genome to be sequenced^{44–46}, which will facilitate the integration of diverse disciplines. This review focuses on this gene-to-ecosystem integration and the implications of these links. We also discuss how similar findings in other systems support a community and ecosystem genetics perspective, suggesting that these findings are widely applicable.

The study of poplars — in the wild, in common gardens with replicated clones and with crosses of known pedigree — has allowed three conceptual advances. First, the genetic analysis of foundation species can tell us much about an ecosystem. Ecologists have long recognized that relatively few species ‘drive’ community structure and ecosystem processes⁴⁷. The genetic analysis of poplars, a foundation species, reveals the structure and function of

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Multi-level selection

Selection that occurs when relative fitness depends on the properties of individuals, as well as on the properties of the group(s) to which individuals belong.

Energy flow

The movement of energy from one species to another throughout an ecosystem (see also 'trophic interactions').

Quantitative trait locus

A genetic locus that is identified through statistical associations between mapped genetic markers and complex traits (such as growth rate or body form).

Common garden

An experimental approach involving planting individuals at the same field site so that all individuals experience the same environmental conditions. Observed differences in the phenotypes among plants are assumed to be genetically based rather than environmentally based.

Foundation species

Species that structure a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes.

Community and ecosystem phenotypes

The effects of genes at levels higher than the population. These phenotypes result from interspecific indirect genetic effects, which can be summarized as a univariate trait.

a diverse ecosystem. Second, the predictable effects of genes in foundation species extend to higher levels, which can be quantified as community and ecosystem phenotypes. Just as the genotype might have a 'traditional' phenotype that is expressed within the individual and its population, gene expression that leads to interactions with other species extends to levels that are higher than the population to produce community and ecosystem phenotypes²⁷. Third, the community and ecosystem heritability of these phenotypes can be quantified using standard community statistical tools, which can then be analysed using established methods for population and quantitative genetics analysis^{20,21}. Documenting heritability at levels higher than the population is an important advance in community and ecosystem genetics.

Because so few studies have merged the continuum from gene to ecosystem, we believe advances with the *Populus* model system can illustrate emerging concepts and areas for research in other systems. Although there are many challenges to this level of integration (see final section), the widespread recognition of the importance of integration by researchers and funding agencies provides new opportunities that were previously unavailable. Here we examine the logical and sometimes controversial implications of community and ecosystem phenotypes. Do they feed back to affect the fitness of the individual expressing the trait? Do communities and ecosystems evolve? Will the community and ecosystem phenotypes of genetically modified organisms negatively affect the environment? Is it important to conserve genetic variation in foundation species that are common?

In the next three sections we argue that community and ecosystem phenotypes exist, that their heritability can be quantified, and that the interactions of species can lead to community evolution. We emphasize that this trait-based approach, although computationally analogous to the analysis of quantitative traits, does not imply or require that communities themselves have fitness, or that communities evolve like populations.

Our approach is based on concepts of phenotype, selection and trait evolution as they are understood within individual species. However, because individual heritable phenotypes can influence the fitness and phenotypes of individuals in other species, we suggest that such selection occurs within a community context. Moreover, when

such selection changes the nature of genetic interactions among species, community evolution occurs.

Community and ecosystem phenotypes of genes

The traditional phenotype is the sum of direct genetic and environmental influences on individual trait expression. By contrast, community and ecosystem phenotypes arise from interactions with other species that comprise the community. Whether particular species contribute to community phenotypes depends on how genetically based traits within species interact to influence the fitness of other species. Recent findings suggest that the variation in community and ecosystem phenotypes that is associated with a foundation species can indeed have a genetic basis and result from indirect genetic effects (IGEs), in which the phenotype of one organism is part of the environment of another³⁶. This hypothesis is supported by studies of multi-level selection^{33–35,48,49} in which the fitness consequences of IGEs among individuals of the same species are important in group and social evolution⁵⁰.

An analogous mechanism involves IGEs among species, or interspecific indirect genetic effects (IIGEs)²⁰, wherein the environmental influences on the phenotype of one species are due to the expression of genes in another species. When IIGEs exist, genetically based ecological interactions between individuals in different species can evolve^{27,51}. Therefore, IIGEs provide a means for communities to become genetically and demographically distinct. In other words, these indirect interactions result in different communities of organisms (such as insects or microbes) becoming associated with genetically distinct plants^{9,12,13,17,20,21} or animals to form unique community phenotypes. Genetically based variation in community and ecosystem phenotypes have so far been found in eight systems (BOX 2).

Effects of tannin levels in leaves as an example. If the expression of genes is limited to the individual or population (the traditional phenotype of population genetics), then understanding the structure of communities and ecosystem processes requires a complex analysis of the genetic interactions of all the component species. However, if gene expression extends beyond the individual to produce predictable community and ecosystem phenotypes, and a few foundation species define the system, then we predict that the analyses will be greatly simplified. The *Populus* example supports this simplified approach in which a mapped phytochemical trait (levels of condensed tannins in plant tissues) in a foundation species seems to have predictable community and ecosystem phenotypes (BOX 3).

Although encouraging, this example will need to be investigated further to test the alternative hypothesis of random linkage of genes for tannin production with other traits, and to better separate cause and effect. It will also be important to confirm experimentally the underlying genetic determinants of these myriad effects (for example, by knocking out the genes that control condensed tannin production).

Because of the ubiquitous presence of condensed tannins in nature and their extensively studied effects

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environmental influences on trait expression. By contrast, community phenotype is the product of heritable traits in a foundation species and the influence these traits have through IIGEs on the fitness of other species that comprise the community. Whereas the broad-sense heritability of quantitative traits measures the extent to which the variation in individual phenotypes is determined by their genotypes, broad-sense community heritability measures the extent to which variation in community phenotypes is determined by genetic variation within the foundation species²⁰.

Quantifying community heritability

Broad-sense community heritability. For community and ecosystem phenotypes to have evolutionary significance, they must be heritable. Just as the heritability of a traditional phenotype can be calculated, so can we

calculate the heritability of community and ecosystem phenotypes (BOX 4). In its simplest form, broad-sense community heritability (H^2_c) is the tendency for related individuals to support similar communities of organisms and ecosystem processes²⁷. Furthermore, the interactions of species across trophic levels might also be heritable^{21,56}. For example, heritable variation in plant resistance affects the distribution of a herbivore, which in turn affects the distribution of a predator. So, selection could favour plant genotypes that promote increased predator abundances that then reduce herbivore populations. Demonstrating heritability in any of these categories — community, ecosystem or trophic interactions — constitutes an important advance as it allows us to apply the principles of population and quantitative genetics to study variation in community structure and ecosystem processes.

Box 2 | Generality of community and ecosystem phenotypes

This review concentrates on *Populus* as a model system, but other systems show similar patterns, suggesting that these findings are general. The table illustrates the number and diversity of studies that have examined how plant genetic factors affect community composition across eight well-studied natural systems that range from herbs to trees. We have included only studies of community composition that use ordination techniques as we believe this is the best way to represent a community phenotype²⁰ (BOXES 4,5).

The communities examined in these systems include microbes, plants, arthropods, birds and mammals. For example, Johnson and Agrawal¹³ found that with the evening primrose (*Oenothera biennis*) traditional plant phenotypic traits (for example, plant architecture and phenology) also had community phenotypes (for example, arthropod diversity, richness, abundance and biomass). Furthermore, they found that an important community phenotype (that is, arthropod diversity) was highly heritable ($H^2 = 0.41$, where H^2 is the broad-sense heritability of the community phenotype; see BOX 4 for a development of heritability methods). Other examples with willow, eucalyptus, pine, oak and goldenrod also demonstrate that plant genetics can influence the associations and interactions of the communities associated with these species^{3,4,9,16}.

Although studies at the ecosystem level are even less common, plant genetic factors have been found to affect processes such as decomposition and nutrient cycling. For example, Madritch and Hunter²⁶ found that genetic distance between oak phenotypes (in *Quercus laevis*) was related to litter chemistry, which had predictable effects on both carbon and nitrogen fluxes in oak forest soils. Examples with a tropical tree (*Metrosideros polymorpha*) and aspen (*Populus tremuloides*) also demonstrate that individual plant genotypes can influence both litter decomposition and nutrient flux as mediated by differential colonization (or activity) by microbial communities^{25,32}. Although no ecosystem study has published the heritability of an ecosystem process, the demonstration of heritability at this level would suggest the potential for feedbacks on individual genotypes, which has important implications for the evolution of ecosystem processes.

All but one of these study systems involve foundation species, which supports our hypothesis that these species are most likely to have community and ecosystem phenotypes. Although evening primrose is not a foundation species, it still has significant community phenotypes¹³. This example is especially significant because it demonstrates that a community genetics perspective need not be restricted to foundation species alone.

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.

Trophic interactions
Interactions within a community of species, each of which occupies a particular level in a food chain. Interaction across trophic levels represents the transfer of energy from primary producers to predators of herbivores.

Ordination technique
The ordering of multivariate data with respect to one or more axes.

Phenology
The study of the relationship of periodic biological phenomena such as flowering, breeding and migration to climatic conditions.

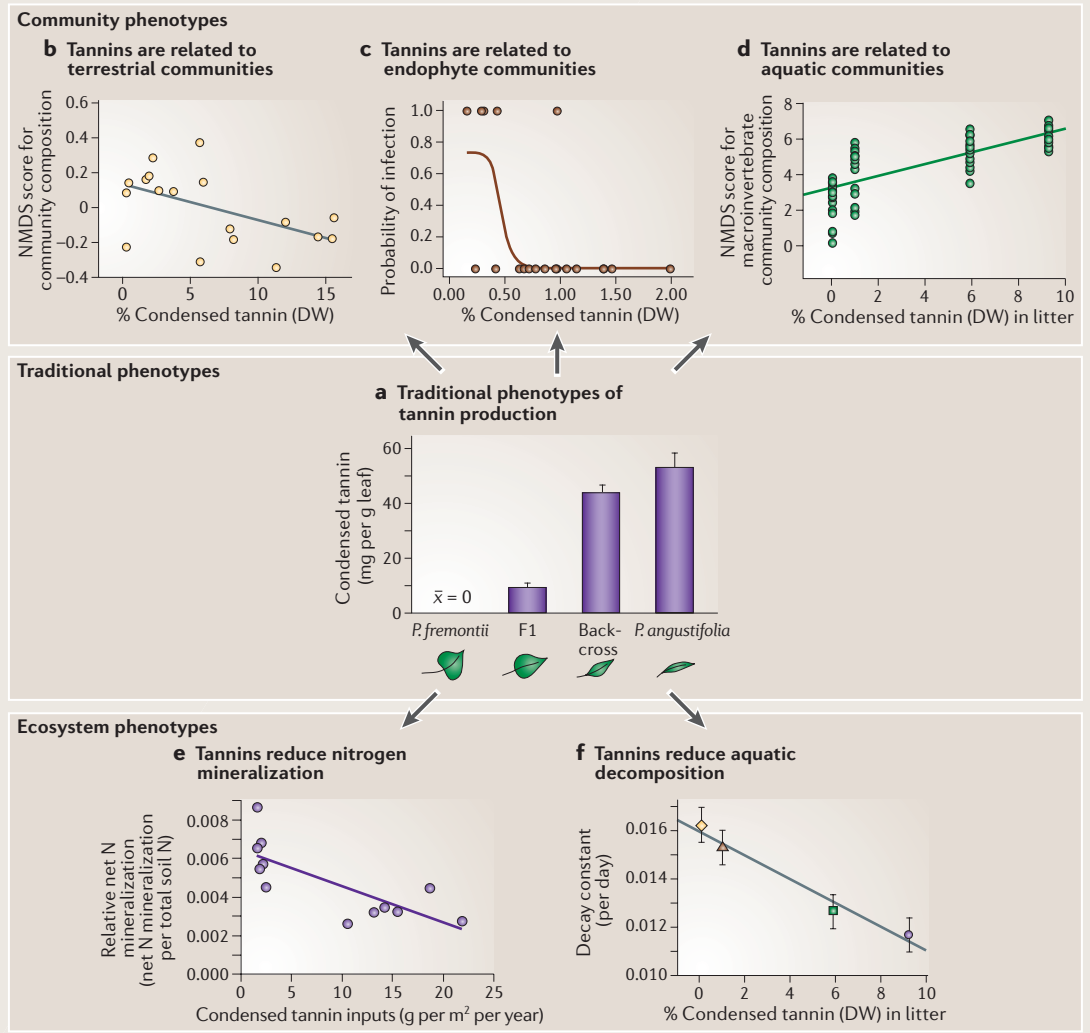
Level of investigation	Plant species	Plant type	Organisms/processes	Heritability measured	References
Community	<i>Populus</i> spp.	Tree	Arthropods, microbes, fungi and vertebrates	Yes	17,19–21,43, 57,68,83,101
	<i>Eucalyptus</i> spp.	Tree	Arthropods	No	9
	<i>Salix</i> spp.	Tree	Arthropods	No	3,12
	<i>Pinus sylvestris</i>	Tree	Plants	No	16
	<i>Oenothera biennis</i>	Herb	Arthropods	Yes	13,18
	<i>Quercus</i> spp.	Tree	Arthropods	No	84,115
	<i>Solidago altissima</i>	Herb	Arthropods	No	4
Ecosystem	<i>Populus</i> spp.	Tree	Litter decomposition, energy flow and nutrient cycles	No	19,23,28–32
	<i>Quercus laevis</i>	Tree	Energy flow and nutrient cycles	No	26
	<i>Metrosideros polymorpha</i>	Tree	Nutrient cycles	No	25

Box 3 | Predictable community and ecosystem phenotypes of a foundation species

Using experimental crosses of *Populus angustifolia* and *Populus fremontii*, a single quantitative trait locus²⁷ was correlated with the phenotypic variation in condensed tannins, where approximately fourfold differences in concentration were observed between two pure species of *Populus* and their naturally occurring hybrids²³ (panel a shows *P. fremontii*, F1 hybrids, backcross hybrids and *P. angustifolia*; ANOVA: $F = 18.64$, $P < 0.0001$, where F is the statistic and P is the probability). Furthermore, this trait also demonstrates significant broad-sense heritability at the finest level of a pure species²¹ (*P. angustifolia* $H^2 = 0.52$; heritability was not calculated for *P. fremontii* as this species typically does not produce condensed tannins). Condensed tannins have been extensively studied and are known for their ecological, economic (tanning leather, wine) and generally inhibitory effects on organisms ranging from microbes to vertebrates^{52,53}.

In a series of studies in the field and in common gardens we found that the traditional phenotype of condensed tannins was significantly correlated with community phenotypes among diverse organisms. The variation in condensed tannins was associated with different community phenotypes of terrestrial arthropods living in tree canopies (panel b; $r^2 = 0.51$, $P < 0.001$, where r^2 is the correlation coefficient), endophytic fungi inhabiting tree bark¹⁰² (panel c; $r^2 = 0.54$, $P < 0.001$), and aquatic macroinvertebrates feeding on the leaves after they fall into an adjacent stream¹⁹ (panel d; $r^2 = 0.56$, $P < 0.001$). See BOX 4 for an explanation of non-metric multidimensional scaling (NMDS).

Similarly, we found significant ecosystem phenotypes. Because important ecosystem processes such as nitrogen mineralization (that is, the conversion of organic nitrogen to plant-preferred inorganic nitrogen) and decomposition are mediated by the microbial community, they are removed by one more step from the condensed tannin quantitative trait locus and might be expected to be weaker than community phenotypes. However, the effects of condensed tannins explained 63% of the variation in net nitrogen mineralization in the soil²⁸ (panel e; $r^2 = 0.63$, $P < 0.003$) and 97% of the variation in decomposition of leaves in the stream¹⁹ (panel f; $r^2 = 0.98$, $P < 0.013$). Therefore, contrary to the general belief that genetic effects would be difficult to detect beyond the population level, these examples argue that a genetically based trait could affect an entire community and ecosystem. DW, dry weight; \bar{x} , indicates the mean concentration of condensed tannin in leaves. Panel a is modified with permission from REF. 23 © (2000) Springer Verlag; panel c is modified with permission from REF. 102 © (2005) NRC Research Press; panel e is modified with permission from REF. 28 © (2004) Blackwell Publishing.



Endophyte
 Describes organisms that at some time in their life cycle live within plant tissues without inducing symptoms in the host.

Box 4 | Detecting and quantifying community heritability

The genetic basis of community phenotypes can be measured by using standard quantitative genetic methods^{103–105}. Standard ecological methodology can be used to quantify traits that are associated with a specific community, such as community composition for arthropods, either directly or through the use of surrogates (for example, phospholipid profiles or microarray data). Once the experimental design is established and the community data (such as arthropod species abundance per foundation individual) are collected, several options for analysis are possible.

Conventional quantitative analysis

Simple, univariate community traits (such as species richness or total abundance) can be analysed using standard methods for quantitative genetic analysis¹⁰⁶. These analyses are also useful for multivariate community data, provided that the multidimensional data are first summarized in matrix or univariate form. This approach involves an initial analysis of multivariate community data, such as the Bray–Curtis similarity coefficient (BOX 5), to calculate the pair-wise similarity between the communities present on each individual of the foundation species (for example, the pair-wise similarity between the arthropod community found on an individual tree and the arthropod community on another individual tree). Depending on the nature of the data, other distance (for example, the Euclidean distance; BOX 5) or similarity measures could be used. The resulting similarity matrix allows tests of overall differences in communities between genetic or pedigree classes of the foundation species with randomization procedures such as analysis of similarity^{107–109} or with more complex models¹¹⁰.

Non-metric multidimensional scaling

Alternatively, or complementary to the above approach, variation in community phenotypes can be quantified using an ordination procedure, called non-metric multidimensional scaling. Non-metric multidimensional scaling is commonly used to summarize variation in community data^{107,108,111} and represents the community associated with each individual of the foundation species as a score on one or more axes that best summarize the compositional variation between individuals of the foundation species. Using ANOVA models, these univariate scores can then be partitioned into variance components that are attributed to variation within and between genetic classes (for example, genotypes, half-sib or full-sib families) of the foundation species. Unlike the direct analysis of similarity measures described above, the reduction of the community variation to a univariate trait(s) allows the application of standard methods for quantifying the heritability of quantitative traits to community data. In the case of clonally replicated genotypes, this allows estimation of the proportion of the total variance in the community trait that can be explained by variation between foundation species genotypes (that is, broad-sense heritability). Such estimates of broad-sense community heritability, that is, $H^2_C = \sigma^2_{\text{among foundation genotypes}} / \sigma^2_{\text{total}}$ measure the proportion of variance in the community or ecosystem phenotype that is attributable to genetic variance in the host²⁰.

Only recently have scientists begun to examine the broad-sense heritability of complex communities in the field^{13,20–21} (BOX 2). These studies showed significant broad-sense heritability of the community phenotypes of species composition, species richness and abundance. An example is provided by the poplar study mentioned in the previous section: individual poplar genotypes were cloned and planted in a common garden, and then the composition of their arthropod communities was analysed, as described in the next section.

Measuring heritability at the community level. Three methods of increasing genetic resolution demonstrated that genetic variation within plant species accounted for more of the total variation in the arthropod community than genetic variation between plant species. First, a line cross analysis and joint scaling test showed no significant additive or dominant effects between the two poplar species (FIG. 1), indicating that differences among species are less important in determining community structure

than differences within plant species. Second, a nested ANOVA of non-metric multidimensional scaling (NMDS) (BOX 4) scores with genotypes that are nested within cross types showed that tree genotype accounted for approximately three times as much of the total variation in arthropod community phenotypes as tree cross type. Third, a one-way ANOVA of NMDS scores of genotypes within each cross type showed that genetic variance within individual plant species accounts for variation among dependent arthropod communities. We calculated significant broad-sense community heritability estimates from this last analysis for each of the parental species²⁰ (*Populus fremontii* $H^2_C = 0.65$; *Populus angustifolia* $H^2_C = 0.60$), and also within the backcross hybrids ($H^2_C = 0.80$). These findings demonstrate heritability at two levels — among hybrids between two species and at the finest scale of an individual species. Similarly, plant genotype also predicts the composition of the associated soil microbial community within backcross hybrids and within pure *P. angustifolia*, demonstrating that the genetic variation within plant species affects their associated microorganisms in the soil⁵⁷. The fact that similar patterns occurred both in each parental species and in their hybrids also suggests that the genetic mechanisms involved are similar at both levels.

Measuring heritability across trophic levels. The outcome of IIGEs across trophic levels is also quantifiable using H^2_C . IIGEs were documented among poplar genotypes, a foundation insect herbivore (*Pemphigus betae*) and avian predators of the insect. When the outcomes of these interactions (that is, herbivory and predation) were summarized with NMDS, we found significant heritability²¹ of the trophic interactions (*P. angustifolia* $H^2_C = 0.70$; backcross hybrid $H^2_C = 0.83$). Again, these findings demonstrate broad-sense heritability at two levels. These findings, which link plant genetics to avian foraging, show that trophic interactions can be quantified as heritable community phenotypes that are predicted by plant genotype. Because interactions across trophic levels are intrinsically tied to the ecosystem process of energy flow⁵⁸, the finding that trophic interactions exhibit broad-sense heritability indicates that ecosystem processes, including nutrient cycling, could be linked to heritable plant traits. The broad-sense heritabilities of these ecosystem processes have yet to be quantified.

The results of using replicated clones in an experimental common garden setting are important for separating cause and effect. In multiple studies it has been shown that community associations are not due to chance, but are based largely on the underlying genotypes of individual plants in the population. The rejection of the null hypothesis indicates that community-level selection has occurred, which in turn could lead to genetic changes within individual species that comprise the community. If this is so, then particular plant genotypes are expected to favour particular genotypes of dependent species — a genetic correlation between species that can be called ‘genetic covariance.’

Line cross analysis and joint scaling test

A method of analysis that identifies the relative contributions of additive and dominant effects to the expression of a phenotype.

ANOVA

Analysis of variance. A statistical model for data analysis.

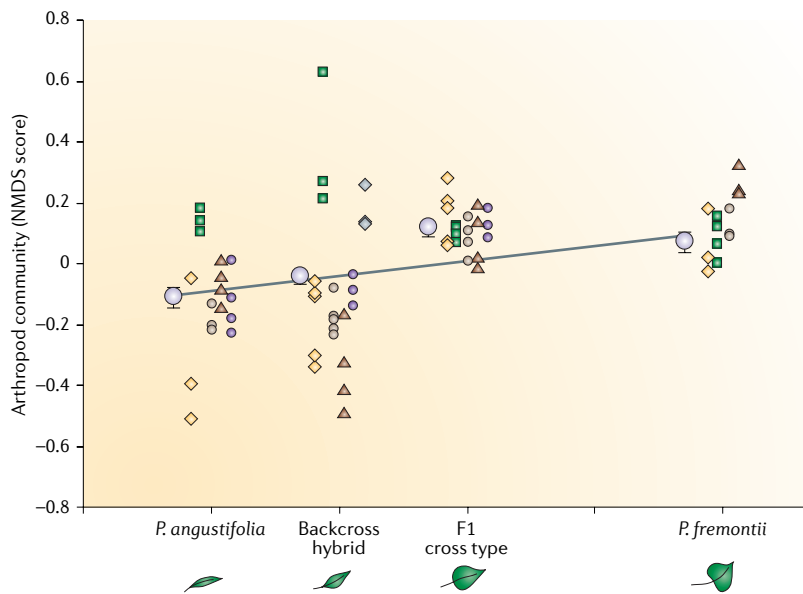


Figure 1 | Genetic variation within species structures the arthropod community. Genetic variation within, rather than between, individual tree species structures the dependent arthropod community in a poplar hybrid system. A line cross analysis and joint scaling test showed that the simplest additive (that is, linear) model could not be rejected ($\chi^2 = 1.68$, $df = 2$, $P = 0.43$) indicating non-significant additive and dominant effects between *Populus angustifolia* and *Populus fremontii*. Broad-sense community heritability estimates for each parental type (*P. fremontii* $H^2_c = 0.65$; *P. angustifolia* $H^2_c = 0.60$), and the backcross hybrid ($H^2_c = 0.80$) were significant. There was no significant heritability within the F1 cross type. Large, filled circles represent adjusted means of the arthropod community for each cross type \pm the standard error from a nested ANOVA. Replicated clones of the same genotype are indicated by the same symbol within each of the four cross types. Different symbols within each of the four cross types indicate different genotypes; similar symbols in different cross types do not represent similar genotypes. Modified with permission from REF. 20 © (2006) Society for the Study of Evolution. No backcrosses between F1 and pure *P. fremontii* are shown because this hybrid cross type does not naturally occur.

Selection, feedback and community evolution

Understanding how complex ecological communities form is a recognized frontier in biology⁵⁹. Three questions that are central to this problem concern how genetic interactions between species (IIGEs) might influence community structure. First, how do genetically based interactions that affect foundation species select for specific communities and ecosystem processes? Second, how might selection proceed within a community context when interspecific interactions have a genetic basis? Third, is it possible for genetically based influences from the community and ecosystem to feed back to affect the fitness of the foundation species? Stated differently, can interactions at these three levels provide a means for communities to become genetically and ecologically distinct (BOX 4)?

Interactions with foundation species. Because of their potential to affect many other species through IIGEs, any genetic responses to selection pressures that are exerted on foundation species are especially important to quantify. For example, the beaver *Castor canadensis* is a species that fells poplars for food and to build

dams, so beavers have the potential to be important agents of natural selection as well as affect other species that depend on the poplar. Indeed, beavers avoid felling poplar genotypes that are high in condensed tannins⁴¹ (FIG. 2a) and, after just 5 years of selective herbivory, there was a three to sixfold increase in poplar cross types that are high in condensed tannins (FIG. 2b). Because different tree cross types and genotypes support different communities of arthropods^{17,20} and facilitate different ecosystem processes^{23,28–32}, selective beaver herbivory might markedly shift the frequency of the community and ecosystem phenotypes. As even small genetic changes in foundation species can have ripple effects at higher trophic levels²¹ through IIGEs, such shifts are important to keep in mind when we later consider the importance of anthropogenic effects on the landscape.

Feedback loops. Although the genetic interactions of foundation species can characterize a community and ecosystem, feedback loops from the community and ecosystem might reinforce genetic interactions^{24,60}. Although examples of feedback loops from plants to ecosystems and back to plants are rare^{61,62}, genetically based feedback loops might occur as a result of variation in phytochemistry. For example, because increased condensed tannin levels are associated with reduced decomposition and nutrient release^{30,31} and reduced nitrogen mineralization²⁸ (FIG. 2c), we propose that poplar genotypes that invest more into tannin production would also have higher fine-root production as a compensatory response to the need to forage for limiting nutrients. As nutrient availability is mediated by microorganisms, this interaction is a potential IIGE. Consistent with this hypothesis, fine-root production is most strongly correlated with tree genotypes that produce high levels of foliar condensed tannins⁴² (FIG. 2d). As most leaves fall beneath the tree that produced them, and nitrogen is the most limiting nutrient in most soils, the individual variation in the expression of condensed tannins could ultimately affect nitrogen availability, which could feed back to affect the performance of individual trees.

Evolution in a community context. We define community evolution as a genetically based change in the ecological interactions that occur between species over time^{20,48,49,63}. What constitutes evidence for evolution in a community context? We propose that three lines of evidence support a community evolution hypothesis: changes in community heritability in the broad or narrow sense; feedback loops between foundation species and dependent community members (that is, selection within a community context); and genetic covariance between community members. The first two conditions have been discussed in previous sections, and the third, genetic covariance, is addressed here.

Genetic covariance occurs when genotypes in one species become associated with genotypes in another species, as is known to occur between arthropods and their host plants in other systems^{64–66}. Three categories of results indicate that IIGEs have led to community

Narrow-sense heritability
The genetic component of phenotypic variance (additive only under random mating) that responds to natural selection.

evolution. First, the documenting of covarying traits and their associated genetic markers between species within a community. Second, the demonstration of coadaptation between community members through reciprocal transplant experiments. Third, a demonstration of progressive changes in broad-sense community heritability over time. Although this third category could be considered to be a succession, such changes are also consistent with a community evolution hypothesis.

As new genetic technologies and candidate model systems emerge, it will become increasingly important to demonstrate the scale at which community evolution occurs. One probable way for this to occur is when geographical structure⁶⁷ creates a selection mosaic and different trajectories in the IIGEs. For example, in the arid southwest of the United States there is extensive genetic structure in poplars across different river systems. We found that arthropod communities are a function of both poplar cross type and the genetic structure of poplar populations within watersheds^{43,68}. This variation indicates a geographical mosaic of IIGEs that could result in different evolutionary trajectories for different river systems⁶⁹.

Community and ecosystem genomics

Advances in community and ecosystem genetics have been paralleled by the simultaneous development of genomics and bioinformatics technology. These advances have converged to form the nascent field of community and ecosystem genomics. Methods such as high-throughput sequencing and assembly, comprehensive expression profiling, and high-throughput genotyping are allowing the fine description of the molecular basis of adaptive variation in a wide variety of model organisms that have ecological significance^{70,71}. In this review we have shown that genetic variation in a foundation species can affect an entire community and ecosystem. Therefore, the combination of genomics approaches with community and ecosystem genetics could lead to new mechanistic insights into the formation, function and diversification of biotic communities.

Candidate gene discovery. Initial steps in community genomics have been taken in the *Populus* system. For example, using mapping and bulked segregant analysis, a locus for resistance to *Melampsora x columbiana* leaf rust in *Populus trichocarpa* was shown to contain

Reciprocal transplant experiment

An experimental approach, which in this case involves quantifying the performance of individuals of two species when they are raised together. If coadaptation has occurred, individuals of both species that have had prolonged evolutionary contact should perform better together than individuals of the same species that have only recently come together or have not previously lived in association.

Geographical mosaic hypothesis

States that because species interactions vary geographically, a mosaic of population genetic structure will result that leads to different evolutionary trajectories.

Community and ecosystem genomics

The study of the composition and function of whole ecosystems using genomic data and methodology.

Bulked segregant analysis

A genome-wide scan for markers that differentiate pooled samples that have contrasting phenotypes.

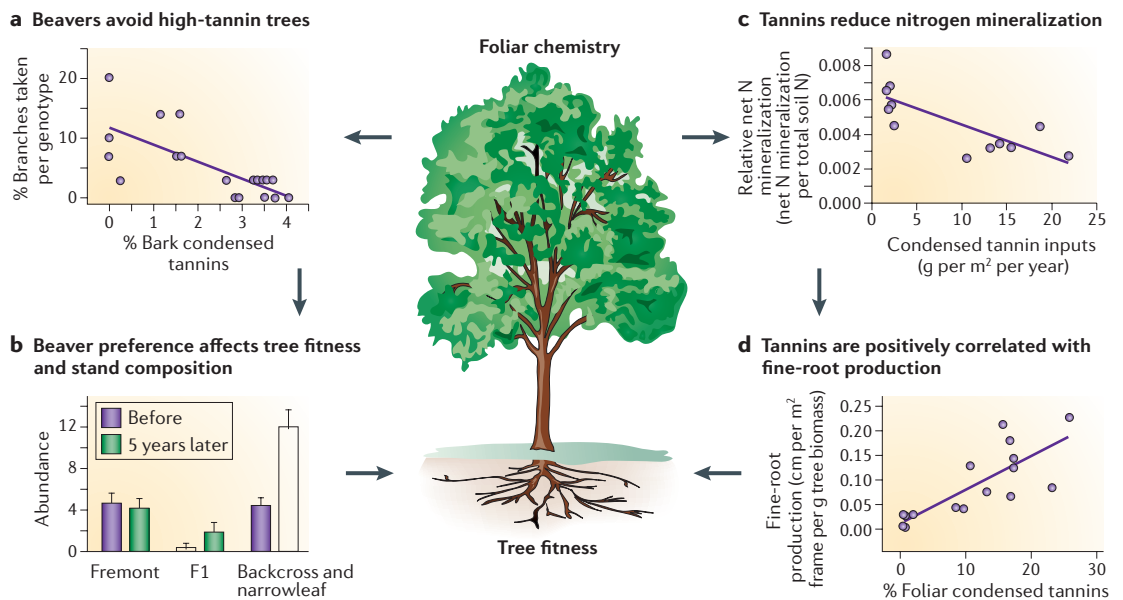


Figure 2 | Feedback relationships. Selection pressures that are exerted on foundation species can affect interactions with other species, which in turn might feed back to affect the fitness of the individual that produced the phenotype. Here we show how the condensed tannin phenotype in the poplar could affect the foraging of an important herbivore, nutrient cycling and nutrient acquisition. Panels **a,b** show that the beaver *Castor canadensis* is an important agent of natural selection in which interactions with a foundation tree species could affect many other species that depend on the tree for their survival⁴¹. Beavers selectively fell trees low in condensed tannins ($r^2 = 0.52, P < 0.001$), which in turn affects the fitness of different tree genotypes and cross types. After 5 years of selective felling of trees, cross types that were high in condensed tannins (backcross hybrids and *Populus angustifolia*) had nearly tripled in abundance, whereas the cross type lowest in condensed tannins (*Populus fremontii*) had significantly declined in abundance, and the cross type intermediate in condensed tannins (F1 hybrids) showed an intermediate increase in abundance (whole-model ANOVA test, change in cross types; $F = 15.66, P < 0.0001$). Panels **c,d** illustrate a potentially important feedback loop that presumably interacts through the microbial community to affect the tree's performance. Panel **c** suggests that an increased concentration of condensed tannins in leaves of individual trees can inhibit the microbially mediated process of nitrogen mineralization²⁸ ($r^2 = 0.65, P < 0.003$). In turn, variation in soil nutrients could feed back to affect the tree's investment into fine-root production to forage for limiting nutrients⁴² (panel **d**; $r^2 = 0.60, P < 0.001$), which can affect tree performance. Panel **a** modified with permission from REF. 41 © (2004) Ecological Society of America; panel **c** modified with permission from REF. 28 © (2004) Blackwell Publishing; panel **d** modified with permission from REF. 42 © (2006) Springer Verlag.

Biodiversity

The number of species in an environment and their individual abundances.

Community metagenome

The amalgamated genetic composition of co-occurring species.

Microarray

A highly compact representation of a large number of diagnostic macromolecules (usually DNA) on glass slides or other solid substrates, allowing the assay of thousands of molecules simultaneously.

Genetic similarity rule

A rule according to which genetically similar plants should support similar communities, whereas genetically dissimilar plants should support dissimilar communities.

several candidate disease-resistance genes, including one with a novel combination of protein domains⁷². These candidates can now be assessed using gene knockouts and upregulation through the high-throughput transformation systems that are available for *Populus*⁷³. The availability of transgenics with single-gene alterations will allow direct assessment of the roles of individual genes at community and ecosystem levels⁷¹. Furthermore, *Melampsora larici-populina* is currently being sequenced, thereby creating the possibility of identifying corresponding avirulence genes in the fungus. Although development in this area is in its early stages, the functional characterization of these genes will enable investigation of detailed coevolutionary interactions between the host and pathogen. Similar future applications of this technology to other associated organisms can ultimately provide mechanistic explanations for community phenotypes.

Community sequencing. Ecosystem genomic approaches could also become possible as sequence information accumulates for other interacting species. Several key fungi associated with *Populus* are currently being sequenced, including mycorrhizal mutualists (*Laccaria bicolor* and *Glomus intraradices*)⁷⁴, as well as the aforementioned *M. larici-populina*. In addition, a community of microbes that are associated with the roots of *Populus* is currently being sequenced, with plans to explore leaf-associated and stem-associated microbes in the near future. However, exhaustive genome sequencing for all organisms in an ecosystem is not currently possible, nor is it necessary for the immediate future of ecosystem genomics. Rather, shallow sequencing of anonymous consortia of organisms can yield valuable

insights about the biodiversity and genomic composition of a community and their possible effects on ecosystem processes^{75,76}.

Towards the community metagenome. The concept of the community metagenome, which is prevalent in microbial ecology^{77,78}, could be extended to higher organisms to provide a new, mechanistic way of describing the composition and structure of ecosystems. The DNA barcoding initiative is an initial first step in this direction, which is aimed at creating a database of diagnostic DNA signatures for all organisms⁷⁹. In addition, the development of high-throughput methods to assay genes that have important functional roles in ecosystems will provide a powerful tool for mechanistic ecological studies. One exciting development in this area is the use of functional gene microarrays to simultaneously assay the abundance of tens of thousands of gene transcripts that are involved in nitrogen and carbon cycling⁸⁰. Similarly, the use of whole-genome microarrays for SNP characterization opens up the possibility of simultaneously assaying molecular variation and differential expression in thousands of candidate genes⁸¹, thereby paving the way for ecosystem genomics studies on a broad scale. A great challenge remains to develop rational, biologically based analytical approaches to organize and analyse these vast quantities of data to provide insights into the organization and functioning of ecosystems.

Applications of community genetics approaches

Conservation biology. A heritable basis for community and ecosystem phenotypes has important conservation implications. For example, how do we conserve biodiversity in the face of habitat destruction, climate change and other anthropogenic alterations of the environment? If individual plant genotypes have different community and ecosystem phenotypes and if these phenotypes are heritable, then genetic diversity in a foundation species should affect the diversity of the dependent community in two ways. First, genetically similar plants should support similar communities. The relationship between plant genetics and the associated community has been identified as the genetic similarity rule⁴³. FIGURE 3a shows that the genetic differences between individual trees, on the basis of molecular markers, are strongly associated with differences in the arthropod communities they support (see methods in BOX 5). This relationship is consistent for trees in a common garden, for trees in the wild and along six river systems in the western United States⁸². Moreover, this relationship holds true when the genetic differences among individuals are associated with the differences in the arthropod communities they support ($r = -0.43, P < 0.001$).

Second, on the basis of this rule, increased genetic diversity within the plant population should be positively correlated with increased species diversity of the dependent community. In support of this hypothesis, studies of natural populations showed that genetic variation in poplars accounted for nearly 60% of the variation in an arthropod community of 207 species⁸³ (FIG. 3b), and similar findings were obtained with oaks

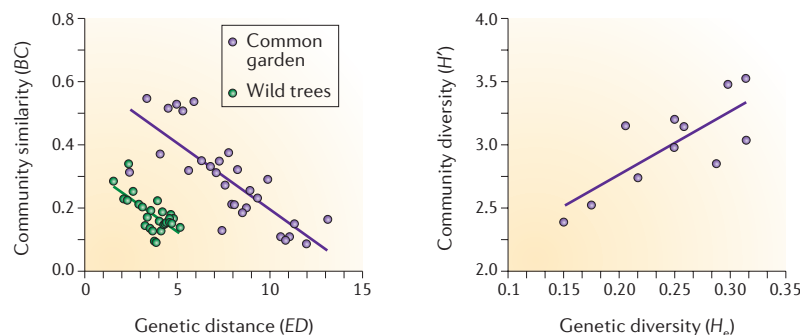


Figure 3 | Arthropod composition is correlated with genetic composition and diversity. a | The genetic similarity rule indicates that, on average, arthropod communities become more similar as the plants they utilize become genetically more similar. High Bray–Curtis (BC) values indicate similar communities (BOX 5) and low Euclidean distance (ED) indicates small genetic distance or more closely related trees (BOX 5). This pattern is observed in common garden trees ($r^2 = 0.622, P < 0.001$) and trees growing naturally in the wild ($r^2 = 0.449, P < 0.001$). Only F1 and backcross hybrids were included in the wild trees, therefore removing the leverage of the two pure parental species from the analysis. Moreover, the relationship is as strong within the Fremont or F1 trees alone. **b** | The diversity of the arthropod community is strongly affected by the genetic diversity of the tree population within individual stands. Stands with greater genetic diversity (high H_g ; BOX 5) support communities with greater arthropod diversity (high H' ; BOX 5) ($r^2 = 0.591, P = 0.006$). Panel **a** is modified with permission from REF. 43 © (2006) Blackwell Scientific Publications; panel **b** is modified with permission from REF. 83 © (2004) Blackwell Publishing.

Box 5 | Quantifying multivariate relationships between genetic and community components

Quantifying the multivariate relationships between molecular markers, phenotypic traits and community traits can be done easily using multivariate data analysis techniques. By correlating matrices of pair-wise similarities or distances between individuals derived from different trait types, such as genetic markers, phytochemistry or insect abundances, we can examine the partial correlation coefficients to determine the relative effect of each trait type while controlling for effects of the others^{43,108,112}.

First, Euclidean distance (*ED*) is a common metric used to calculate genetic composition and measures the genetic distance between two individuals^{108,113,114} with the familiar distance formula in equation 1.

$$ED = \sqrt{\sum_{j=1}^P (y_{aj} - y_{bj})^2} \quad (1)$$

y_{aj} represents an individual *a* and marker *j*, and y_{bj} represents an individual *b* and the marker, summed over all markers. The more related the two individuals (for example, trees), the smaller the Euclidean distance between them. Second, a community similarity matrix is calculated between each pair of the same trees using the Bray–Curtis similarity coefficient (*BC*)^{43,107,108} (equation 2).

$$BC = \frac{2W}{(A + B)} \quad (2)$$

W is the sum of the minimum abundances between samples *A* and *B*, divided by the total abundance of species on the two trees, and scales between 0 and 1. This measures the proportional similarity between two samples. Similarity is a complementary concept to distance where units that are more similar have a high similarity value.

Mantel correlations

To evaluate the overall relationship between molecular markers, phenotypic traits and community traits, Mantel tests are applied to the similarity and distance matrices. Mantel tests are analogous to Pearson's correlation and provide a realistic way to study these complex relationships. The expectation for a correlation between distance and similarity is a negative slope. A significant relationship indicates that closely related trees have associated arthropod communities that are similar.

Genetic and community diversity

Another approach to quantifying the relationship between genes and communities is with diversity indices. Shannon's diversity index (*H'*) comes from information theory and measures diversity such that both the total number of species found in a community and the way in which individuals in the community are distributed across species (that is, evenness) are accounted for. Communities with more species and with all individuals more evenly distributed across species have higher diversity than communities with fewer species and in which there are more individuals distributed between only a few species. Population genetic variation can be estimated from the expected heterozygosity (*H_e*), or gene diversity, which is derived from the frequency of alleles in the population. Therefore, it can be proposed that community diversity increases with gene diversity⁸³.

(*Quercus* spp.)⁸⁴. Furthermore, experimental studies with evening primrose, *Oenothera biennis*, showed that genetically diverse patches supported significantly greater species richness than monocultures¹⁸.

Although conservation biologists recognize that there is a minimum viable population size necessary for the continued existence of a species⁸⁵, this population size might be inadequate for the dependent community. For example, studies of the mite *Aceria parapopuli* showed that <1% of the poplar genotypes could support this arthropod⁸⁶. Because the 'actual' host population for these mites is a small subset of the larger poplar population, the minimum viable population size of poplars is probably inadequate to support its interactions with mites. To support such dependent species, we proposed the concept of a minimum viable interacting population²⁷, which represents the size of a population necessary to maintain the genetic diversity at levels required by 'other' interacting species. These findings argue that genetic diversity in common and non-endangered foundation species is important for maintaining biodiversity⁶⁸.

Anthropogenic effects. Because anthropogenic effects, such as exotic introductions, genetically engineered organisms (GEOs) and climate change, are widespread

and might affect foundation species, it is crucial to evaluate how a change in the community and ecosystem phenotypes of these organisms might alter the environment. For example, the introduction of an exotic genotype of the common reed *Phragmites australis*, combined with anthropogenic environmental disturbances (such as agricultural drainage and urbanization), has resulted in this species now dominating wetlands in the United States and southern Canada⁸⁷. The increased competitive abilities of this exotic genotype has resulted in a new community phenotype that is associated with a striking decrease in the diversity of wetland plant and bird communities⁸⁸ and the apparent disappearance of native *P. australis* genotypes from New England⁸⁹. This example and others^{90,91} indicate that the genotypic composition of an exotic might be a determinant of invasiveness.

GEOs are a special case of exotic introductions in which the genetic differences confer ecological novelty with several uncertain effects on community and ecosystem phenotypes. First, the genes introduced into GEOs are intended to have significant effects, such as reducing herbivory (for example, BT corn), reducing competition (for example, Roundup ready crops and turf grasses) or increasing biomass (for example, growth hormone genes in fish). Second, if these transgenes are beneficial, they

Minimum viable population size

The number of individuals required to sustain a population for a specific amount of time; for example, a probability of extinction of 1% in 1,000 years.

Minimum viable interacting population

The minimum size of a population that is required to maintain the genetic diversity at levels required by dependent and interacting species.

Exotic

A non-native species or even a gene that has been introduced into areas that are outside its native geographical distribution.

BT corn

Corn that has been genetically transformed with genes encoding insecticidal endotoxins that are derived from the bacterium *Bacillus thuringiensis*.

Roundup ready crops

Plants that have been genetically engineered to be resistant to the herbicide glyphosate.

could be passed on to future generations of the GEO and potentially to wild relatives through hybridization, thereby causing sustained changes in community and ecosystem phenotypes^{92–94}. Third, although studies on GEOs are limited, they significantly alter communities. Below ground, Bt corn plants and their residues influence bacterial communities, the establishment of mycorrhizal fungi and soil respiration⁹⁵, and above ground they alter interactions between insects⁹⁶. These potential effects on community phenotypes are important considering the 35-fold increase in transgenic crops from 1996 to 2002 (REF. 97).

Perhaps the most important anthropogenic effect of this century is global climate change. Rapid changes in global climate will create new selection pressures on foundation species that can affect the evolution of the

community. For example, over the past 30 years, the climate of the Galapagos Islands has changed, which has altered the availability of seeds of different sizes that Darwin's finches (*Geospiza* spp.) depend on for their survival. This change has resulted in the evolution of different bill and body-size traits to utilize the change in available resources⁹⁸, which demonstrates that climate change has had important evolutionary consequences⁹⁹. Current rates of climatic change are likely to cause local extinctions¹⁰⁰ and alter IIGEs. Because few studies have examined the consequences of changes in the community and ecosystem phenotypes of foundation species, we can only conclude that the potential for anthropogenically caused changes are great and once they occur they might be impossible to reverse.

Future directions and challenges

The explosion of genetics research in the past 50 years has centred on population genetics and the exploration of factors that affect the expression and heritability of the 'traditional' phenotype. With the advent of genomic technology, the past decade has focused inwards to understanding how individual genes and genomes control the phenotype. By contrast, community and ecosystem genetics looks outwards, beyond the phenotype, to examine links at higher levels. Now that we appreciate that genetically determined phenotypes can have community and ecosystem phenotypes, many of the issues that have been explored at lower levels must be investigated at these higher levels of organization. There are significant challenges in this outwards approach. So far the emphasis has been on quantifying broad-sense community heritability, which includes additive and non-additive genetic variation. This approach is most applicable to species that reproduce asexually and evolve through hybridization events, of which there are many, especially among plants. A challenge will be to demonstrate the existence of narrow-sense community heritability, which is best studied with randomly mating populations of pure species. We believe that the methods described in BOXES 4,5 can be directly applied to quantify community heritability in diverse communities that have the appropriate genetic resources (for example, common gardens with individuals of replicated and known pedigree and/or replicated clones).

The importance of an accepted terminology. There are also important terminology issues to be considered. For example, the meaning of community heritability and community evolution can be misinterpreted. To some these terms imply differential group fitness or proliferation, and are summarily dismissed. However, we emphasize that our approach is fundamentally based on individual measures of trait expression and fitness. Any new terminology that is based on an existing one requires some effort to see where the similarities and differences lie for each lexicon.

Demonstrating causal relationships. In integrating studies across the gene-to-ecosystem continuum, the problems in demonstrating causality rather than just

Box 6 | A checklist for community and ecosystem genetics research

Because the field of community and ecosystem genetics is multidisciplinary, few individuals are likely to have all the necessary skills, or the physical and social requirements. The following checklist of requirements is intended as a 'primer' for those interested in embarking on this approach.

- A system with one or more target species that are thought to be foundation species.
- A common garden using individuals of replicated and known pedigree and/or replicated clones combined with observational studies in the wild.
- An understanding of the potential ecological interactions and ecosystem processes that are likely to be important.
- The ability to experimentally manipulate foundation species to test the interactions and feedback relationships among species.
- The identification of genetically controlled traits that are strong candidates for affecting interacting community members and ecosystem processes.
- The development of molecular tools for characterizing individuals, and studying population genetic structure and genetic covariance among species.
- The potential for developing the mechanistic basis of interactions within and between species (for example, phytochemistry).
- A commitment to long-term studies that allows new collaborators to utilize ongoing experiments and previously collected data bases.
- A collaborative vision that emphasizes integration and the use of modern tools in genetic, community and ecosystem methodologies.
- The maintenance of regular and, importantly, effective communication among collaborators.
- An atmosphere of creativity that embraces the merging of disciplines, the application of novel tools and independence from established paradigms.

These points emphasize the choice of a system in which a broad array of genetic, community and ecosystem parameters can be studied, and a common garden approach, which allows the variance in community and ecosystem phenotypes to be partitioned into genetic and environmental components. If an individual or small group makes the commitment to establish the initial genetic resources (for example, a common garden), it is much easier to attract collaborators to use these resources for other purposes.

Although our group has remarked that collaboration is an exercise in herding cats, we recognize that it is a continual effort to promote a creative atmosphere that respects and rewards the contributions of all participants and pushes everyone to appreciate each other's disciplines and to exploit integrative issues. As interdisciplinary studies expand, academic cultures also need to expand. University review and promotion boards need to recognize the importance of collaborations, accept the reality that a faculty member will not be first author on most papers, and recognize the important role each individual has in multi-authored papers. Hiring committees need to appreciate that scientists early on in their career who embrace interdisciplinary research will have multiple authors on their dissertation or postdoctoral papers. Finally, funding agencies need to earmark resources for large projects and promote continuity over the long term.

correlational relationships are magnified. For example, although we can be confident of our findings of broad-sense community heritability, the precise mechanisms that result in community heritability (for example, condensed tannins as proposed in BOX 3) are subject to alternative interpretation until experiments such as those involving knockout studies of genes can be used. Nevertheless, we now have the methodological tools to critically address these issues and move towards large-scale integration.

If the validity of a community and ecosystem genetics approach is borne out, then new allied fields of study such as community and ecosystem genomics will emerge. This approach will require new levels of experimentation, methodology and collaboration. For example, we will need to simultaneously study many foundation species and quantify their ecological interactions at the genetic level. To do this, experimental forests (or their equivalents in prairie, marine and other systems) will need to be established in which the pedigree and genetic structure of the foundation species are quantified and replicated in different environments. Similarly, greater emphasis should be placed on quantifying their diverse communities, and within these communities target species should be selected for studies of genetic covariation.

The need for new models. Many of the traditional model systems have been selected because of their ease of manipulation and fast generation times, and so many

might be inappropriate as they are not known to be foundation species. Therefore, to critically address higher-order genetic effects with complex communities, new model systems and integrative collaborations will be necessary (BOX 6). Such model systems will allow us to mechanistically address how complex communities evolve.

Implications of future studies. By studying the genetic interactions of foundation species and their dependent community members through time, we can critically address how gene–environment interactions affect community structure, ecosystem processes such as nutrient cycling, and evolution in the context of both communities and ecosystems. In turn, these studies should allow us to address applied issues on how to best preserve biodiversity and ecosystem function in the face of climate change, exotic invasions and GEOs. The long-term genetic resources of such sites will become an important research platform for the future, and they should be incorporated into the National Ecological Observatory Network in the United States and its equivalents in other countries. Such experiments will allow us to achieve a true gene-to-ecosystem integration of diverse disciplines, which is especially important for fields that have typically lacked a genetically based perspective. Because we now have the study systems and technologies to merge fields of study as never before, the quagmire mentioned at the beginning of this review might be far more navigable than previously thought.

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