



Tansley insight

A community genetics perspective: opportunities for the coming decade

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Summary

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Community genetics was originally proposed as a novel approach to identifying links between genes and ecosystems, and merging ecological and evolutionary perspectives. The dozen years since the birth of community genetics have seen many empirical studies and common garden experiments, as well as the rise of eco-evolutionary dynamics research and a general shift in ecology to incorporate intraspecific variation. So what have we learned from community genetics? Can individual genes affect entire ecosystems? Are there interesting questions left to be answered, or has community genetics run its course? This perspective makes a series of key points about the general patterns that have emerged and calls attention to gaps in our understanding to be addressed in the coming years.

I. Introduction

For decades, if not longer, ecologists have sought novel approaches or techniques that shed new light on the diversity of life around us, how it varies in space and time, or help predict which species are important or critical for their respective ecosystems. Proposed by

Antonovics (1992) and featured more broadly in the early 2000s, 'community genetics' was one such approach, with the basic premise that genetic variation is a major driver of phenotypic variation, which, in turn, has consequences that extend well beyond the population level (Whitham *et al.*, 2003). Therefore, by understanding the heritability and genetic architecture of variation within species, we would ultimately have a clearer picture of the links between the hierarchies of ecological organization, from genes to ecosystems, and would be better able to place ecology into an evolutionary framework (Whitham *et al.*, 2006; Johnson & Stinchcombe, 2007; Hughes *et al.*, 2008).

Gregory Crutsinger was a finalist for the 2015 *New Phytologist* Tansley Medal for excellence in plant science, which recognises an outstanding contribution to research in plant science by an individual in the early stages of their career; see the Editorial by Lennon & Dolan, **210**: 5.

Since its early days, community genetics has been heavily weighted towards the study of genetic variation within plants and bottom-up effects. Terrestrial plants will thus be the main focus of this perspective, although recent illustrations have occurred for higher trophic levels (discussed below in relation to eco-evolutionary dynamics, see Section IX). Much of the empirical evidence stems from dominant and foundation plant species, as these species support a diverse array of associated organisms and contribute strongly to ecosystem functioning (Ellison *et al.*, 2005). Thus, if genetic variation is going to be important at the community or ecosystem level, it will likely be in species such as cottonwoods, oaks or eelgrass first and foremost (Whitham *et al.*, 2006). Intuitively, it makes sense to start with foundation species, even though we may still lack any formal community genetic comparisons within less dominant players.

Given the series of case studies in the literature documenting the ecological consequences of genetic variation, what have we really learned about how communities are assembled in space and time or the links between genes and ecosystems? This perspective is not meant to be a comprehensive literature review of community genetics studies, as there is already a high ratio of reviews of this topic already compared to empirical examples. Rather, my goals are to summarize the general patterns that have emerged from the field, emphasize a variety of gaps in our understanding, and present opportunities for future questions to be answered.

II. Plant genotype effects are common, especially on herbivores

Links between plant genetic variation and herbivore communities have been a major focus of community genetics studies (Fig. 1a). There is now a laundry list of examples where different herbivores exhibit varying degrees of host-plant genetic specificity, with genotype explaining anywhere from *c.* 0 to over 80% of the variation in community-level parameters, such as richness, abundance, evenness and composition (Johnson & Agrawal, 2005; Barbour *et al.*, 2015). Early adoption of community genetics by plant–herbivore researchers probably resulted from a longer history of the study of heritable resistance/susceptibility to herbivores, with some of the earliest cases of community-level effects of genetic variation made well before the term ‘community genetics’ was coined (Maddox & Root, 1987). Although invertebrates continue to be disproportionately represented in community genetics studies, many different assemblages have now been shown to exhibit responses to intraspecific genetic variation, including understory plants, epiphytes, endophytes, soil microbes and vertebrates (Whitham *et al.*, 2012).

III. From prey to predators, genetic effects cascade up the food chain

Within the empirical support for plant genetic effects on higher trophic levels, arthropods are also disproportionately represented in field studies (Fig. 1b). Classic work on the *Solidago altissima* system remains one of the best case studies of the interactions between plant genetic variation, galling herbivores and parasitoids

(Abrahamson, 1997). This line of questioning has now been expanded to diverse predator assemblages (Crutsinger *et al.*, 2006; Moreira & Mooney, 2013). Plant genetic effects on predators occur both directly through phenotypic variation in plants themselves, such as in flowering or plant architecture (Crutsinger *et al.*, 2014a), and indirectly through effects on the abundance of herbivorous prey (Moreira & Mooney, 2013) or modification of herbivore phenotypes, such as gall size that mediates parasitism rates (Abrahamson, 1997). What remains notably absent from community genetics studies, however, is the adoption of more encompassing food-web approaches. Integrating a network perspective would begin to unravel the complex interactions between genetic variation in producers and the higher trophic levels they support (Melián *et al.*, 2014). For example, the extent to which genetic variation increases the complexity of networks or alters network stability and persistence remains untested in the field.

IV. Genetic effects rain down from the canopy to soil

Concurrent with community genetics, understanding above- and belowground linkages has been a major initiative in ecology over the past decade, revealing many paths by which plants shape the soil around them (Bardgett & Wardle, 2010). Genetic variation can play an important role in shaping belowground communities and processes (Schweitzer *et al.*, 2012) (Fig. 1c). For instance, variation in the quality or amount of litter inputs can influence decomposers, including litter invertebrates and soil microbes (Schweitzer *et al.*, 2011), and decomposition and nutrient mineralization (Silfver *et al.*, 2015). In addition, genetic variation can directly and indirectly (via herbivore resistance) influence crown architecture, thereby altering the understory microenvironment and belowground interactions (Whitham *et al.*, 2006; Crutsinger *et al.*, 2014a). Madritch *et al.* (2014) recently used image spectroscopy to distinguish between different aspen (*Populus tremuloides*) clones by the spectral signature of both their foliar chemistry and effects on adjacent soils, indicating that the genetic basis of belowground interactions scales to the landscape level. Nevertheless, there continues to be a unidirectional bias toward the effects of plants on soil, and major gaps remain in understanding the genetic basis of plant–soil feedbacks (Schweitzer *et al.*, 2012). Further empirical studies are needed that examine genetic variation within both above- and belowground organisms (e.g. plants, herbivores, bacteria, invertebrates, fungi) and the interactions/feedbacks between the two on plant fitness, the structure of different communities, and how terrestrial ecosystems function.

V. The dampening of the extended phenotype

The current paradigm is that the ecological effects of genetic variation tend to dampen with distance from the source, such as moving up the food chain, from above- to belowground, or from terrestrial to aquatic habitats (Bailey *et al.*, 2009). However, we are missing rigorous tests of the extent to which genetic effects ripple out through most ecosystems. For example, above- and

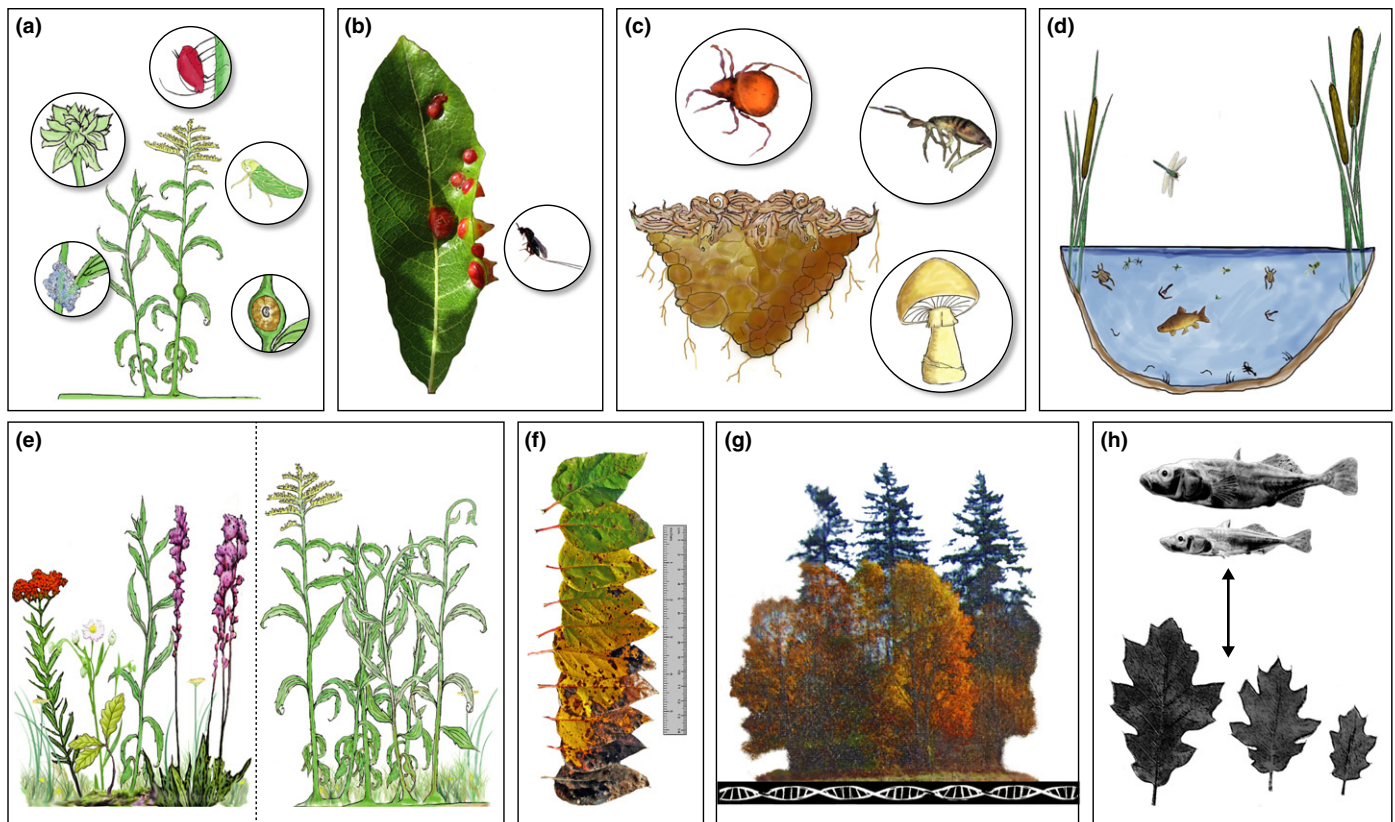


Fig. 1 The figure depicts the key points about the general patterns that have emerged from community genetics research over the past decade (artwork by G. M. Crutsinger unless otherwise noted). These include (a) the effects of host-plant genetic variation on herbivores and (b) predators (photo credit: M. Barbour). The ecological consequences of genetic variation extend both (c) belowground and (d) across terrestrial–aquatic boundaries, with (e) patterns of plant genetic diversity mirroring those of species diversity. However, (f) the underlying phenotypes within community genetics studies, as well as (g) the links between specific genes and ecosystems, remain poorly explored. Finally, (h) the rise of eco-evolutionary dynamics (stickleback photo credit: S. Rudman) research reveals the need to study genetic and phenotypic variation across multiple trophic levels concurrently.

belowground responses are rarely measured simultaneously in the same study (Crutsinger *et al.*, 2014a) and only a handful of studies have explored how the genetics of riparian plants spill over into aquatic ecosystems (LeRoy *et al.*, 2006; Crutsinger *et al.*, 2014b; Jackrel & Wootton, 2014)(Fig. 1d). Moreover, community genetics studies have acknowledged that phenotypic variation is determined not only by genetic variation (G), but also by the biotic and abiotic environments (E) in which individuals and species occur. Although comparisons of the ecological effects of genetic variation on other environmental factors are growing (Johnson & Agrawal, 2005; Silver *et al.*, 2015), there is still not a concerted effort aimed in partitioning $G \times E$ interactions (Hughes *et al.*, 2008; Hersch-Green *et al.*, 2011). To date, empirical work has occurred in a limited number of ecosystems (namely low-diversity temperate grasslands and forests), aimed at community and not ecosystem responses, and focused primarily on abiotic and not biotic environments. There is also a significant need to identify the spatial scale of genetic and environmental variance, and to relate this scale to the context of common garden experiments (Tack *et al.*, 2012). Thus, although we know that genetic effects are common and can be important ecologically, many questions remain as to how genetic effects compare or interact with other factors and at what scale?

VI. From genetic to species, diversity begets diversity

The positive relationship between plant and animal diversity has long fascinated ecologists and large field experiments at the plant species level have shed light on the mechanisms driving this pattern (Haddad *et al.*, 2009). Smaller experiments at the genetic level have (sometimes) revealed analogous effects of diversity within plant species (Fig. 1e), with increasing animal diversity and primary productivity being associated with increasing number of plant genotypes (i.e. genotypic diversity) (Crutsinger *et al.*, 2006; Hughes *et al.*, 2008). Meanwhile, only a handful of studies have manipulated both genetic and species diversity together (Fridley & Grime, 2010; Cook-Patton *et al.*, 2011; Crawford & Rudgers, 2013; Abdala-Roberts *et al.*, 2015), mainly because the logistical challenges of doing so are not trivial. As a result, many interesting questions are still unanswered about the relationship between genetic and species diversity (Vellend & Geber, 2005), the interactions between the two, and how and when these interactions shape communities and ecosystems (Crawford & Rudgers, 2013). Moreover, genetic diversity experiments tend to consist of a random selection of genotypes. It is unclear what the community- and ecosystem-level impacts would be if experiments more closely represented how genetic diversity actually varies natural

populations, for example, mirroring patterns of relatedness or structure within and among populations. Finally, genetic diversity experiments have occurred over short timescales relative to species-level experiments (Haddad *et al.*, 2009). The long-term consequences of genetic diversity, as well as how changes in population genetic structure over time influence the diversity and stability of communities and ecosystems, are only beginning to be explored (Agrawal *et al.*, 2012). All told, we know that there can be parallel patterns between genetic and species diversity, but there are clear opportunities to further explore the causes and consequences of the interaction between the two.

VII. It's the traits that matter ... but which ones?

Community genetic studies have done a fairly thorough job of characterizing species responses to the genetics of host plants, but the effort to partition the relevant phenotypes mediating ecological patterns continues to be poor. Studies have either measured one or a few traits or have failed to measure traits altogether, simply documenting a genotype effect. This is in spite of repeated calls for better trait screening in community genetics research (Hughes *et al.*, 2008; Hersch-Green *et al.*, 2011) and a growing interest in traits in ecology more generally. Studies have tended to concentrate on traits such as secondary metabolites, perhaps as a consequence of the interest in plant–herbivore interactions. By contrast, other key aspects of plant physiology, morphology and phenology have been relatively ignored (Fig. 1f). As a result, we have limited understanding for most study systems of the amount of intraspecific variation, the degree to which it is heritable and the extent to which different members of a community are associated with different traits (but see Johnson & Agrawal, 2005; McKown *et al.*, 2014; Barbour *et al.*, 2015). I note that this lack of trait screening is in the context of community genetics research, as there are significant resources from the plant functional trait literature to draw upon for estimating trait variation and the patterns of plant community assembly (Kraft *et al.*, 2015), including a push to incorporate intraspecific variation (Violle *et al.*, 2012). Community genetics studies simply need a broader approach to trait screening and for detailed screenings to occur in all future studies.

VIII. There are many, many genes for ecosystems

In community genetics research, there has been the appeal of the 'genes-to-ecosystems' concept (Fig. 1g). Yet, in spite of huge strides in genomics over the past decade, there have been limited attempts to link the underlying genetic architecture with patterns of community assembly or ecosystem function. Studies have focused almost exclusively on variation among different genotypes, genotypic richness or other measures, such as hybridization or ploidy. Of the systems (namely *Populus* and *Eucalyptus*) with the genomic resources necessary for identifying the genes associated with ecologically relevant traits, most traits have been found to be highly polygenic, with only a small fraction of phenotypic variability accounted for by a single gene (Külheim *et al.*, 2011; DeWoody *et al.*, 2013; McKown *et al.*, 2014). As a consequence, linking one or a few genes to community or ecosystem responses may not be likely or at least ecologically meaningful (Crutsinger

et al., 2014b). However, with few examples available, whether linking genes to ecosystem is a valid approach or not is debatable, although rapidly advancing genomic methodologies will soon validate this approach for a range of systems.

IX. From the community-genetic caterpillar to the eco-evolutionary butterfly

The study of eco-evolutionary dynamics has emerged to reveal the reciprocal relationship between evolutionary change and ecology (Schoener, 2011). Eco-evolutionary dynamics (eco-evo) research overlaps almost entirely with the goals of community genetics in understanding the ecological consequences of phenotypic variation; however, eco-evo studies explicitly target evolutionary processes, such as local adaptation, as the driving force underlying trait variation. To date, the best case studies of eco-evolutionary interactions stem from local adaptation in predator species, such as alewives, guppies and sticklebacks (Schoener, 2011), with strong top-down consequences observed for lower trophic levels, such as invertebrate prey, as well as ecosystem processes, such as primary productivity and nutrient cycling (Harmon *et al.*, 2009; Bassar *et al.*, 2010). Pooled, both community genetics and eco-evo dynamics create a framework in which trait variation, either as a result of drift or natural selection, shapes contemporary ecological patterns and processes from the bottom up, the top down, or laterally. Incorporating a multi-trophic approach in the study of genetic and phenotypic variation, where variation in multiple species within an ecosystem is considered simultaneously (Fig. 1h), is an obvious next step in understanding the interplay between ecology and evolution, and empirical efforts will likely be productive.

X. Conclusions and future directions

So what have we learned from community genetics? Certainly, we understand now that genetic variation can play a much stronger role in ecology than previously anticipated. We have observed how genetic effects can cascade up trophic levels or spill over the boundaries of ecosystems and that an impressive amount of variation can be explained by incorporating intraspecific differences (or at least controlling for them). However, it remains complicated. Interactions among co-occurring genotypes can result in nonadditive effects (Crutsinger *et al.*, 2006; Johnson *et al.*, 2006), many traits and genes are likely involved, and the strength of genetic effects can vary among study systems, over space, and with time. As such, these general patterns need further testing and expanded upon.

Perhaps one of the most important legacies of community genetics is its contribution to a general trend in many areas of ecology of incorporating intraspecific variation. Areas such as trait-based community ecology (Violle *et al.*, 2012), biodiversity–ecosystem function (Crutsinger *et al.*, 2006), metacommunity ecology (Urban *et al.*, 2008), network theory (Melián *et al.*, 2014), and above- and belowground linkages (Schweitzer *et al.*, 2012) all share common ground in incorporating differences among individuals, at least the portion of which is genetically based. Given the broader context being applied by eco-evolutionary dynamics

studies, it is likely that community genetics will not stand on its own and will be assimilated into this newest approach. Yet, regardless of the terminology, there are more questions than answers about the role of heritable trait variation in structuring communities or driving ecosystem processes. As such, the future remains bright for this avenue of research with many opportunities to expand on the framework that community genetic studies have built.

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