EVOLUTIONARY ECOLOGY OF PLANT DEFENCES

Genetic variation and community change – selection, evolution, and feedbacks

Mark A. Genung*,[1], Jennifer A. Schweitzer[1,2], Francisco Úbeda[1], Benjamin M. Fitzpatrick[1], Clara C. Pregitzer[1], Emmi Felker-Quinn[1] and Joseph K. Bailey[2]

[1]*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996, USA; and*
[2]*School of Plant Science, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia*

Summary

1. There is relatively little information on how evolutionary processes that alter genetic variation in a focal species may affect interactions with other species, impact the structure or function of the community and ecosystem, and affect evolutionary feedbacks among interacting species through time.

2. Because evolution can occur at ecological time-scales, it is important to understand how major selective events, such as climatic changes, can impact the community of interacting species and ecosystem processes by changing intraspecific genetic variation.

3. The evidence linking genetic variation and evolution to community change and feedbacks has arisen from several different approaches whose results have not been synthesized into one conceptual framework, and whose commonalities may not be fully understood.

4. This review synthesizes several different experimental approaches on how evolution may impact communities and ecosystems and focuses on five main issues: (i) the genetic basis to communities and ecosystems; (ii) the community and ecosystem consequences of among-population genetic differentiation; (iii) the role of local adaptation and co-evolution; (iv) the effects of trans-generational feedbacks and the eco-evo dynamic and; (v) the integration of community and ecosystem genetics and multi-level selection.

5. Evolution can alter intraspecific genetic variation to affect indirect genetic effects and feedbacks. Future studies should investigate how communities and ecosystems are affected when evolution causes the strength of feedbacks to change.

Key-words: co-evolution, community and ecosystem genetics, eco-evo interactions, feedbacks, genes to ecosystems, genetic differentiation, genetic variation, multi-level selection, Price equation

Introduction

An important current issue in community and ecosystem genetics research is determining the relevance of intraspecific genetic variation (i.e. polymorphism) and *genetic differentiation* (i.e. divergence) (Table 1) to ecological and evolutionary processes at the community and ecosystem level. Intraspecific genetic variation in a focal species not only affects the composition of associated communities, but can cause community members to evolve in response to genetic differentiation across the focal species' range, which provides a strong argument for the necessity of considering intraspecific genetic variation in ecological studies. The

genetic analysis of ecological and evolutionary interactions involving multiple species may seem complicated, because *community and ecosystem phenotypes* represent complex traits related to genetically based interactions among species, and because abiotic and biotic environmental variation have a large effect on their expression. However, in both controlled *common garden* environments and across broad biogeographic regions, genetic variation in one species can have predictable and heritable effects on associated communities and ecosystems (Whitham *et al.* 2003, 2006; Johnson & Stinchcombe 2007; Bangert *et al.* 2008; Bailey *et al.* 2009; Johnson, Vellend & Stinchcombe 2009). It is crucial that we further our understanding of these processes, because when genetic variation in one species drives the expression of community and ecosystem phenotypes, selection can alter

*Correspondence author. E-mail: mgenung@utk.edu

Table 1. Lexicon of terms used in this review which are commonly used in ecological genetics studies

All home and away	An experimental design in which common gardens are established at every location from which individuals were collected
Co-evolution	Evolutionary changes in traits of one population followed by an evolutionary change in traits of a second population to the first
Common garden	An experimental design in which environmental differences are minimized by planting all individuals in a common site
Community heritability	The degree to which genetically related individuals support similar communities and drive similar ecosystem processes
Community and ecosystem phenotypes	The effects of genes on levels of organization above the population; occur due to species interactions in which the genes of one species affect the phenotype of the other species
Diffuse co-evolution	Selection imposed reciprocally by one species on another is dependent on the presence or absence of other species
Eco-evo feedback	Reciprocal interactions between ecology and evolution in which populations alter their environment and those changes subsequently affect the evolution of the population
Feedback	Change in fitness of an organism due to its alteration of its biotic and abiotic environments
Genetic cline	A gradual change in allele frequencies across a portion of a species' geographic range
Genetic differentiation or divergence	Genetic differences between populations across the geographic range of a species
Indirect genetic effect	Genotype of one individual affects the phenotype and fitness of an associated conspecific individual
Interspecific indirect genetic effect	Environmental influences on the phenotype of one species are due to expression of genes in another species
Local adaptation	Higher fitness, within a given habitat, of individuals born in that habitat relative to individuals from other habitats

that genetic variation, resulting in evolution in one species which will further affect associated communities and ecosystems (Bailey *et al.* 2011).

The attempt to understand how evolution acts on genetic variation within a species to affect associated communities is not a new endeavour – for decades, both ecologists and evolutionary biologists have been interested in understanding how evolution in one species affects other species in the community (e.g. Pimentel 1961, 1968; Janzen 1980; Reznick & Endler 1982; Antonovics 1992; Thompson 1998; Grant & Grant 2002; Whitham *et al.* 2006). For example, Pimentel (1968) proposed that evolution in one species could regulate the population of another through a 'genetic feedback mechanism' through which the selective pressure on host plants increases with herbivore densities, causing changes in the genetic makeup of the host populations such that they become more resistant. This change, in turn, imposes selection on herbivores to overcome plant resistance. Moreover, it has been clearly shown that evolution can occur at ecologically relevant time-scales (Thompson 1998; Hendry & Kinnison 1999; Bohannan & Lenski 2000; Kinnison & Hendry 2001; Grant & Grant 2002; Yoshida *et al.* 2003; Hairston *et al.* 2005) and this observation is a unifying element to every approach linking ecology and evolution, including the geographic mosaic theory of *co-evolution* (Thompson 1999), *diffuse co-evolution* (Janzen 1980; Fox 1981; Herrera 1982; Strauss, Sahli & Connor 2005; Wade 2007), *community heritability* (Whitham *et al.* 2003, 2006; Shuster *et al.* 2006), and *eco-evo feedbacks* (Post & Palkovacs 2009). This has important implications because it suggests that major selective events such as climate change, increased habitat fragmentation, and species invasions can have extended ecological consequences by changing intraspecific genetic variation. While rapid evolution has already been incorporated into invasion biology through the 'evolution of increased competitive ability' hypothesis (see review by Boss-

dorf *et al.* 2005) and the 'hybridization increases invasiveness' hypothesis (see review by Ellstrand & Schierenbeck 2000) the demonstration that rapid evolution can alter species interactions and ecosystem properties has broad implications that are not commonly addressed in many other subfields of ecology including conservation biology, plant-pollinator interactions, and restoration ecology.

Although decades of research clearly shows that intraspecific genetic variation has community-level consequences, the extent to which evolutionary forces change genetic variation in one species and affect associated communities, and whether these changes feed back to affect the original species, is less clear. One conceptual model for understanding the extended effects of evolution acting on intraspecific genetic variation involves expanding Lewontin's (1974) representation of population genetic transformations occurring in genotype and phenotype space to include another level of 'community space' (Fig. 1). In this diagram, 'spaces' represent a set of possible values for genotypes, phenotypes, and communities, respectively, and arrows represent the 'transformations' between different spaces. For example, the transformation beginning in genotype space and ending in phenotype space represents the results of different genotypes developing in various environments (Lewontin 1974). In the expanded version the transformation beginning in phenotype space and ending in community space represents the community phenotype of genes being expressed by the species of interest. In this model, we assume that all community-level effects of genotype are mediated through the expressed phenotypes. In some systems, intraspecific genetic variation may have little or no effect on associated communities (Fig. 1a), suggesting that other ecological factors determine community composition. For example, Tack *et al.* (2010) reported that insect communities associated with *Quercus robur* were determined more by an environmental factor, spatial connectivity, than by
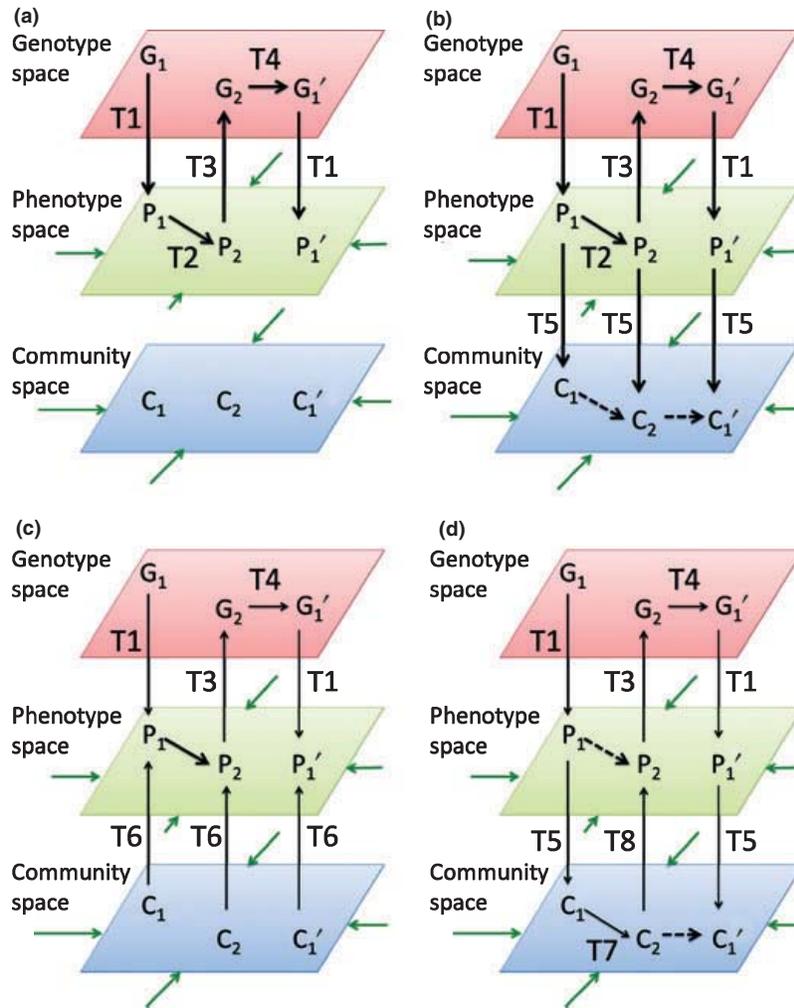
Fig. 1. Genetically based feedbacks through which one species alters its associated community, and community changes exert a reciprocal effect on the fitness of the original species, may occur when a series of conditions are met. In this diagram, 'spaces' represent a set of possible values for genotypes, phenotypes, and communities. Transformations are represented by arrows and refer to changes either within or between spaces; for example, a transformation beginning in phenotype space and ending in community space represents the community phenotype of genes in the species of interest. Dashed arrows represent transformations which are driven, at least primarily, by dynamics in another space. G_1 and G_1' represent the beginning of new generations, while G_2 or P_2 represents the second value for a genotype or phenotype within a generation. The transformations involving genotype and phenotype space are (modified from Lewontin 1974): [T1] laws that give the distribution of phenotypes that result from the development of various genotypes in various environments; [T2] laws of mating, migration, and natural selection which transform the distribution of phenotypes within one generation; [T3] relations which allow inference of a distribution of genotypes corresponding with a distribution of phenotypes; [T4] genetic rules which allow the prediction of genotypes in the next generation, given the array of parental genotypes. The transformations involving phenotype and community space describe: [T5] the community phenotypes associated with a species based on the distribution of phenotypes (i.e. community heritability); [T6] environmental factors driving differences in the phenotype of the plant independent of plant genetics; [T7] the differential fitness values of community members associated with a species which transform the distribution of communities within one generation; [T8] how changes in community composition feed back to affect the distribution of phenotypes in the species of interest. (a) represents a system in which plant genetic variation does not affect associated communities; (b) represents a system in which plant genetic variation affects associated communities but there are no feedbacks; (c) represents a system in which the herbivore community drives differences in a plant's phenotype; and (d) represents a system in which plant genetic variation affects herbivore communities and these changes feed back to affect the plant species. Arrows pointing inwards to the boundaries of phenotype and community space are placeholders for extrinsic effects of the biotic and abiotic environment on expression of phenotypes and community structure.

host-plant genotype. When intraspecific genetic variation does affect associated communities, then evolution can lead to changes in the associated community (Fig. 1b), represented by transformations between the phenotype and community spaces. Transformations can also begin in community space and end in phenotype space, if the community repre-

sents an environmental factor driving differences in an organism's phenotype independent of genetics (Fig. 1c). In some cases, evolution in a community context will feed back to affect the fitness and performance of the focal species (Fig. 1d). In this case, the transformation in phenotype space (dashed arrow) is primarily driven by the transformation in

Table 2. Experimental approaches which address how evolution in one species changes associated communities and how these changes can feed back to affect the original species. A small number of key studies and information which can be inferred strongly are included for each approach

	Description	Example studies	Genetic basis of communities and ecosystems	Evolutionary process	Co-evolutionary process	Eco-evo feedbacks	Eco-evo feedback dynamics
Local common garden studies	Collect individuals locally and plant in local garden(s) to minimize influence of environmental differences	Whitham et al. (2003, 2006), Johnson & Agrawal (2005)	Yes	Yes*	No	No	No
Genetic differentiation studies	Collect individuals from across the range of a species and plant them in one environment	Pennings, Siska & Bertness (2001); Barbour et al. (2009a,b)	Yes	Yes	No	No	No
Local adaptation studies	Collect and grow individuals and associated species in all home and away environments	Johnson et al. (2010)	Yes	Yes	Yes	Yes	No
Trans-generational feedback Studies	Examine systems in which genetic differentiation has occurred in multiple environments and infer the effects on trans-generational feedbacks	Palkovacs & Post (2008) ; Post & Palkovacs (2009) ; Pregitzer et al. (2010)	Yes	Yes	Yes	Yes	Yes

*Assumptions of evolution in common garden studies may be too strong, due to the effects of gene flow between genetic individuals being stronger than selection.

community space, which represents natural selection acting to change the composition of associated communities.

The perspective outlined in Fig. 1 is valuable because understanding how this range of *indirect genetic effects* and *feedbacks* varies spatially and temporally (e.g. Thompson 2005) in response to abiotic and biotic environmental variation represents an important frontier. Each of the possibilities listed above have been detected in different experimental designs, each with its own strengths and weaknesses, and each one providing different information about how evolution in one species may affect community and ecosystem properties in associated species (Table 2). For example, designs that provide valuable information about co-evolutionary processes and feedbacks are considerably more expensive and labour-intensive than a single-location common garden study, so investigators should consider the experimental scale at which their question can be best addressed.

Of all the above approaches, studies examining how feedbacks affect co-evolution and eco-evo interactions have received the least attention (but see Lankau & Strauss 2007; Palkovacs & Post 2008; Palkovacs *et al.* 2009; Post & Palkovacs 2009; Pregitzer *et al.* 2010); however, these studies are crucial to linking ecological and evolutionary processes. Although ecological feedbacks in natural systems are just beginning to be formally studied at the genetic level (e.g. Lankau & Strauss 2007; Pregitzer *et al.* 2010), studies of this nature have broad implications to many scientific disciplines, some of which currently do not incorporate genetic variation as a part of their research. Many types of feedbacks exist, but a common feature is that feedbacks occur when an organism modifies its abiotic (e.g. increased leaf area causes decreased ground temperature) or biotic (e.g. changes in prey community structure due to predation pressure) environment, and that modification in turn affects the fitness of the organism or other community members (Van der Putten, Vandijk & Peters 1993; Bever 1994; Jones, Lawton & Shachak 1997; Post & Palkovacs 2009). Feedbacks are fundamental to the co-evolutionary process (Thompson 2005) and local adaptation (Clausen, Keck & Hiesey 1940; Gandon & Nuismer 2009) because in each of these cases the interacting species can exert reciprocal fitness consequences. Additionally, feedbacks are an important part of the maintenance of biodiversity (Bascompte & Jordano 2007; Lankau & Strauss 2007; Duffy & Forde 2009; Laine 2009). For example, in a recent review, Laine (2009) reported that variation in the strength of feedbacks led to population-level divergence in the traits of interacting species. Finally, there has been virtually no consideration of the extended consequences of particular feedbacks in community or ecosystem ecology; for example, if a feedback alters the fitness and performance of one species, how does that alter interactions with other species and the ecosystem services they mediate? Although recent studies have begun to address the dynamic nature of ecological and evolutionary feedbacks (e.g. Lankau & Strauss 2007; Palkovacs & Post 2008; Pregitzer *et al.* 2010), a more complete understanding of these feedbacks remains a major challenge.

As the field of community and ecosystem genetics is currently focused on documenting the extended effects of genetic variation in a focal species, this review provides a broad conceptual framework for understanding how evolution may impact communities and ecosystems. We discuss five main elements relating to 'genes to ecosystems' research, including: (i) intraspecific genetic variation affects communities and ecosystems, although these effects can be dependent on abiotic and biotic environmental context; (ii) evolution in one species across its native range leads to genetic differentiation which affects associated communities; (iii) genetically differentiated populations of species can co-evolve interactions with other species which maximize the focal species' fitness in a given environment; (iv) genetically differentiated populations can affect the success of subsequent generations of their offspring and the offspring of other community members through trans-generational feedbacks; and lastly, (v) feedbacks may vary in space and time and may be a consequence of the community of interacting species or even the ecosystem processes that those communities mediate (Lankau & Strauss 2007; Bailey *et al.* 2009). This suggests that the relative fitness of any individual may vary depending upon characteristics of the specific 'group' (i.e. population, community, and ecosystem) to which it belongs and suggests that concepts associated with multi-level selection may be useful for understanding the potential impacts of selection on populations as a consequence of the particular 'groups' with which they are associated. In this last section, we use the Price equation to define mathematically how multi-level selection may act within the context of the community and ecosystem. In this review, we attempted to bring together these five components whose synthesis suggests that if the evolutionary dynamic in a system changes, then the ecological dynamic also likely changes (and vice versa) through indirect genetic effects and feedbacks, with consequences that can extend from the phenotype of an individual within a population to affect associated communities and ecosystem processes. Our examples largely focus upon plant-herbivore interactions, but the ideas and conceptual framework proposed are general and may apply to any system.

Genetic basis to communities and ecosystems

Linking genetic variation within species to patterns and processes that occur above the population level is critical to understanding how genetic changes in one species may affect the ecology of associated species (Bailey *et al.* in press). One approach to this problem involves quantifying the predictability of community and ecosystem responses with respect to genetic factors in a given species. A common experimental approach to this question has been to collect plants from a specific population and then to plant all collected specimens in a 'common garden' at one location. Within the common garden, trait differences across genotypes can be assessed in the absence of high environmental variation. Common garden studies have been instrumental in building our understanding of the extended effects of genotypic variation on

traits at the community (Whitham *et al.* 2003, 2006; Johnson & Agrawal 2005; Bailey *et al.* 2006; Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006; Tetard-Jones *et al.* 2007; see also Fig. 1a), and ecosystem (Whitham *et al.* 2003, 2006; Crutsinger *et al.* 2006; Madritch, Donaldson & Lindroth 2006; Schweitzer *et al.* 2008; Pregitzer *et al.* 2010) level. However, the effects of genetic variation on associated communities are often context dependent, varying across different environments [genetic (G) × environment (E) interactions, e.g. Johnson & Agrawal 2005; Bangert *et al.* 2008; Bossdorf, Shuja & Banta 2009] or due to the presence of genetic variation in other species in addition to non-genetic biotic and abiotic environmental effects (G × G × E interactions, e.g. Tetard-Jones *et al.* 2007). For example, Tetard-Jones *et al.* (2007) manipulated aphid and barley genotypes, and showed that the presence of rhizobacteria significantly altered the genotype by genotype interactions between aphids and barley. Genetic by environment interactions are important because the context dependency of genetic effects sets up the possibility of community-level responses to genetic differentiation and *local adaptation* if a species' range includes many different environments. These interactions also suggest that studies of *genetic clines* along elevational or latitudinal gradients could improve our knowledge of how strong the effects of genetic variation and differentiation are in the context of varying environmental conditions (Bailey *et al.* in press).

The higher-level ecological effects of genetic variation were first termed 'extended phenotypes' by Dawkins (1982) because they are caused by the expression of genes in an individual. Extended phenotypes have been further characterized as community and ecosystem phenotypes, respectively, which describe the tendency for genetically related individuals to support similar communities and affect ecosystem processes in similar ways (Whitham *et al.* 2003, 2006). A common garden experimental framework allows the estimation of variation in the community or ecosystem phenotype and the extent to which it is explained by variation in underlying genetic factors. The heritability of community phenotypes involves using traditional diversity indices (i.e. Simpson's or Shannon–Weiner) or an ordination technique to convert multivariate community data (associated with individuals of a focal species) into a univariate response which can be analyzed with standard statistical tools, allowing for the estimation of the broad sense heritability of community traits (see Johnson & Agrawal 2005; Shuster *et al.* 2006; Whitham *et al.* 2006 for details). For example, in *Populus* spp., the heritability of communities associated with particular genotypes has been estimated as 0·56–0·63 for arthropod communities and 0·70 for soil microbial communities or microbial pools of nutrients (Shuster *et al.* 2006; Schweitzer *et al.* 2008).

Many investigators argue that community and ecosystem phenotypes represent complex traits related to variation in the fitness consequences of indirect genetic effects (IGEs) among species (Thompson 2005; Shuster *et al.* 2006; Whitham *et al.* 2006; Tetard-Jones *et al.* 2007). In their most basic form, IGEs are environmental influences of genes in one individual on the phenotype and fitness of an associated

conspecific individual (Moore, Brodie & Wolf 1997; Agrawal, Brodie & Wade 2001). When IGEs occur between different species, they are referred to as *interspecific IGEs* (IIGEs, Shuster *et al.* 2006; Whitham *et al.* 2006). Based on theory outlined by Shuster *et al.* (2006), genetically based variation in community phenotypes provides evidence that: (i) fitness effects arise due to IIGEs, and (ii) through differential fitness consequences of IIGEs, selection can occur in a community context. While it has been suggested that a finding of significant community heritability provides evidence of evolution in a community context, in practice, the relationship between community heritability and co-evolution by natural selection is less clear.

For associated species to evolve in response to underlying plant genetic variation there are four important requirements. First, plant genotypes have to act as an agent of selection affecting the fitness and phenotype of the associated species (described in the preceding paragraphs). Second, the effects of plant genetic variation on arthropods must be mediated by genetic variation for arthropod traits (Lewontin 1970). Third, the variation in arthropod traits must also covary with arthropod fitness (Lewontin 1970). Fourth, some spatial isolation or other mechanism is required to prevent gene flow between populations that are evolving in response to different selective environments (i.e. associations with different host-plant genotypes). For example, Heschel & Paige (1995) showed that introducing pollen from a larger population of scarlet gilia (*Ipomopsis aggregata*) to a smaller population was enough to ease extinction risk caused by small population size, illustrating the well-known principle that even very low levels of gene flow can have relatively large effects on the genetic structure of populations (Wright 1931; Hartl & Clark 1997). Although divergent adaptation in the face of gene flow is possible, and often observed in phytophagous insects (see reviews by Dres & Mallet 2002; Coyne & Orr 2004; Bolnick & Fitzpatrick 2007), the conditions are restrictive (Lenormand 2002) and the strength of selection needed to overcome gene flow might be rare among genotypes of a single host plant population (but see Van Zandt & Mopper 1998). Immigration can affect the rate at which arthropod populations became locally adapted to host plant genotypes. For example, Tack & Roslin (2010) reported that arthropod abundance was higher on local genotypes of *Quercus robur*, compared to genotypes transplanted from different parts of the species' range, when immigration rates were low; however, the opposite pattern was observed (higher arthropod abundance on transplanted genotypes than local genotypes) when immigration rates were high. The effects of immigration on community heritability are important because most estimates of community heritability are from within a single common garden site where gene flow among the pool of possible herbivore populations is not limited. A better understanding of how genetic variation in one species affects associated community members requires that experiments are carried out at larger spatial scales (i.e. along environmental gradients or among races) such that realistic levels of gene flow can be compared with the effects of selection.

Community and ecosystem consequences of among population genetic differentiation

Identifying and understanding genetic differentiation along specific environmental gradients (Endler 1977; Storfer 1999; Foster *et al.* 2007) provides an important tool for addressing the hypothesis that evolution in one species can lead to change at the community and ecosystem level. One promising approach to examining how evolution in one species leads to change in associated communities and ecosystem processes involves investigating whether a species is genetically differentiated across its geographic range and then determining whether that genetic differentiation has affected associated communities and ecosystem processes. For example, in a 15-year-old plantation forest trial, Barbour *et al.* (2009a) found that (i) genetically based variation in *Eucalyptus globulus* expressed at the race and family level was correlated with differences in the associated arthropod community; (ii) community divergence among races was correlated with leaf physical and chemical traits; and (iii) community dissimilarity was correlated with neutral marker and quantitative genetic dissimilarity. Because variation among populations as well as between families was detected, this indicates that *E. globulus* had genetically differentiated across its range, and that this differentiation had led to changes in the associated community. This type of experiment is represented in Fig. 1b, in which the transformations in genotype and phenotype space represent the process of genetic differentiation, and the subsequent transformations in community space represent the unique community composition of each family of *E. globulus*. Using the same plantation forest, differences among races in litter arthropod communities (Barbour *et al.* 2009b) and soil nitrate (NO_3^-) availability (Bailey *et al.* 2011) were also detected, demonstrating broad community and ecosystem phenotypes of *E. globulus*. Genetic differentiation along latitudinal gradients can also affect plant palatability to herbivores (B. T. Moles, S. P. Bonser, I. R. Wallis & W. J. Foley, unpublished data). For example, Pennings, Siska & Bertness (2001) allowed herbivorous insects to choose between conspecific plants collected from northern and southern environments within the United States and reported that herbivores preferred the northern plants, a pattern which held across herbivore species. These studies indicate that genetic differentiation across broad geographic ranges can result in variation to foliar and litter arthropod communities and soil nitrogen availability (Bailey *et al.* in press). Based on theory established in Shuster *et al.* (2006), one may expect that community differences resulting from divergence in one species (e.g. *E. globulus*) suggest that all interacting species are differentiating in a co-evolutionary manner. However, the frequency and intensity of co-evolution will vary; co-evolution is most likely to be observed when the strength of feedbacks is large relative to gene flow. Because genetic variation interacts with differences in the regional species pool, strong inferences about the co-evolutionary dynamics are difficult to make without placing the differenti-

ated population (e.g. *E. globulus*) within all potential communities to test for feedbacks (see local adaptation below).

Another way that evolution can affect change in associated communities is reticulate evolution, which can occur in hybridizing species complexes. In *Populus* (*P. angustifolia* X *P. fremontii*), Bailey *et al.* (in press) showed that introgression at a single molecular marker had important effects on associated arthropod communities; for example, total arthropod richness increased by 23% and gall-forming arthropod abundance increased by 72% on trees carrying the *P. fremontii* allele at the molecular marker RFLP-755. Introgression also caused a 56% increase in ramet production and a 51% decrease in the production of salicortin, an anti-herbivore defensive compound (Palo 1984; Rehill *et al.* 2006; Bailey *et al.* 2007). A multiple regression model indicated ramet production, but not salicortin, predicted arthropod abundance, suggesting that the increase in arthropod abundance was due to increased vegetative branching (Price 1991). Reticulate evolution can also lead to the evolution of invasiveness by introduced species (see review by Ellstrand & Schierenbeck 2000), which is important because of the large effects these invaders can have on associated communities and ecosystems. For example, invasion by a hybrid cordgrass, *Spartina alterniflora × foliosa*, affected sediment properties and associated communities, increasing sediment organic matter and decreasing benthic macrofaunal density by 75% (Neira, Levin & Grosholz 2005). These results indicate that community phenotypes can be sensitive to even small genetic changes, suggesting that evolutionary changes in associated communities may occur more often, and through a simpler mechanism, than previously thought.

Genetic variation may be expressed and evolutionary processes may act in a variety of ways to affect patterns of community structure and ecosystem function. Moreover, there is emerging evidence from a variety of taxa, including vertebrates (e.g. Palkovacs & Post 2008), which clearly indicates that evolutionary dynamics can operate on ecological timescales (Thompson 1998; Hendry & Kinnison 1999; Bohannan & Lenski 2000; Kinnison & Hendry 2001; Grant & Grant 2002; Yoshida *et al.* 2003; Hairston *et al.* 2005). While genetic variation in one species can have community and ecosystem consequences, little is understood about whether there are feedbacks from the community or ecosystem on the fitness and performance of a focal population, and how these feedbacks may affect ecological and evolutionary dynamics.

Local adaptation, the co-evolutionary process, and feedbacks

Genetic differentiation that is a result of natural selection commonly results in strong patterns of local adaptation. Local adaptation occurs when individuals born in a given habitat have higher fitness within that habitat (i.e. 'home' environment), than individuals from other habitats (i.e. 'away' environments). Such local adaptation may be associ-

ated with factors such as differences in temperature or precipitation along elevational or latitudinal gradients. For example, Clausen, Keck & Hiesey (1940) showed that clones of sticky cinquefoil (*Potentilla glandulosa*) performed better when grown near their native elevation than at other elevations, suggesting that the populations were adapted to local abiotic environmental conditions.

Local adaptation can also occur in response to biotic environmental variation, and this type of local adaptation can result in the co-evolutionary process. Local adaptation associated with biotic environmental variation is largely associated with species interactions which vary across a species' range (Pennings, Siska & Bertness 2001; Thompson 2005; Johnson *et al.* 2010; Bailey *et al.* 2011). For example, Johnson *et al.* (2010) collected ecotypes of *Andropogon gerardii* from across its range and planted them in *all home and away* conditions with respect to both soils and arbuscular mycorrhizal (AM) fungi inoculates, and showed that ecotypes were adapted to local soil environments and AM fungi communities to maximize transfer of the most limiting nutrients between plants and fungi. Because this study manipulated ecotype identity in 'all possible home and away' environments from which individuals were collected, it confirms that subpopulations of *A. gerardii* had both genetically differentiated and co-evolved interactions with particular AM fungi strains in different environments across its range. However, the 'all possible home and away' approach can be financially and logistically intractable depending upon the number of families collected from each population, the number of populations sampled across the range of the species and the number of different abiotic and biotic environments that are tested (Barbour *et al.* 2009a).

When local adaptation and co-evolution are detected in genetically differentiated populations (e.g. Johnson *et al.* 2010), genetically based feedbacks can be inferred because certain populations display greater fitness and performance in their 'home' environment (biotic and abiotic) vs. an 'away' environment. When a population performs better in its home environment relative to away conditions it experiences a *positive feedback*. When a population performs better under away conditions, it experiences a *negative feedback*. Similar to the design of local adaptation studies, experiments to test for feedbacks would be conducted by establishing common gardens at every location from which a subpopulation was collected; however, in contrast to local adaptation studies, feedback studies examine the dynamic nature of organisms' modifying their environment and the fitness consequences of those modifications.

Feedbacks could be observed in a variety of species interactions, including those between plants and herbivores, plants and their soil communities, plants and neighbouring plants, animals and their prey, and many others. It is likely that species experience multiple positive and/or negative feedbacks from many different interactions simultaneously, and understanding how multiple feedbacks may interact is largely uninvestigated. For example, a plant may experience a positive feedback in genotype monocultures because it is able to

cultivate a specific microbial community below-ground (Johnson *et al.* 2010); conversely, a plant may experience a negative feedback in a genotype mixture due to temporal and spatial partitioning of resource acquisition (Crutsinger *et al.* 2006). Theoretically, feedbacks with fitness consequences are implicit in the measurement of the heritability of community composition because different communities are assumed to have different fitness consequences for any given species. However, quantification of such feedbacks requires the experimental manipulation of the associated community and the subsequent measurement of the original species' fitness and performance. Furthermore, even if plant fitness and performance change with the removal of the associated community, understanding the strength of the feedback through time is an additional challenge.

Trans-generational feedbacks and the eco-evo dynamic

Feedbacks involving reciprocal interactions of ecology and evolution over relatively short time-scales have been termed eco-evo feedbacks, which are defined as occurring when a population alters its environment (abiotic or biotic) and those environmental changes influence the fitness of the original population (Post & Palkovacs 2009) or subsequent generations (i.e. trans-generational feedback, Pregitzer *et al.* 2010). While community and ecosystem phenotypes clearly indicate the potential of feedbacks to occur between associated species, simply detecting a community or ecosystem phenotype does not specifically examine such interactions or speak to the dynamic nature of eco-evo feedbacks. Intraspecific genetic variation provides a means for testing how eco-evo feedbacks affect species and their environments through time, although it is not technically a prerequisite condition for eco-evo feedbacks to occur (Post & Palkovacs 2009). Examples of systems with a high potential for eco-evo feedbacks include those in which intraspecific genetic variation is high (Yoshida *et al.* 2003) or species interactions are continuous throughout the year, rather than intermittent (Palkovacs & Post 2008). One example of eco-evo feedbacks comes from Lankau & Strauss (2007), who showed that genetic variation for sinigrin content in *Brassica nigra* is responsible for a feedback which maintains diversity in plant communities, due to an intransitive (i.e. rock-paper-scissors) competitive relationship in which high-sinigrin *B. nigra* individuals can invade patches of heterospecific neighbours, low-sinigrin *B. nigra* individuals can invade patches of high sinigrin *B. nigra*, and heterospecific neighbours can invade patches of low-sinigrin *B. nigra*. This result indicates that genetic variation for sinigrin content is responsible for feedbacks which maintain genetic diversity in *B. nigra*, and species diversity in neighbouring plants. This type of experiment is represented in Fig. 1d, in which genetic variation in *B. nigra* for sinigrin content drives changes in the associated plant community, which in turn affects which genotypes of *B. nigra* will perform well in the next generation. While we recognize that *B. nigra* may reduce the species diversity by

outcompeting its neighbours in some cases, we discuss this study to illustrate the potential for genetic differentiation to cause community changes which feedback to affect traits in the original species.

Another mechanism through which transgenerational feedbacks can operate involves offspring performing better in their parent's soil than in an 'away' soil environment. For example, Pregitzer *et al.* (2010) showed that *P. angustifolia* seedlings performed better when grown in soil conditioned by their parent trees compared with soil conditioned by other *Populus* species, even though the 'home' soils were the most N-limited (i.e. highest C : N ratio and highest microbial N pools, Fig. 2). Because parent species affect soil microbial
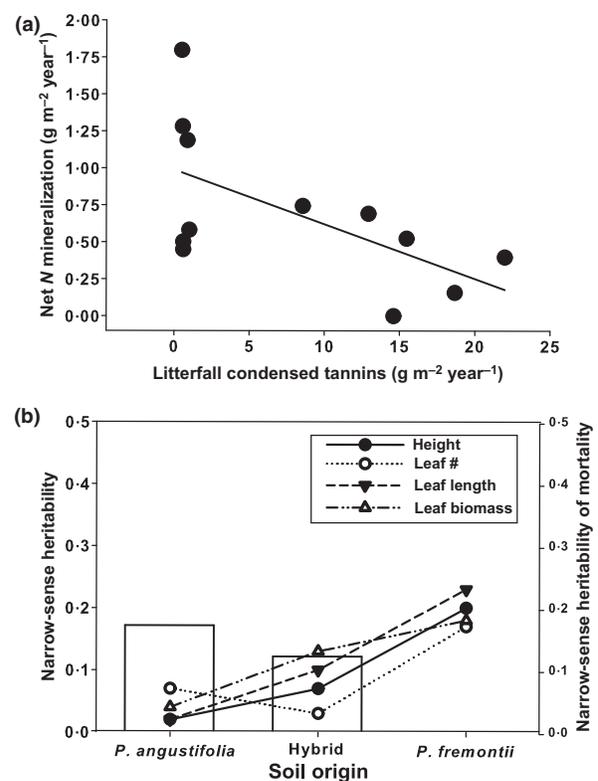

Fig. 2. Genetic variation in *Populus* can affect soils, and these changes can feed back to affect fitness and performance of the next generation of *Populus* trees. In field and laboratory incubations, condensed tannin in litterfall was best related to soil net N mineralization. Condensed tannin in litterfall explained 65% of the variation in annual rates of net N mineralization in soils from 12 stands of gallery cottonwood forests (a, Schweitzer *et al.* 2004). Trees with low condensed tannins were from the *P. fremontii* zone, trees with high tannins were from the *P. angustifolia* zone, with hybrids intermediate, on average. Soils were collected from all three zones, and *P. angustifolia* seedlings were planted in each soil type. *P. angustifolia* survived best in its own soil type, even though these soils were the most nutrient limited; additionally, *P. angustifolia* also experienced the most mortality in soils collected from beneath *P. fremontii*, even though these soils were the least nutrient limited (b, Pregitzer *et al.* 2010). Bars represent the narrow-sense heritability of seedling mortality. Symbols represent the narrow-sense heritability of performance traits. Originally published in Schweitzer *et al.* (2004), *Ecology Letters* (a) and Pregitzer *et al.* (2010), *Evolutionary Ecology* (b).

communities and nutrient cycling (Schweitzer *et al.* 2004, 2008; Whitham *et al.* 2006), these results indicate that soils, which are a common abiotic and biotic environment for both parents and their offspring, can act as agents of selection (Pregitzer *et al.* 2010). In the same sense that we must determine the relative importance of intraspecific genetic variation, future studies should investigate the importance of feedbacks as agents of selection, relative to 'traditional' (i.e. unidirectional) ecological and evolutionary factors. Because genetic variation in one species can have community and ecosystem phenotypes that affect genetic variation in subsequent generations, it becomes difficult to determine at which level of organization (e.g. population, community, or ecosystem) the relative fitness of an individual depends.

Multi-level selection…whose phenotype is it and how is selection acting?

While no experimental approach for multi-level selection is widely accepted, multi-level selection provides an important theoretical framework for understanding how higher level selection may influence individual level evolutionary processes. Multi-level selection is generally defined as variation in an individual's relative fitness that can be partitioned into within-group and between-group components, with 'level' defined by the question to be addressed (Keller 1999; Collins & Gardner 2009). Partitioning variation in fitness is an important approach if we are to model the change in the average value of a specific character across all individuals, in all species, in all communities in an ecosystem (i.e. a phenotype that is common to all organisms in an ecosystem such as biomass, plant and soil nutrient content (i.e. carbon, nitrogen, phosphorous), body size, or offspring). We recognize that ecosystems are more than a set of communities, and that some ecosystem properties would go unmeasured even if every parameter at the community level was assessed. Our approach is only one method of using the flexible Price equation to partition across levels of organization. This approach provides an all-encompassing view of natural selection by recognizing that organisms are embedded not only in a complex abiotic environment, but also a matrix of interacting species in which the phenotype of one organism is the environment of another (i.e. the relative fitness of an individual depends on the group to which it belongs). One common theoretical framework for understanding multi-level selection is the Price equation (Price 1972; Frank 1998; Gardner 2008; Collins & Gardner 2009). The Price equation mathematically describes change via natural selection in a completely general way and has recently been applied successfully in the field of community ecology (Loreau & Hector 2001; Fox 2006; Collins & Gardner 2009) and its use for understanding how evolutionary processes may alter communities and ecosystem function may be fundamental.

Consider an ecosystem formed by a set of communities C, in which each community is assigned a unique index $i \in C$. Each community contains a set of species S_i and we assign each species a unique index $j \in S_i$. Each species contains a set

of different individual phenotypes P_{ij}, to which we assign each phenotype a unique index $k \in P_{ij}$. Notice that for our purposes communities are mutually exclusive groups of species and phenotypes within an ecosystem, and species are mutually exclusive groups of individuals within a community. Communities can be defined in different ways depending on the character considered and the interest of the researcher as long as they retain their hierarchical and mutually exclusive nature.

Let w_{ijk} be the fitness of an individual with phenotype k in species j in community i. The average (arithmetic mean) fitness of all individuals in species j in community i is $w_{ij} = E_{P_{ij}}[w_{ijk}]$ (where E_A denotes the statistical expectation taken over the set A). Set A is a generic set which can refer to phenotypes (P), communities (C), or ecosystems (E). The average fitness of all species in community i is $w_i = E_{S_i}[w_{ij}]$. The average fitness of all phenotypes in the ecosystem is $\bar{w} = E_C\big[E_{S_i}\big[E_{P_{ij}}[w_{ijk}]\big]\big]$.

Let z_{ijk} be the value of the character of interest corresponding to phenotype k in species j in community i. The average value of character z in species j in community i is $z_{ij} = E_{P_{ij}}[z_{ijk}]$. The average value of character z in community i is $z_i = E_{S_i}[z_{ij}]$. The average value of character z in the ecosystem is $z = E_C[z_i] = E_C\big[E_{S_i}\big[E_{P_{ij}}[z_{ijk}]\big]\big] = \bar{z}$.

Consider the value of the character of interest z and z' in times t_1 and t_2 respectively. Let $\Delta z = z' - z$ be the change of the character value from one generation to the next. A species changes when the frequency of the different phenotypes within the species changes over time. A community changes when its constituent species change and/or when the frequency of species changes over time. Finally, an ecosystem changes when the frequency of communities changes over time.

We applied the Price equation (Price 1972; Frank 1998; Gardner 2008) to model the change in the average value of a specific character across a whole ecosystem. In particular, the total effect of selection can be partitioned into among-community, among-species within communities, and among-phenotypes within species of a community (Frank 1998; Gardner 2008):

$$\Delta \bar{z} = E_C\left[E_{S_i}\left[C_{P_{ij}}\left[\frac{w_{ijk}}{\bar{w}}, z_{ijk}\right]\right]\right]$$
$$+ E_C\left[C_{S_i}\left[\frac{w_{ij}}{\bar{w}}, z_{ij}\right]\right] + C_C\left[\frac{w_i}{\bar{w}}, z_i\right]$$

where C_A denotes the statistical covariance taken over the set A. Here, we assumed that there is no environmental induction or bias in the transmission of a particular phenotype between generations (i.e. $E_{P_{ij}}[w_{ijk}\Delta z_{ijk}] = 0$) but an additional partition could be added to account for such changes (Collins & Gardner 2009).

This equation shows that the change, owing to selection, in the average value of a character across the whole ecosystem during the time considered is given by the sum of three terms. The first term is the covariance between a phenotypic character value (z_{ijk}) and its fitness relative to the average fitness of all phenotypes in the ecosystem considered ($\frac{w_{ijk}}{\bar{w}}$) averaged over all species and all communities in the ecosystem. This term

captures whether phenotypes with higher character value increase or decrease within their species and community and describes the average change in phenotypic composition within species. It represents the change in the total or average phenotype of the ecosystem that can be explained by variation in fitness within species.

The second term is the covariance between the average character in each species (z_{ij}) and the average fitness of that species relative to the overall average fitness in the ecosystem ($\frac{w_{ij}}{\bar{w}}$) averaged over all communities in the ecosystem. This term captures whether species with higher character value increase or decrease within their community and describes the change in species composition of a community. The third term is the covariance between the average character in each community (z_i) and the fitness of that community relative to the average fitness in the ecosystem ($\frac{w_i}{\bar{w}}$). This term captures whether communities with higher character value increase or decrease within the ecosystem and describes the change in community composition of an ecosystem. Note that covariance between a trait and fitness need not imply that the trait is responsible for variation in fitness (Lande & Arnold 1983). Particularly for more inclusive partitions (i.e. species), strong covariances among traits make correlated responses to selection highly likely. For example, average biomass might change owing to differential extinction of prokaryotes and eukaryotes driven by a chemical with physiological effects functionally unrelated to size. Because phenotypic covariances are often different at different levels, partitioning the Price equation can help expose effects of correlated selection (Collins & Gardner 2009).

Note also that the average within-species selection might often be very near zero if different species are changing in opposite directions. Thus, the degree of inclusiveness, detail, and manner of partitioning must all be chosen carefully to most effectively address any specific question. The Price equation is a 'statistical tautology' that follows from the definitions of the phenotype, fitness, and grouping variables (Gardner 2008; Collins & Gardner 2009). As such, it is both general and exact, but does not specify mechanisms or functional forms of selection. The levels-of-selection partition of the Price equation shows how the contribution of natural selection to changes at the phenotype, species, and community levels can be distinguished and combined additively to explain the total change of a character value over time. The equation provides a foundation for creating a theoretical framework whereby changes in the phenotypic composition of a population (evolutionary processes) can affect the species and community composition of the ecosystem (ecological processes) and *vice versa* through ecological and evolutionary dynamic feedbacks. Specifically, this partition allows us to assess eco-evo feedbacks because it separates the contributions of ecological and evolutionary components to the total change. This allows us to determine how a particular set of evolutionary conditions affects the ecological properties of a community or ecosystem, and vice versa. Such processes may favour one species or community over another (sensu Swenson, Wilson & Elias 2000) resulting in changing patterns on the landscape. The total change in a system will be affected most by whichever covariance is greatest.

Conclusions

In this review, we have synthesized evidence from different sub-fields of research to provide a broad conceptual framework in which to consider how evolution may impact communities and ecosystems. We focused on five main issues: (i) Within local populations, intraspecific genetic variation affects community and ecosystem properties, although these effects can be dependent on abiotic and biotic environmental context; (ii) across a species' range, genetically differentiated populations have different effects on associated communities, showing that evolution in one species can drive community change; (iii) genetically differentiated populations can also co-evolve interactions with other species, resulting in feedbacks and strong patterns of local adaptation; (iv) the effects of feedbacks can alter the environment in a way which affects future generations; and (v) multi-level selection, which provides a framework for considering how the fitness of an individual depends on the group (i.e. population, community, or ecosystem) of which it is a part.

The evidence linking genetic variation and evolution to community change and feedbacks comes from several different approaches whose results have not been synthesized into one conceptual framework, and whose commonalities may not be fully understood. Together, this synthesis suggests that the evolutionary and ecological dynamics of systems are connected through species interactions, specifically indirect genetic effects and feedbacks, and the consequences of this ecological-evolutionary linkage begin with the phenotype of an individual within a population and extend to the associated community and ecosystem. Potential research questions for future studies in this field include: (i) how does the strength of indirect genetic effects and feedbacks change over time; (ii) if a feedback alters the fitness and performance of one species, how does that alter interactions with other species and the ecosystem functions they mediate; and (iii) what are the consequences of multiple feedbacks (i.e. feedbacks from insect herbivores, neighbouring plants, and soil microbial communities) acting on a population simultaneously? Understanding the linkages between evolutionary processes and ecological outcomes is particularly important given the continuing global loss of genetic variation (Butchart *et al.* 2010), as well as the potential for community and ecosystem-level consequences when large selective events change the range of genetic variation present in a species.

Acknowledgements

References

Agrawal, A.F., Brodie, E.D. & Wade, M.J. (2001) On indirect genetic effects in structured populations. *American Naturalist*, **158**, 308–323.

Antonovics, J. (1992) Toward community genetics (eds R.S. Fritz & E.L. Simms). *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago, IL, USA.

Bailey, J.K., Wooley, S.C., Lindroth, R.L. & Whitham, T.G. (2006) Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecology Letters*, **9**, 78–85.

Bailey, J.K., Schweitzer, J.A., Rehill, B.J., Irschick, D.J., Whitham, T.G. & Lindroth, R.L. (2007) Selective herbivory by elk results in rapid shifts in the chemical composition of aspen forests. *Biological Invasions*, **9**, 715–722.

Bailey, J.K., Schweitzer, J.A., Úbeda, F., Koricheva, J., LeRoy, C.J., Madritch, M.D., Rehill, B.J., Bangert, R.K., Fischer, D.G., Allan, G.J. & Whitham, T.G. (2009) From genes to ecosystems: a synthesis of the effect of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **364**, 1607–1616.

Bailey, J.K., Schweitzer, J.A., Úbeda, F., Zinkgraf, M., Fitzpatrick, B.M., O'Reilly-Wapstra, J., Rehill, B.J., LeRoy, C.J., Potts, B.M., Whitham, T.G., Genung, M.A., Fischer, D.G., Pregitzer, C.C. & Keith, A. (2011) From genes to ecosystems: emerging concepts bridging ecological and evolutionary dynamics. *The ecology of plant secondary metabolites*: *from genes to landscapes* (eds G.R. Iason, M. Dicke & S.E. Hartley). Cambridge University Press, Cambridge, UK.

Bangert, R.K., Lonsdorf, E.V., Wimp, G.M., Shuster, S.M., Fischer, D., Schweitzer, J.A., Allan, G.J., Bailey, J.K. & Whitham, T.G. (2008) Genetic structure of a foundation species: scaling community phenotypes from the individual to the region. *Heredity*, **100**, 121–131.

Barbour, R.C., O'Reilly-Wapstra, J.M., De Little, D.W., Jordan, G.J., Steane, D.A., Humphreys, J.R., Bailey, J.K., Whitham, T.G. & Potts, B.M. (2009a) A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology*, **90**, 1762–1772.

Barbour, R.C., Forster, L.G., Baker, S.C., Steane, D.A. & Potts, B.M. (2009b) Biodiversity consequences of genetic variation in bark characteristics within a foundation tree species. *Conservation Biology*, **23**, 1146–1155.

Bascompte, J. & Jordano, P. (2007) Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology and Systematics*, **38**, 567–593.

Bever, J.D. (1994) Feedback between plants and their soil communities in an old-field community. *Ecology*, **75**, 1965–1977.

Bohannan, B.J.M. & Lenski, R.E. (2000) Linking genetic change to community evolution: insights from studies of bacteria and bacteriophage. *Ecology Letters*, **3**, 362–377.

Bolnick, D.I. & Fitzpatrick, B.M. (2007) Sympatric speciation: models and empirical evidence. *Annual Review of Ecology, Evolution and Systematics*, **38**, 459–487.

Bossdorf, O., Shuja, Z. & Banta, J.A. (2009) Genotype and maternal environment affect belowground interactions between Arabidopsis thaliana and its competitors. *Oikos*, **118**, 1541–1551.

Bossdorf, O., Auge, H., Lafuma, L., Rogers, W.E., Siemann, E. & Prati, D. (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrell, T.D., Vie, J.C. & Watson, R. (2010) Global biodiversity: indicators of recent declines. *Science*, **328**, 1164–1168.

Clausen, J., Keck, D.D. & Hiesey, W.M. (1940) *Experimental Studies on the Nature of Species. 1. Effects of Varied Environments on Western North American Plants*. Carnegie Institute of Washington, Washington DC, USA.

Collins, S. & Gardner, A. (2009) Integrating physiological, ecological and evolutionary change: a Price equation approach. *Ecology Letters*, **12**, 744–757.

Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates, Sunderland, MA, USA.

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006) Genotypic diversity predicts community structure and governs an ecosystem process. *Science*, **313**, 966–968.

Dawkins, R. (1982) *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford University Press, New York, USA.

Dres, M. & Mallet, J. (2002) Host races in plant-feeding insects and their importance in sympatric speciation. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **357**, 471–492.

Duffy, M.A. & Forde, S.E. (2009) Ecological feedbacks and the evolution of resistance. *Journal of Animal Ecology*, **78**, 1106–1112.

Ellstrand, N.C. & Schierenbeck, K.A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Science of the United States of America*, **97**, 7043–7050.

Endler, J.A. (1977) *Geographic Variation, Speciation and Clines*. Princeton University Press, Princeton, NJ, USA.

Foster, S.A., McKinnon, G.E., Steane, D.A., Potts, B.M. & Vaillancourt, R.E. (2007) Parallel evolution of dwarf ecotypes in the forest tree *Eucalyptus globulus*. *New Phytologist*, **175**, 370–380.

Fox, L.R. (1981) Defense and dynamics in plant-herbivore systems. *American Zoologist*, **21**, 853–864.

Fox, J.W. (2006) Using Price equation to partition the effects of biodiversity loss on ecosystem function. *Ecology*, **87**, 2687–2696.

Frank, S.A. (1998) *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ, USA.

Gandon, S. & Nuismer, S.L. (2009) Interactions between genetic drift, gene flow, and selection mosaics drive parasite local adaptation. *American Naturalist*, **173**, 212–224.

Gardner, A. (2008) The Price equation. *Current Biology*, **18**, R198–R202.

Grant, P.R. & Grant, B.R. (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, **296**, 707–711.

Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, **8**, 1114–1127.

Hartl, D.L. & Clark, A.G. (1997) *Principles of Population Genetics*, 3rd edn. Sinauer Associates, Sunderland, MA, USA.

Hendry, A.P. & Kinnison, M.T. (1999) Perspective: The pace of modern life: measuring rates of contemporary microevolution. *Evolution*, **53**, 1637–1653.

Herrera, C.M. (1982) Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology*, **63**, 773–785.

Heschel, M.S. & Paige, K.N. (1995) Inbreeding depression, environmental stress, and population size variation in scarlet gilia (*Ipomopsis aggregata*). *Conservation Biology*, **9**, 126–133.

Janzen, D.H. (1980) When is it coevolution? *Evolution*, **34**, 611–612.

Johnson, M.T.J. & Agrawal, A.A. (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology*, **86**, 874–885.

Johnson, M.T.J., Lajeunesse, M.J. & Agrawal, A.A. (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters*, **9**, 24–34.

Johnson, M.T.J. & Stinchcombe, J.R. (2007) An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology & Evolution*, **22**, 250–257.

Johnson, M.T.J., Vellend, M. & Stinchcombe, J.R. (2009) Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **364**, 1593–1605.

Johnson, N.C., Wilson, G.W.T., Bowker, M.A., Wilson, J.A. & Miller, R.M. (2010) Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 2093–2098.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as ecosystem engineers. *Ecology*, **78**, 1946–1957.

Keller, L. (1999) *Levels of Selection in Evolution*. Princeton University Press, Princeton, NJ, USA.

Kinnison, M.T. & Hendry, A.P. (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica*, **112**, 145–164.

Laine, A.L. (2009) Role of coevolution in generating biological diversity: spatially divergent selection trajectories. *Journal of Experimental Botany*, **60**, 2957–2970.

Lande, R. & Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.

Lankau, R.A. & Strauss, S.Y. (2007) Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science*, **317**, 1561–1563.

Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends in Ecology and Evolution*, **17**, 183–189.

Lewontin, R.C. (1970) The units of selection. *Annual Review of Ecology and Systematics*, **1**, 1–18.

Lewontin, R.C. (1974) *The Genetic Basis to Evolutionary Change*. Columbia University Press, New York, NY, USA.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.

Madritch, M., Donaldson, J.R. & Lindroth, R.L. (2006) Genetic identity of *Populus tremuloides* litter influences decomposition and nutrient release in a mixed forest stand. *Ecosystems*, **9**, 528–537.

Moore, A.J., Brodie, E.D. & Wolf, J.B. (1997) Interacting phenotypes and the evolutionary process. 1. Direct and indirect genetic effects of social interactions. *Evolution*, **51**, 1352–1362.

Neira, C., Levin, L.A. & Grosholz, E.D. (2005) Benthic macrofaunal communities of three sites in San Francisco Bay invaded by hybrid Spartina, with comparison to uninvaded habitats. *Marine Ecology-Progress Series*, **292**, 111–126.

Palkovacs, E.P. & Post, D.M. (2008) Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feed back to shape predator foraging traits? *Evolutionary Ecology Research*, **10**, 699–720.

Palkovacs, E.P., Marshall, M.C., Lamphere, B.A., Lynch, B.R., Weese, D.J., Fraser, D.F., Reznick, D.N., Pringle, C.M. & Kinnison, M.T. (2009) Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **364**, 1617–1628.

Palo, R.T. (1984) Distribution of birch (Betula spp), willow (*Salix* spp), and poplar (*Populus* spp) secondary metabolites and their potential role as chemical defense against herbivores. *Journal of Chemical Ecology*, **10**, 499–520.

Pennings, S.C., Siska, E.L. & Bertness, M.D. (2001) Latitudinal differences in plant palatability in Atlantic coast salt marshes. *Ecology*, **82**, 1344–1359.

Pimentel, D. (1961) Animal population regulation by genetic feedback mechanism. *American Naturalist*, **95**, 65–79.

Pimentel, D. (1968) Population regulation and genetic feedback. *Science*, **159**, 1432–1437.

Post, D.M. & Palkovacs, E.P. (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **364**, 1629–1640.

Pregitzer, C.C., Bailey, J.K., Hart, S.C. & Schweitzer, J.A. (2010) Soils as agents of selection: feedbacks between plants and soils alter seedling survival and performance. *Evolutionary Ecology*, **24**, 1024–1059.

Price, G.R. (1972) Fisher's "fundamental theorem" made clear. *Annals of Human Genetics*, **36**, 129–140.

Price, P.W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos*, **62**, 244–251.

Rehill, B.J., Whitham, T.G., Martinsen, G.D., Schweitzer, J.A., Bailey, J.K. & Lindroth, R.L. (2006) Developmental trajectories in cottonwood phytochemisty. *Journal of Chemical Ecology*, **32**, 2269–2285.

Reznick, D. & Endler, J.A. (1982) The impact of predation on life-history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, **36**, 160–177.

Schweitzer, J.A., Bailey, J.K., Rehill, B.J., Martinsen, G.D., Hart, S.C., Lindroth, R.L., Keim, P. & Whitham, T.G. (2004) Genetically based trait in a dominant tree affects ecosystem processes. *Ecology Letters*, **7**, 127–134.

Schweitzer, J.A., Bailey, J.K., Fischer, D.G., Leroy, C.J., Lonsdorf, E.V., Whitham, T.G. & Hart, S.C. (2008) Plant-soil-microorganism interactions: heritable relationship between plant genotype and associated soil microorganisms. *Ecology*, **89**, 773–781.

Shuster, S.M., Lonsdorf, E.V., Wimp, G.M., Bailey, J.K. & Whitham, T.G. (2006) Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution*, **60**, 991–1003.

Storfer, A. (1999) Gene flow and local adaptation in a sunfish-salamander system. *Behavioral Ecology and Sociobiology*, **46**, 273–279.

Strauss, S.Y., Sahli, H. & Connor, J.K. (2005) Toward a more trait-centered approach to diffuse (co)evolution. *New Phytologist*, **165**, 81–89.

Swenson, W., Wilson, D.S. & Elias, R. (2000) Artificial ecosystem selection. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 9110–9114.

Tack, A.J.M. & Roslin, T. (2010) Overrun by the neighbors: landscape context affects strength and sign of local adaptation. *Ecology*, **91**, 2253–2260.

Tack, A.J.M., Ovaskainen, O., Pulkkinen, P. & Roslin, T. (2010) Spatial location dominates over host plant genotype in structuring an herbivore community. *Ecology*, **91**, 2660–2672.

Tetard-Jones, C., Kertesz, M.A., Gallois, P. & Preziosi, R.F. (2007) Genotype-by-genotype interactions modified by a third species in a plant-insect system. *American Naturalist*, **170**, 492–499.

Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology & Evolution*, **13**, 329–332.

Thompson, J.N. (1999) Specific hypotheses on the geographic mosaic of coevolution. *American Naturalist*, **153**, S1–S14.

Thompson, J.N. (2005) Coevolution: the geographic mosaic of coevolutionary arms races. *Current Biology*, **15**, R992–R994.

Van der Putten, W.H., Vandijk, C. & Peters, B.A.M. (1993) Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, **362**, 53–56.

Van Zandt, P.A. & Mopper, S. (1998) A meta analysis of adaptive deme formation in phytophagous insect populations. *American Naturalist*, **152**, 595–604.

Wade, M.J. (2007) The co-evolutionary genetics of ecological communities. *Nature Reviews Genetics*, **8**, 185–195.

Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M., Wimp, G.M., Fischer, D.G., Bailey, J.K., Lindroth, R.L., Woolbright, S. & Kuske, C.R. (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, **84**, 559–573.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., Lonsdorf, E.V., Allan, G.J., DiFazio, S.P., Potts, B.M., Fischer, D.G., Gehring, C.A., Lindroth, R.L., Marks, J.C., Hart, S.C., Wimp, G.M. & Wooley, S.C. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**, 510–523.

Wright, S. (1931) Evolution in Mendelian populations. *Genetics*, **16**, 97–159.

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G. (2003) Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, **424**, 303–306.