

## CLIMATE CHANGE AND SPECIES RANGE SHIFTS

**Indirect genetic effects: an evolutionary mechanism linking feedbacks, genotypic diversity and coadaptation in a climate change context****Joseph K. Bailey\***, Mark A. Genung, Ian Ware, Courtney Gorman, Michael E. Van Nuland, Hannah Long and Jennifer A. Schweitzer*Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996-0001, USA***Summary**

1. Predicting the response of communities and ecosystems to range shifts as a consequence of global climate change is a critical challenge confronting modern evolutionary ecologists.
2. Indirect genetic effects (IGEs) occur when the expression of genes in a conspecific neighbouring species affects the phenotype of a focal species, and the same concept applies for interspecific indirect genetic effects (IIGEs) except that the neighbouring species is then required to be heterospecific.
3. Theory and empirical data indicate that indirect genetic effects and interspecific indirect genetic effects have fundamental roles in understanding the consequences of genotypic diversity, evolutionary feedbacks, the co-evolutionary process and coadaptation and are a primary mechanism for the broad ecological and evolutionary dynamics that are likely to be a consequence of climate change.
4. When indirect genetic effects and interspecific indirect genetic effects occur along environmental gradients, both positive and negative feedbacks can evolve, resulting in regions of strong local adaptation and competition as well as regions of complementarity and facilitation. Such evolutionary dynamics have direct consequences for how individuals interact and evolve in mixture and drive the services ecosystems provide.
5. Integrating indirect genetic effects and interspecific indirect genetic effects, feedbacks and diversity effects along environmental gradients represents a major conceptual, theoretical and empirical frontier that must be considered to understand the whole-system consequences of climate change on biodiversity and the services ecosystems provide.

**Key-words:** coadaptation, community genetics, eco–evo dynamics, elevation gradients, extended phenotype, feedbacks, genotypic diversity, indirect genetic effects

*Uva uvam vivendo varia fit – ‘It’s a motto. It just says itself’*  
Gus McCrae

**Introduction**

Predicting the evolutionary response of communities and the ecosystem services they provide to range shifts as a consequence of global climate change is among the most challenging and pressing problems confronting modern evolutionary ecologists (Gilman *et al.* 2010; Lavergne *et al.* 2010). The study of *genetic divergence* along environ-

mental gradients is fundamental to understanding adaptive evolution and diversification (Endler 1977; Storfer 1999), and contemporary evolution (Pelletier, Garant & Hendry 2009) particularly as it relates to range shifts that are driven by climate change. While much adaptive evolution research has focused on speciation, there is little understanding of how evolutionary dynamics may impact contemporary ecological interactions or ecosystem processes (Thompson 2005; Whitham *et al.* 2006; Harmon *et al.* 2009; Pelletier, Garant & Hendry 2009). Connecting historical evolutionary dynamics (e.g. genetic divergence) and contemporary ecological interactions is critical if we are to

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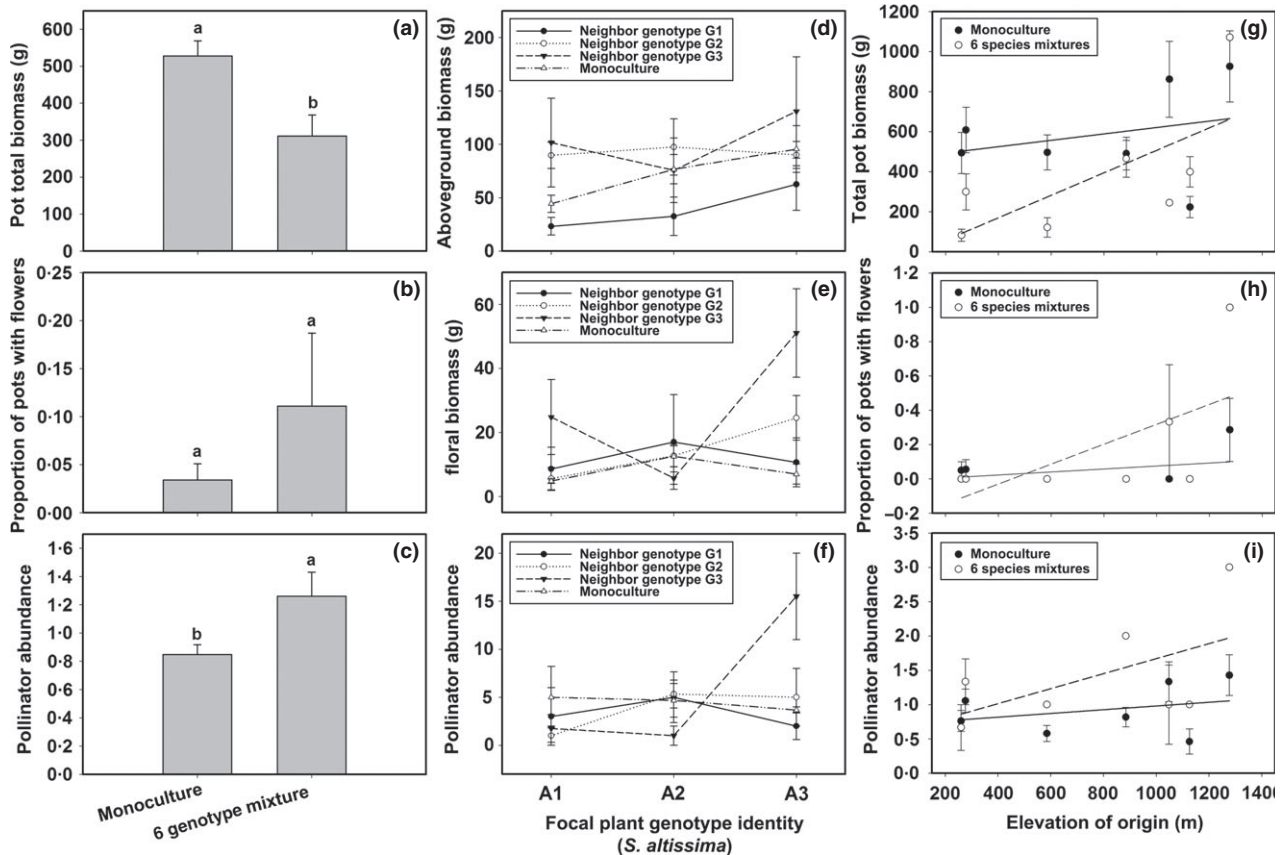
build synthesis and develop a basic understanding of how evolutionary drivers of *functional traits* affect biodiversity and ecosystem function.

Recent research linking ecological interactions and evolutionary dynamics clearly shows that among-population genetic divergence can drive change in functional traits and associated biodiversity and ecosystem function (Harmon *et al.* 2009; Bailey *et al.* 2012). For example, using a nested approach, which accurately partitioned genetic variation into family and population-level components, Barbour *et al.* (2009) found that genetic differentiation among *Eucalyptus globulus* trees collected from different provenances in southeastern Australia and grown in a common garden environment, supported different canopy communities of arthropods. Similarly, using ion-exchange resins to estimate differences in soil inorganic nitrogen from soils beneath individual trees (due either to differential nutrient turnover or differential nutrient uptake; Binkley & Hart 1989), provenance-level variation in soil nitrate  $\text{NO}_3^-$  was also found (Bailey *et al.* 2012). Community- and ecosystem-level effects similar to these have been shown in other plant (Johnson, Lajeunesse & Agrawal 2006) and animal groups (Post *et al.* 2008; Harmon *et al.* 2009; Palkovacs *et al.* 2009; Post & Palkovacs 2009; Bassar *et al.* 2010), suggesting that links between genetic divergence and community- and ecosystem-level dynamics are likely to be common. Results, such as these, indicate that (i) evolutionary processes have acted on contemporary time-scales (hundreds or thousands of years, as opposed to millions); (ii) there is a genetic basis to biodiversity and ecosystem function, although in the animal groups (see above citations) variation between populations may be due to plasticity rather than genetic divergence; and (iii) as climate change drives species range shifts, population fragmentation and genetic differentiation, associated patterns of biodiversity and ecosystem function can change.

Understanding broad geographical patterns of genetic variation associated with species ranges is critical to linking ecology and evolution in a changing global climate. Recent research suggests that patterns of genetic variation may depend on where in the geographical range of a species an individual occurs (Hampe & Petit 2005; Aitken *et al.* 2008; Eckert, Samis & Loughheed 2008). It is thought that individuals that occupy the leading edge of a geographical range have likely gone through a strong selective filter resulting in overall low genetic variation, but positively influencing dispersal traits (Eckert, Samis & Loughheed 2008; Hargreaves & Eckert, in press) which enable those individuals to be fit in novel environments. Negative feedbacks, which occur when an individual has greater fitness in an environment other than its parents, likely applies to plants of the leading edge of range expansions, where dispersal traits are of particular importance. The continuous zone of a species distribution is thought to have high levels of additive genetic and phenotypic variation and gene flow within and among populations (Hampe & Petit 2005). Finally, those individuals and populations

in the trailing edge of a geographical range are thought to be fragmented remnants of a once intact continuous zone. Populations in the trailing edge of a species distribution are thought to demonstrate low gene flow among populations and be locally adapted to the particular environmental conditions in which they persist. While this conceptual model provides hypotheses for how neutral and quantitative genetic variation may be distributed throughout a species range, geographical distributions are influenced by a host of biotic and abiotic factors that are more complex than simple linear gradients of elevation and latitude. In addition, much of the relationship between evolutionary processes and ecological interactions depends upon how distributions of interacting species (and populations) will overlap in the new climate context (e.g. novel interactions; see Rasmann *et al.*, in press). Developing an understanding of how genetic and phenotypic variation in one species may influence the fitness and phenotype of interacting intra- or interspecific individuals and the ecosystem processes they mediate along these gradients remains a frontier linking ecology and evolution and may be even more important as it allows for a better understanding of interactions that change with changing species distributions. Such interactions may ultimately determine the ability of an individual to persist on the landscape, through complementary or facilitative interactions (Aitken *et al.* 2008; He, Bertness & Altieri 2013; Schweitzer *et al.*, in press).

Indirect genetic effects (IGEs) provide a mechanism for understanding the links between ecology and evolution that are driven by range shifts due to a changing global climate (Fig. 1). Indirect genetic effects are *not* indirect ecological interactions where the effect of one species on another is mediated by a third as defined in the ecological literature (Ricklefs 2008). Instead, IGEs occur when the fitness and phenotype of one individual changes due to the genetic identity of interacting individuals (Moore, Brodie & Wolf 1997; Wolf *et al.* 1998; Bailey *et al.* 2009, 2012; Wolf, Mutic & Kover 2011). This concept was first developed in the context of maternal effects from parent to offspring but the concept is broadly applicable across ecological and evolutionary disciplines (see review by Bailey 2012). For example, IGEs are fundamental for social evolution and coadaptation (shared fitness effects among individuals within a population related to genotype  $\times$  genotype interactions that vary along a particular ecological gradient; McGlothlin *et al.* 2010; Pruitt & Reichart 2011), sexual selection and the evolution of mate choice (Bonduriansky & Chenoweth 2009) and the evolution of parental care (Rauter & Moore 2002). They are also fundamental to nonbehavioural interactions such as niche construction and the *extended phenotype* (the idea, first proposed by Dawkins (1982), that the effects of genes extend beyond the individuals to affect associated communities and ecosystems; Odling-Smee, Laland & Feldman 2003; Bailey 2012) and to the nonadditive effects of individuals and species when they co-occur in mixture (i.e.



**Fig. 1.** Data from two experiments (a–c and g–i methods in Appendix S1, Supporting information; d–f Genung, Bailey & Schweitzer 2012) suggest that ‘mixture effects’ (i.e. the degree to which traits in monoculture differ from additive expectations) can vary significantly along ecological gradients due to indirect genetic effects (IGEs). Genotypes of *Solidago altissima* collected along an elevational gradient that were then planted in both genotype monocultures and six-genotype mixtures in a common garden (at roughly the lowest elevation) show that mixtures of different genotypes often display different traits than would be expected under additive expectations (a–c). These results suggest that the genotypes in mixture are interacting in ways that affect their fitness and performance. IGEs serve as the most parsimonious explanation for how genotypes may interact in mixtures (Genung, Bailey & Schweitzer 2012) as these interactions may occur when one genotype affects trait expression in its neighbours. Panels d–f demonstrate that manipulated focal-plant and neighbour-plant identity in two species – *Solidago altissima* and *Solidago gigantea* (*Solidago altissima* genotypes are labelled A1–A3 and *S. gigantea* genotypes are labelled G1–G3) can change mean plant and community traits (Genung, Bailey & Schweitzer 2012). Interestingly, the effects of genotypic diversity change along environmental gradients (g–i). Plant traits differed between monocultures and mixtures depending upon the elevation from which the plants were collected, such that genotype interactions were more facilitative at higher elevations than at lower elevations. [Correction added on 18 October 2013, after first online publication: x-axis label changed from ‘6 species mixture’ to ‘6 genotype mixture’.]

diversity effects; Laine 2009; Bailey *et al.* 2009). Among species, interspecific indirect genetic effects (IIGEs; Shuster *et al.* 2006) represent the fundamental unit of the co-evolutionary process (Thompson 2005) and are important in plant–soil feedbacks (Johnson *et al.* 2010; Pregitzer *et al.* 2010; Andonian *et al.* 2011; Schweitzer *et al.* 2012, in press), plant–plant (Genung *et al.* 2011; Rowntree, Shuker & Preziosi 2011; Whitlock *et al.* 2011; Genung, Bailey & Schweitzer 2012, 2013), plant–herbivore (Tétard-Jones *et al.* 2007; Duffy & Forde 2009) and plant–pollinator interactions (Thompson 2005; Shuster *et al.* 2006; Genung, Bailey & Schweitzer 2012) and even ecosystem processes such as decomposition (Genung, Bailey & Schweitzer 2013). For example, utilizing genotypes of *Solidago altissima* and *Solidago gigantea* (Genung, Bailey & Schweitzer 2013) tested whether IIGEs that had affected

living focal plants would affect litter decomposition rate, as well as nitrogen (N) and phosphorus (P) dynamics after the focal plant senesced. Consistent with the effects of IGEs and IIGEs, genetically based species interactions that occurred while plants were alive had afterlife consequences that affected N release; similarly, and genotype interactions that occurred while plants were alive affected P immobilization. While the genetic influence of neighbours on a given individual has been frequently studied, there is limited awareness that these types of interactions are a common evolutionary mechanism that (i) drives a diverse series of behavioural and ecological interactions, (ii) links ecological and evolutionary (eco–evo) dynamics and (iii) may be particularly important when species range shifts due to climate change (Moya-Laraño 2012; Schweitzer *et al.*, in press).

Here, we examine and synthesize emerging eco–evo concepts, that link climate change, species range shifts and biodiversity and ecosystem function, focusing on the role of IGEs and IIGEs as mechanisms of (i) ecological and evolutionary feedbacks at the leading and trailing edge of a species distribution; (ii) intra- and interspecific *genotypic diversity* effects; and (iii) the continuum of competition–facilitation along environmental gradients that can lead to coadaptation. Throughout the manuscript, we will refer to feedbacks as any effect (e.g. plant–soil interactions, plant–plant interactions) that changes an individual’s fitness in a ‘home’ versus ‘away’ environment; positive feedbacks result when an individual is more fit in its home environment and negative feedbacks result when an individual is less fit in its home environment. These feedbacks can be viewed as genotype by environment ( $G \times E$ ) interactions through which the biotic (e.g. Genung, Bailey & Schweitzer 2012) environment affects an individual’s fitness. Overall, the theory and empirical data, to date, indicate that IGEs and IIGEs have fundamental roles in ecological and evolutionary feedbacks, the genotypic diversity effects found in plant mixture experiments, the co-evolutionary process and coadaptation and may be fundamental to understanding the broad ecological and evolutionary dynamics that are likely to be a consequence of climate change.

### **IGEs and IIGEs as mechanisms of ecological and evolutionary feedbacks**

IGEs and IIGEs may dramatically influence the direction and pace of evolutionary change among interacting individuals when there is direct–indirect genetic covariance. Genetic covariance occurs when (i) the fitness of one species is related to heritable variation in a phenotype(s) that influences the fitness and phenotype of interacting individuals; and (ii) there is a feedback where the community of interacting individuals influences the fitness of the focal individual/species that created the original environment, reinforcing the interactions and resulting in an eco-evolutionary feedback loop (Johnson, Lajeunesse & Agrawal 2006; Wade 2007; McGlothlin *et al.* 2010; Genung *et al.* 2011; Moya-Laraño 2012). Eco–evo feedbacks can be either positive or negative and are similar to classic local adaptation studies (Kawecki & Ebert 2004), the difference being that feedback studies compare the performance of an individual in home vs. away environments while local adaptation studies compare the performance of local vs. foreign individuals in one given environment. Therefore, feedback studies inform whether selection will favour a species moving from one site to another (assuming the sites are close enough that movement is possible), while local adaptation studies inform whether selection will favour local individuals over foreign individuals that attempt to colonize. It is certainly possible that positive feedbacks could lead to local adaptation in the classic sense, but this is not guaranteed. While feedback studies often involve

reciprocal transplants, we stress that feedbacks can frequently occur in natural systems without any manipulation and here, we discuss feedbacks in the natural rather than experimental context. When these eco–evo feedbacks persist through time there are (at least) two major outcomes. When the fitness of individuals within populations is better-suited to ‘home’ than ‘away’ conditions, positive feedbacks and potentially local adaptation occur. In contrast, when the fitness of individuals within population are negatively affected by their parents environment (Connell 1970; Janzen 1970), or well suited to the environment created by another individual, negative feedbacks are expected to occur and selection is expected to favour those individuals that coexist (resulting in increased diversity). At local scales, when eco–evo feedbacks persist they can influence the competitive or facilitative characteristics of communities (Fridley, Grime & Bilton 2007), potentially leading to co-evolution and coadaptation among interacting individuals (Thompson 2005). Importantly, these feedbacks may be fundamental to leading- and trailing-edge dynamics, diversity effects and competition to facilitation along environmental gradients as species ranges shift.

Historically, species ranges have changed dramatically in response to climate (Davis & Shaw 2001; Davis, Shaw & Etterson 2005), which has consequences for genetic structure and novel species interactions. As species ranges change, species in expanded ranges will interact with and influence a different suite of species than their (co-evolved) community in the native range (Engelkes *et al.* 2008; Van der Putten 2012). Consistent with the hypothesis that individuals at the leading edge of their distribution survive and perform better ‘away’ than they do at ‘home’, McCarthy-Neumann & Ibanez (2012) found a negative plant–soil feedback where seedlings of dominant trees had higher survival when they established in novel territory that was not previously influenced by mature individuals of the same species. There are three important considerations associated with negative feedbacks at the leading edge that are important to consider. First, by definition, negative feedbacks indicate that an individual survives and performs better in the environment created by other individuals, which should lead to increased diversity. Secondly, within a population or among species, increased diversity as a consequence of negative feedbacks is likely to lead to ‘diversity effects’ and thus an increased chance of nonadditive responses due to facilitation among individuals. Thirdly, because persistent eco–evo feedbacks can influence characteristics of communities (Aarssen 1989; Fridley, Grime & Bilton 2007), consistent negative feedbacks among species may lead to coadaptation among interacting individuals. Additionally, it is worth noting that species’ ability to respond to climatic changes may be restricted by genetic variation (e.g. Kellermann *et al.* 2009). Species with lower amounts of genetic variation (especially for traits related to dispersal, temperature tolerance, etc.) may not be able to expand in response to climate change and therefore may not show the patterns detailed above.



In contrast to range expansion associated with feedbacks at leading edge populations, understanding the genetic consequences of populations in the trailing edge, including local adaptation and the evolution of endemics, is critical for understanding the evolutionary and biodiversity implications of modern global climate change. Trailing-edge populations are those that remain in their original distributions after species range shifts, meaning that they are remnants of a once intact continuous population. These populations usually occur in regions that have experienced long-term climatic stability (Tzedakis *et al.* 2002; Hampe & Petit 2005), which allows them to function as refugia that conserve biodiversity, contribute to landscape-scale patterns of genetic diversity (Hampe & Petit 2005) and can therefore serve as buffers to extinction events during species range shifts. Trailing-edge populations are usually small and prone to isolation, which can lead to reduced genetic variation within populations (Petit *et al.* 2003; Chang *et al.* 2004); however, prolonged isolation can often result in high levels of genetic differentiation among populations (Hampe & Petit 2005). Long-term isolation of these small populations can drive local adaptation to unique environments that often lead to the evolution of *ecotypes* and *endemic species* (Sexton *et al.* 2009). Because local adaptation occurs when local individuals are more fit than foreign individuals, positive feedbacks that cause an individual to be more fit in the biotic environment of conspecifics could lead to local adaptation if these feedbacks allow an individual to be more fit than foreign individuals. This suggests that while IGEs are not essential to local adaptation, they can in some cases speed the process by increasing the fitness of a given genotype or species. For example, in a greenhouse experiment, Pregitzer *et al.* (2010) planted seedlings from 20 randomly collected *P. angustifolia* genetic families in soils conditioned by *Populus* species in the field and measured subsequent survival and performance. Even though *P. angustifolia* soils were less fertile overall, *P. angustifolia* seedlings grown in *P. angustifolia*-conditioned soils were twice as likely to survive, grew 24% taller, had 27% more leaves, and 29% greater above-ground biomass than *P. angustifolia* seedlings grown in non-native *P. fremontii* or hybrid soils. While these were not isolated populations, positive feedbacks such as these are thought to be (i) more common in the trailing edge of species range; (ii) be drivers of local adaptation and persistence as species ranges shift; and (iii) if they persist through time may result in the evolution of endemic species. Importantly, while the ecological outcome of genetically based positive and negative feedbacks is remarkably different, they are driven by the same IGE and IIGE mechanism (Wade 2007; Genung *et al.* 2011; Moya-Laraño 2012).

### Genotypic diversity effects as a consequence of IGEs and IIGEs

Because species ranges are predicted to shift in response to climate change, it is pressing to resolve how the role of

IGEs and IIGEs vary along species distributions, to understand how plant genotype and species mixture effects (i.e. positive diversity effects measured in plant genotype or species mixtures) will operate in a changing climate. Plant–plant interactions, such as those commonly quantified in genotypic diversity studies, can be considered IGEs, as an individual's phenotype and fitness is due to the expression of genes in an interacting individual (Moore, Brodie & Wolf 1997; Wolf *et al.* 1998). For example, Genung, Bailey & Schweitzer (2012) showed that IIGEs could influence pollination dynamics and plant biomass production, indicating that influences on plant biomass can come from genetic factors in focal and interacting individuals (Fig. 1). Further, these changes in biomass were correlated with shifts in plant litter quality that affected decomposition and nitrogen cycling after plant senescence (Genung, Bailey & Schweitzer 2013). The effects of plant genotypic diversity have been detected in many systems, and for many response variables (e.g. Johnson, Lajeunesse & Agrawal 2006; Madritch, Donaldson & Lindroth 2006; Hughes *et al.* 2008; Genung *et al.* 2010). For example, Schweitzer *et al.* (2005) mixed leaf litter from five genotypes (backcross hybrids of *Populus angustifolia* and *Populus fremontii*) to examine the effects of genotype mixtures on microbe-mediated decomposition and showed that leaf litter decomposed faster, and released more phosphorus and nitrogen, in mixtures than in monocultures (i.e. the single genotype treatment). At the community level, Crutsinger *et al.* (2006) showed that common garden plots containing higher levels of genotypic diversity (i.e. 3, 6 or 12 genotypes) supported more diverse arthropod communities. These studies indicate the important role of IGEs and IIGEs in plant communities and highlight the potential for species interactions to vary along environmental gradients and to mediate the effects of climate change depending upon the strength and direction of the genetic covariance among the interacting individuals.

Nonadditive outcomes in genotypic diversity studies are, by definition, examples of either IGEs or IIGEs because individuals display different trait values in genotype mixtures than in monocultures (Bailey *et al.* 2009). Importantly, the effects of genotypic diversity are often greater than expected based on the additive components of the genotypes in mixture, indicating that there are nonadditive, synergistic outcomes of the genetic neighbourhood (Schweitzer *et al.* 2005; Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006; Madritch, Donaldson & Lindroth 2006; Hughes *et al.* 2008). From an ecological standpoint, combinations of genotypes often show nonadditive effects at the community (Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006; Genung *et al.* 2010) and ecosystem (Madritch & Hunter 2002; Schweitzer *et al.* 2005; Madritch, Donaldson & Lindroth 2006) level that cannot be predicted based on information about the component species or genotypes measured alone; this illustrates the importance of considering genotypic variation to understand complex ecological processes. In the context of

plants, the links between IGEs/IIGEs and genotypic diversity effects suggest that the simplest explanation for nonadditive outcomes involves plant–plant interactions between as few as two genotypes, and these plant–plant interactions may also have co-evolutionary consequences when heritable traits related to fitness vary in the environment of interacting genotypes. If the consequences of IGEs/IIGEs vary and persist along strong environmental gradients such as elevation or latitude, then  $G \times E$  effects could arise at the trailing edge as small populations persist in certain environments. Similarly,  $G \times G \times E$  effects could give rise to locally coadapted populations at the leading edge of species ranges where the fitness of individuals increases in the environment created by other individuals relative to ‘home’ conditions.

### Coadaptation and genotypic diversity effects along elevational gradients

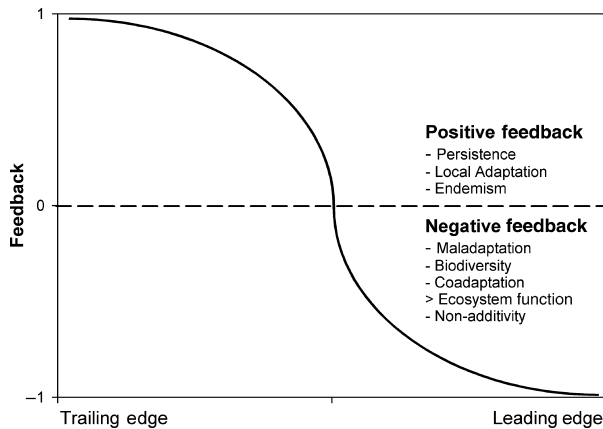
Integrating genetically based diversity experiments along environmental gradients, critical for investigating climate change, represents an important frontier linking ecology and evolution. Because genetic divergence and population genetic structure in one species can impact associated species interactions and ecosystem processes, evolutionary processes that act on the focal species may alter the effects of genotypic diversity on associated communities and ecosystem processes. For example, Lankau *et al.* (2009) showed that selection against phytochemical production in the invasive plant *Allaria petiolaris* allowed native plant communities to recover over time. In a different system, Callaway (1998) demonstrated that competitive interactions were more common among low-elevation plants and that facilitative interactions occurred more commonly in high-elevation settings. In particular, competitive interactions tended to prohibit plants from moving from higher to lower elevation conditions, but facilitative interactions enabled migration of plants up elevation gradients (see also Michalet *et al.*, in press). While this work is suggestive of an evolutionary mechanism, whether there is a genetic component to these interactions is still unclear (but see Fig. 1). However, as the feedback section indicates, negative feedbacks, and thus facilitation, can theoretically evolve. Recent research supports this contention and indicates that there can be population-level genetic variation for facilitation (sensu Michalet *et al.* 2011). For example, using an alpine cushion plant (*Geum rossii*) that expresses significant phenotypic variation for ‘cushion’ morphology (i.e. density of the plant’s rosettes that determines whether other plants can grow in the ‘cushion’), Michalet *et al.* (2011) found that cushion morphology impacted the distribution and abundance of associated plant species as well as the reciprocal effects of plant species on the fitness of *G. rossii* (IIGE). They found genetic variation for facilitation in this species, as well as significant reciprocal effects of the plant community on *G. rossii* that depended upon the degree of facilitation. This work clearly shows that

positive, community-level interactions such as facilitation can be viewed as products of genetic variation within a focal species. This represents a new direction in evolutionary research about which little is known and, because of the feedback effects of genetic variation at the community level, suggests some degree of co-evolution (Thompson 2005). If these effects were also correlated with the elevation from which the plants were collected, then it would suggest that the co-evolution between the cushion plants and associated plant communities may be coadaptive. Such interactions may dramatically influence the direction and pace of evolution among the interacting species and impact range expansion in unusual ways.

Traits of competition and facilitation may evolve within a population along a gradient, resulting in coadaptation among individuals within a particular location. For example, using a genotypic diversity experiment with multiple populations of *Solidago altissima* collected along an elevational gradient, there was among-population level variation for genotypic diversity effects (Fig. 1; Appendix S1, Supporting information). Importantly, the genotypic diversity effect (and thus IGEs) was correlated with the elevation from which the population was collected suggesting a pattern of local coadaptation. In particular, low-elevation plants tended to show competitive interactions and negative genotypic diversity effects, while high-elevation populations tended to show more facilitative genotypic diversity effects (sensu Callaway 1998; Michalet *et al.* 2011, in press). These results are consistent with predictions from range shifts, where negative feedbacks are most likely to occur on the leading edge of species ranges and local adaptation is predicted to occur more commonly at the trailing edge (Hampe & Petit 2005). In combination, these studies suggest that the ‘competition to facilitation gradient’ is one important, conceptual model that can inform the potential community and ecosystem consequences of evolution in dominant species (Callaway 1998; Choler, Michalet & Callaway 2001; Michalet *et al.* 2011). Moreover, these results across environmental gradients suggest that understanding the effects of climate change on genotypic diversity is critical and has not been well integrated into studies of diversity along environmental gradients.

### Conclusions and implications

It is well-established that climatic variation affects the ability of plants to adapt to environmental gradients by changing plant traits and the broad geographical patterns of plant distributions (Clausen, Keck & Heisey 1940; Davis, Shaw & Etterson 2005; Gitlin *et al.* 2006; Jump & Peñuelas 2006; Hargreaves & Eckert, in press; Ikeda *et al.*, in press; Michalet *et al.*, in press; Potts *et al.*, in press; Rasmann *et al.*, in press; Read *et al.*, in press; Schweitzer *et al.*, in press). Research over the last 50 years indicates that the global climate is rapidly changing, affecting patterns of temperature and precipitation at many



**Fig. 2.** Conceptual model integrating range shifts with ecological and evolutionary dynamics. Here, we hypothesize that indirect genetic effects (IGEs) represent the evolutionary mechanism that may change ecological processes following range shifts. The outcomes of IGEs vary such that at the trailing edge, positive feedbacks and local adaptation are predicted to be the norm. At the leading edge of a species distribution, it is predicted that negative feedbacks will arise due to maladaptation between individuals at the leading edge and novel environments into which they are expanding. Negative feedbacks occur when individuals from one population perform better in the environment created by individuals from a different population (presumably through plant–soil biota interactions) and are thought to be critical to range expansion. Here, IGEs may lead to complementarity and facilitation and genetic covariance among genotypes and species, giving rise to increased diversity, potential coadaptation, higher overall ecosystem function and greater provisioning of ecosystem services at the leading edge.

geographical scales (Morgenstern 1996; Pitelka & Plant Migration Workshop Group 1997; IPCC 2007). The implications of these projections are that future climate changes have the potential to greatly modify plant species ranges (Allen & Breshears 1998; Bachelet *et al.* 2001; Breshears *et al.* 2005; Gitlin *et al.* 2006) and/or alter the ability of plants to adapt to future changes (Davis & Shaw 2001; Jump & Peñuelas 2005; Krauss *et al.* 2006). Importantly, a changing climate can also change the community context of other species with which an individual or species interacts, creating novel genetically based interactions that may shape their shared evolutionary fates.

Recently, there have been calls for greater integration of ecology and evolution particularly as it relates to global change factors (Sutherland *et al.* 2013). This is a great challenge due to the diversity of disciplines that inform these questions including quantitative and molecular genetics, eco-physiology, mathematical modelling, climate science, as well as community and ecosystem ecology. IGEs and IIGEs may be fundamental, but generally overlooked mechanism, to understanding the broad ecological and evolutionary dynamics that are likely to be a consequence of climate change that warrants much more research attention. IGEs and IIGEs represent a mechanism for the evolution of feedbacks that result in patterns of local adaptation (positive feedbacks) and diversity effects (nega-

tive feedbacks) that are thought to predictably vary throughout the range of a species (Fig. 2). The theoretical and empirical results to date indicate that IGEs and IIGEs have primary roles in genotypic diversity effects, feedbacks, the co-evolutionary process and coadaptation as well as nonadditive interactions. If the effects of IGEs and IIGEs are persistent across scales of space and time they may dramatically impact the community context within which species evolve resulting in unpredictable consequences for the success of species in expanded ranges. Novel studies integrating IGEs and IIGEs along environmental gradients are critical to linking ecology and evolution in a changing global climate, placing genetically based species interactions along a continuum from adaptation to maladaptation (Schweitzer *et al.*, in press) and may represent a fundamentally new explanation for patterns of biodiversity on the landscape.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** In 2008 we established a common garden where clonal replicates of 9 (site 1277) to 15 (site 260) individual, randomly selected plants (from rhizome cuttings) of *S. altissima* were collected from seven locations along a 1000 m elevational transect in the southern Appalachian mountains of Tennessee and randomly planted in 40 gallon pots.

**Table S1.** Evolution of diversity effects along elevational gradients.