

Meetings

New frontiers in community and ecosystem genetics for theory, conservation, and management

Community and ecosystem genetics: the extended genetic effects of plant species, XVII International Botanical Congress 2011, Melbourne, Australia, August 2011

The effects of genetic variation in species can have large impacts on direct and indirect species interactions, associated biodiversity and ecosystem function. Biodiversity and ecosystem function can change as a consequence of evolutionary dynamics (Barbour *et al.*, 2009), thus, linking evolution strongly with community and ecosystem ecology. At the 2011 International Botanical Congress in Melbourne, Australia, a symposium entitled, 'Community and ecosystem genetics: the extended genetic effects of plant species', examined new research in the field of community and ecosystem genetics. Talks focused on: links between contemporary ecological interactions and historic evolutionary dynamics; the role of feedbacks as mechanisms in driving patterns of biodiversity and ecosystem function; and application of these approaches to management and conservation issues as they relate to global change. The symposium concluded that an understanding of evolutionary divergence and adaptation, and the role of ecological feedbacks in natural systems, will be fundamental to successful outcomes in future conservation, restoration and management decisions.

'... feedbacks between interacting species may lead to divergence at the population scale and perhaps even in deep evolutionary time.'

Linking contemporary ecological interactions to historic evolutionary dynamics

Links between genetic variation in host plants and associated species interactions, biodiversity, and ecosystem function were demonstrated across several herbaceous and woody species. Two talks linked evolutionary processes in *Eucalyptus* to shifts in biodiversity and ecosystem function. The first of these by Brad Potts (University of Tasmania, Australia) described the

'Extended genetic effects of a forest dominant: The case of *Eucalyptus globulus*', while the second by Joe Bailey (University of Tennessee, USA) on 'Historical evolutionary dynamics result in convergent ecological consequences for biodiversity and ecosystem function' focused on how phylogenetic divergence may lead to change in biodiversity and ecosystem function. Emerging from both talks was the recognition that *Eucalyptus*, as a broad group, represents a model for understanding the genetic basis to biodiversity and ecosystem function irrespective of the genetic scale of interest. *Eucalyptus globulus*, a dominant tree of lowland forests of south-eastern Australia, is widely grown in plantations in temperate regions of the world and its molecular and quantitative genetic diversity are amongst the most extensively studied of any forest tree. The natural colonization of pedigreed field trials by local fungi, insect and marsupial species has provided a robust system in which to study individual species, as well as community responses to genetic variation (Barbour *et al.*, 2009). Community and ecosystem responses have been explored at multiple genetic levels from genetically divergent geographic races, additive genetic effects within-populations and within-races, to within-family quantitative trait loci (QTL) effects. Because of this system's established quantitative and molecular genetics, there is a strong foundation for understanding the genetic drivers of insect, marsupial and fungal responses to genetic variation at the species (including genetic co-variance amongst these organisms) and community level, the relative importance of direct and indirect genetic effects as a mechanism, and the potential for co-evolution through feedbacks on tree fitness.

The role of feedbacks as mechanisms in driving patterns of biodiversity and ecosystem function

There were three talks in the symposium on this topic. First, Jennifer Rowntree (University of York, UK) discussed plant-plant parasite feedbacks, second Mark Genung (University of Tennessee, USA) spoke about plant-plant intra- and inter-specific indirect genetic effects in *Solidago*, and third, Jennifer Schweitzer (University of Tennessee, USA) examined plant-soil genetic feedbacks. Feedbacks among interacting species are fundamental to the co-evolutionary process (Thompson, 2005), local adaptation (Johnson *et al.*, 2010), and the maintenance of biodiversity (Laine, 2009). Little is understood, however, about how feedbacks influence patterns of biodiversity and ecosystem function, or if they stabilize (i.e. by negative feedback) or destabilize (i.e. by positive feedback) eco-evolutionary patterns in community or ecosystem ecology. Genetic variation in a single species can influence many facets of ecological communities and ecosystem function, thus one may expect to observe genetically based feedbacks on ecological communities stemming from a variety of species interactions.

As a consequence of genotype by genotype interactions (i.e. where the fitness and phenotype of an interacting individual or species is affected by the genotype of an associated individual or species), feedbacks between interacting species may lead to divergence at the population scale and perhaps even in deep evolutionary time. For example, the net effects of diverse components of the soil community that either interact with the living plant (including root herbivores, pathogens, mutualists) or plant detritus (heterotrophic decomposers) can result in both positive and negative feedback to plant performance or persistence that can vary through time (Kulmatiski *et al.*, 2008; Diez *et al.*, 2010, Felker-Quinn *et al.*, 2011; Van der Putten *et al.*, 2001). Negative plant–soil feedbacks from accumulation of pathogens or herbivores may largely affect the direction of natural selection and prevent species from persisting at fixed locations or at high abundances and also promote species co-occurrence (Diez *et al.*, 2010). Positive plant–soil feedbacks may affect the direction of natural selection and are mechanisms for persistence and even increased genetic variation (*sensu* Pregitzer *et al.*, 2010).

The importance of ‘plant–neighbor’ interactions in feedbacks has yet to be fully realized, although recent data suggests they may be critical. For example, biodiversity studies that have manipulated genotypic diversity almost always invoke genotype interactions as mechanisms for any observed non-additive (i.e. unpredictable) effects (Bailey *et al.*, 2009). Studies which manipulate $G \times G$ interactions may illuminate mechanisms that are important in mixtures containing greater numbers of genotypes. Additionally, if these $G \times G$ interactions have fitness consequences, such studies can inform how ‘plant–neighbor’ (including parasitic plants, herbivores as well as species at higher trophic levels) interactions affect both the ecology and evolution of the interacting species at small spatial scales (Genung *et al.*, 2011; Rowntree *et al.*, 2011). Recent research, including the talks in this symposium, suggest the novel idea that natural selection in the context of feedbacks is at least partially responsible for the non-additive effects observed in biodiversity studies.

Application of community genetic approaches to management and conservation

Finally, a talk by Tom Whitham (Northern Arizona University, USA) on ‘Conservation issues associated with the community genetics of foundation forest trees as drivers of community diversity, structure, stability and evolution’ raised new issues for our understanding management and conservation in an uncertain climatic future. As genetic variation in species (especially foundation species that are community and ecosystem drivers) can define community structure, ecosystem processes, species interactions, evolution and biodiversity, it is important to consider their management and conservation implications (Whitham *et al.*, 2010). For example, because different plant genotypes can support different communities and ecosystem processes (reviewed by Bailey *et al.*, 2009), genetic diversity in a common foundation species such as a forest tree is likely to be associated with the biodiversity of the dependent community (see review by Hughes *et al.*, 2008). Similarly, with the demonstration that there is a

genetic component to community stability (i.e. the consistent response of arthropod communities across years; Keith *et al.*, 2010), we now realize that so called ‘emergent properties’ of communities such as stability can be due, in part, to underlying plant genetic variation.

A community genetics approach to management and conservation is likely to be productive in three major and interactive areas (climate change, exotic invasions, and habitat restoration). For example, climate change is likely to make locally adapted species locally maladapted (e.g. O’Neill *et al.*, 2008); climate change is thought to interact with exotic invasive species to either promote or hinder their expansion (Bradley *et al.*, 2009); and restoration of endangered habitat types has a strong genetic component with some genotypes of a foundation species far exceeding the performance of other genotypes. Recent studies have even identified specific genes and mutations associated with invasive species that allow them to dramatically alter community structure and/or make them difficult to remove or control (Wymore *et al.*, 2011). Because there are genetic components to understanding the response of plants to climate change, exotic invasions, and habitat restoration, and they can strongly interact, we believe that community genetics has a strong role to play in the successful merger of these fields, which constitute some of the most pressing biological issues of our time.

We predict that two major tools will become increasingly important in merging climate change, exotic invasions, and habitat restoration. First, common gardens that use multiple foundation species and replicated genotypes of species along elevation and latitude gradients are crucial. By incorporating exotic species into these experiments, we can identify the genotypes of native species best able to survive climate change and interactions with exotic species, as well as those genotypes or genotype combinations that support the greatest biodiversity. This approach elevates the time honored provenance trial approach to a new level of complexity to develop management strategies and calibrate climate change models for the more realistic conditions of gene by biotic environment by abiotic environment interactions ($G \times E \times E$). Second, the application of network theory (e.g. Bascompte, 2009) to quantify the interactions among species in a community is crucial to understanding the functioning of an ecosystem. Because climate change, exotic invasions and other anthropogenic factors change species interactions and evolutionary trajectories, the conservation of species interactions may be critically important. Thus, just as population genetics has played a major role in agriculture and the green revolution, we argue that community genetics can play a vital role in the management and conservation of whole ecosystems.

Joseph K. Bailey^{1,2*}, Mark A. Genung², Julianne O’Reilly-Wapstra^{1,3}, Brad Potts^{1,3}, Jennifer Rowntree⁴, Jennifer A. Schweitzer^{1,2} and Thomas G. Whitham^{5,6}

¹School of Plant Science, University of Tasmania, Private Bag 55, Hobart 7001, Tas., Australia; ²Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee, Knoxville, TN 37996, USA; ³CRC for Forestry,

Private Bag 12, Hobart 7001, Tas., Australia; ⁴Department of Biology, University of York, Wentworth Way, York YO10 5DD, UK; ⁵Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA; ⁶Merriam-Powell Center for Environmental Research, Flagstaff, AZ 86011, USA (*Author for correspondence: email Joe.Bailey@utk.edu) All Authors contributed equally to this manuscript; authorship is alphabetical.

References

- Bailey JK, Schweitzer JA, Koricheva J, Madritch MD, LeRoy CJ, Rehill BJ, Bangert RK, Fisher DG, Allen G, Whitham TG. 2009. From genes to ecosystems: synthesizing the effects of plant genetic factors across systems. *Philosophical Transactions of the Royal Society B – Biological Sciences* 364: 1607–1616.
- Barbour RC, O'Reilly-Wapstra JM, De Little DW, Jordan GJ, Steane DA, Humphreys JR, Bailey JK, Whitham TG, Potts BM. 2009. A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. *Ecology* 90: 1762–1772.
- Bascompte J. 2009. Disentangling the web of life. *Science* 325: 416–419.
- Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH. 2009. Predicting plant invasions in an era of global change. *Trends in Ecology and Evolution* 25: 310–318.
- Diez JM, Dickie I, Edwards G, Hulme PE, Sullivan JJ, Duncan RP. 2010. Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters* 13: 803–809.
- Felker-Quinn E, Bailey JK, Schweitzer JA. 2011. Geographic mosaics of plant-soil feedbacks in a highly invasive plant: implications for invasion success. *Ecology* 92: 1208–1214.
- Genung MA, Schweitzer JA, Úbeda F, Fitzpatrick BM, Pregitzer CC, Felker-Quinn E, Bailey JK. 2011. Genetic variation and community change – selection, evolution, and feedbacks. *Functional Ecology* 25: 408–419.
- Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11: 609–623.
- Johnson NC, Wilson GWT, Bowker MA, Wilson J, Miller RM. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences, USA* 107: 2093–2098.
- Keith AR, Bailey JK, Whitham TG. 2010. A genetic basis to community repeatability and stability. *Ecology* 11: 3398–3406.
- Kulmatiski A, Beard KH, Stevens J, Cobbold SM. 2008. Plant–soil feedbacks: a meta-analytical review. *Ecology Letters* 11: 980–992.
- Laine A. 2009. Role of coevolution in generating biological diversity: spatially divergent selection trajectories. *Journal of Experimental Biology* 60: 2957–2970.
- O'Neill GA, Hamann A, Wang T. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology* 45: 1040–1049.
- Pregitzer CC, Bailey JK, Hart SC, Schweitzer JA. 2010. Soils as agents of selection: feedbacks between plants and soils alter seedling survival and performance. *Evolutionary Ecology* 24: 1045–1059.
- Rowntree JK, Cameron DD, Preziosi RF. 2011. Genetic variation changes the interactions between the parasitic plant–ecosystem engineer *Rhinanthus* and its hosts. *Philosophical Transactions of the Royal Society B – Biological Sciences* 366: 1380–1388.
- Thompson JN. 2005. *The geographic mosaic theory of coevolution*. Chicago, IL, USA: University of Chicago Press.
- Van der Putten WH, Vet LEM, Harvey JA, Wäckers FL. 2001. Linking above and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology and Evolution* 16: 547–554.
- Whitham TG, Gehring CA, Evans LM, LeRoy CJ, Bangert RK, Schweitzer JA, Allan GJ, Barbour RC, Fischer DG, Potts BM *et al.* 2010. A community and ecosystem genetics approach to conservation biology and management. In: DeWoody A, Bickham J, Michler C, Nichols K, Rhodes G, Woeste K, eds. *Molecular approaches in natural resource conservation and management*. Cambridge, UK: Cambridge University Press, 50–73.
- Wymore AS, Keeley ATH, Yturralde KM, Schroer ML, Propper CR, Whitham TG. 2011. Genes to ecosystems: exploring the frontiers of ecology with one of the smallest biological units. *New Phytologist* 191: 19–36.

Key words: adaptation, biodiversity, climate change, community and ecosystem genetics, conservation management, ecosystem interactions, exotic invasions, habitat restoration.