

From genes to ecosystems: an emerging synthesis of eco-evolutionary dynamics

Symposium 7, 94th Ecological Society of America Meeting, Albuquerque, New Mexico, USA, August 2009

A synthesis is underway between ecology and evolution, partly brought about by the realization that evolutionary change can take place on ecological timescales (Hairston *et al.*, 2005; Whitham *et al.*, 2006; Carroll *et al.*, 2007). This synthesis attempts to understand the dynamic interplay of ecological and evolutionary processes that results from natural or anthropogenic selective forces (Lankau & Strauss, 2007). Moreover, this synthesis represents an integration of several 'genes to ecosystems' approaches, including 'ecological stoichiometry', 'community genetics' (Whitham *et al.*, 2006) and 'niche construction'. United under the framework of 'eco-evolutionary dynamics', these ideas seek to link genetic and phenotypic variation to population dynamics, biodiversity and ecosystem function, and place these disciplines in a dynamic evolutionary framework (i.e. understanding the ecological consequences of evolutionary processes and the evolutionary consequences of ecological interactions). This is not an easy endeavor because any such synthesis needs to be broadly multidisciplinary and integrative (Whitham *et al.*, 2006). And yet the potential pay offs are large given that genetic variation across plant and animal systems can have extended consequences at the population, community and ecosystem levels. These consequences can come in the form of the vital rates of survival, reproduction and migration, as well as arthropod and aquatic macroinvertebrate diversity, soil microbial communities, trophic interactions, carbon storage, soil nitrogen availability, dissolved organic nitrogen and production of primary producers (Whitham *et al.*, 2006; Bailey *et al.*, 2009; Ezard *et al.*, 2009; Harmon *et al.*, 2009; Johnson *et al.*, 2009; Palkovacs *et al.*, 2009; Post & Palkovacs, 2009). The effects of genetic or phenotypic variation are not limited to single systems or to ecologically important species (i.e. keystone species, dominant species, foundation species, ecosystem engineers), although these are excellent places to start looking. Instead, genetic variation seems to have effects that are broadly distributed across plant and animal systems - and these effects can be similar in magnitude to those of nonevolutionary ecological variables, such as climate, species invasion and habitat quality (Hairston *et al.*, 2005; Bailey *et al.*, 2009; Ezard *et al.*, 2009; Palkovacs *et al.*, 2009; Post & Palkovacs, 2009).

While it is clear from the talks presented in this symposium that genetic variation can have significant impacts on population dynamics, biodiversity and ecosystem services in specific instances, research efforts are increasingly focused more generally on factors that influence the strength and form of eco-evolutionary dynamics (Bailey *et al.*, 2009). Active research topics include (1) how evolution and co-evolution influence biodiversity and ecosystem function, (2) the reciprocal influences of ecological and evolutionary causation (i.e. eco-evolutionary feedbacks) and (3) the relative effect sizes of evolutionary processes. In Fig. 1, for example, genetic variation might influence phenotypic variation, which might influence population dynamics or community structure, leading to variation in ecosystem function that might then impose selection on phenotypic variation and thereby cause genetic change. At the 2009 Annual Meeting of the Ecological Society of America, a symposium entitled 'Eco-Evolutionary dynamics: Should ecologists care?' <http://eco.confex.com/eco/2009/techprogram/S4123.HTM> focused on the state of eco-evolutionary research, and here we outline some of the insights that emerged from that symposium.

'...to show that eco-evolutionary dynamics are taking place in a specific system, it is first important to show that genetic variation influences ecological variables. But how important is this variation or these dynamics at different hierarchies of complexity or in relation to nonevolutionary ecological effects?'

Evolutionary and co-evolutionary effects on biodiversity and ecosystem function

Recent research has shown that extended ecological consequences of standing genetic variation/diversity occur across plant and animal systems and across terrestrial and aquatic biomes. Moreover, empirical, mathematical and theoretical studies suggest an emerging mechanistic framework for the multispecies co-evolutionary process that is associated with interspecific indirect genetic effects (i.e. where the genotype of one species influences the fitness and phenotype of associated interacting species) (Thompson, 2005; Shuster *et al.*, 2006; Wade, 2007). Such work suggests that the co-evolutionary process should be common across the landscape and be important for positive and negative plant-soil feedbacks,

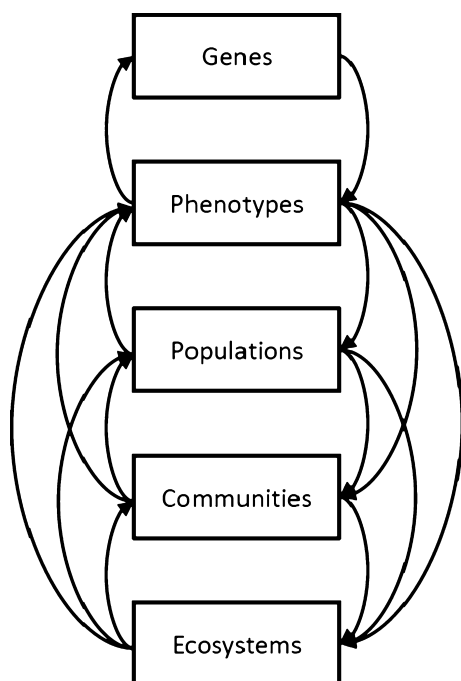


Fig. 1 Conceptual model of dynamic eco-evolutionary feedbacks, demonstrating the potential feedbacks from genes to phenotypes across population, community and ecosystem levels of organization.

plant–plant interactions that range from competitive to complementary, and trophic interactions in plant–herbivore–predator systems. In addition, understanding the indirect consequences of evolution and co-evolution represents an emerging frontier. For example, Palkovacs *et al.* (2009) experimentally compared the effects of two fish species (guppies (*Poecilia reticulata*) and killifish (*Rivulus hartii*)) that had evolved in either the presence or absence of predators (i.e. evolutionary diversity), and under different contexts of sympatry (i.e. co-evolutionary diversity), on aquatic macroinvertebrates and algal biomass. They found that populations which evolved under these different conditions differentially influenced both invertebrate and algal biomass in mesocosms. Overall, three major themes emerged from these and other work on this topic: (1) intraspecific variation can be as important as interspecific variation to ecological processes; (2) the co-evolutionary process is likely to be common across plant and animal systems as more studies specifically begin to address interspecific genotype \times genotype interactions; and (3) the co-evolutionary dynamic may be a particularly important contributor to eco-evolutionary dynamics.

Dynamic ecological and evolutionary frameworks

The demonstration of multiple ecological effects of standing genetic variation within populations, or recently evolved

differences between populations, suggests the potential for true eco-evolutionary dynamics (i.e. ongoing changes in traits influencing ecological interactions, and vice versa), but these dynamics have only rarely been studied explicitly (Pelletier *et al.*, 2009). Very recent examples include empirical analyses of population responses to contemporary trait change (Ezard *et al.*, 2009), mathematical models of population or community dynamics (Johnson *et al.*, 2009; Zheng *et al.*, 2009) and experimental designs that either capture (Jones *et al.*, 2009) or mimic longitudinal time series (Barbour *et al.*, 2009; Harmon *et al.*, 2009). This framework is critical for revealing (1) how ecology and evolution mutually interact to shape population persistence in the face of environmental change, (2) the origins (speciation) and maintenance of biodiversity (Cavender-Bares *et al.*, 2009) and (3) the ecological trajectories of populations, communities and ecosystems (Jones *et al.*, 2009). Although there are a number of nice examples of how genetic and phenotypic variation within species influences ecological processes, as presented in this symposium, the relative rarity of dynamical studies of reciprocal eco-evolutionary feedbacks highlights the difficulty of such work (Post & Palkovacs, 2009). This difficulty probably arises, at least in part, because two-way interactions are difficult to document and disentangle in nature. However, this means that detailed manipulative experiments are called for that also extend to more natural contexts, rather than only the laboratory or field mesocosms that have been used so far (Harmon *et al.*, 2009; Post & Palkovacs, 2009).

Measuring and predicting effect sizes

In order to show that eco-evolutionary dynamics are taking place in a specific system, it is first important to show that genetic variation influences ecological variables. But how important is this variation or these dynamics at different hierarchies of complexity (populations, communities, ecosystems) or in relation to nonevolutionary ecological effects? Only by addressing these questions can we determine the potential importance of eco-evolutionary patterns at different hierarchical levels or in relation to traditional ecological effects. These studies present compelling evidence that eco-evolutionary effects can be surprisingly large, even relative to the effects of traditional ecological factors (Fig. 2; Bailey *et al.*, 2009; Palkovacs *et al.*, 2009). Such effects may be greatest (on average) at the population level and somewhat less intense at levels more removed from variation within a target species, such as community structure or ecosystem function (Bailey *et al.*, 2009). This is not always the case, however, given that genetic variation can sometimes have very large direct effects on community or ecosystem variables that are not simply mediated by population abundance. Quantitative assessments of effect sizes represent a significant advance in the field as it may ultimately enable

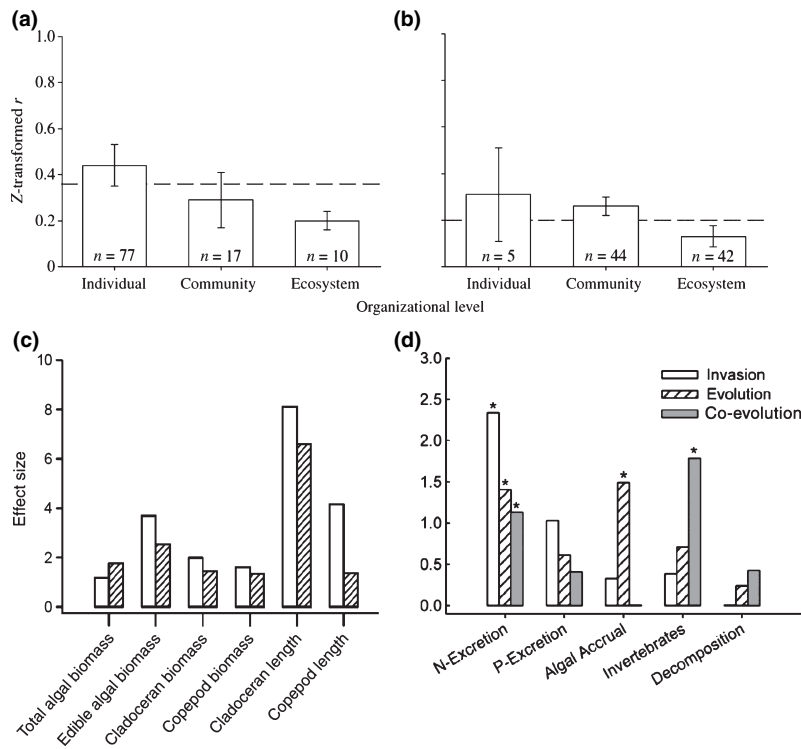


Fig. 2 Ecological effect sizes across population, community and ecosystem response variables in aquatic and terrestrial ecosystems. In terrestrial plant systems the effects of genetic introgression (a) and genotypic diversity (b) demonstrate strong effects across levels of organization (i.e. population, community, ecosystem). Bars represent the mean effect size (\pm 95% CI) while the dashed lines indicate the average effect size across all levels of organization (modified from Bailey *et al.*, 2009). In aquatic systems, large effect sizes (Cohen's *d*) exist on community and ecosystem response variables in association with alewife (c) populations and stream fishes in Trinidad (d). Panel c represents the effect size of the presence/absence or incidence of alewife (open bars) and intraspecific phenotypic variation (i.e. the difference between anadromous and land-locked populations of alewives; hashed bars). The data are modified from Post *et al.* 2008. Panel d represents effect sizes with guppy invasion, guppy evolution and *Rivulus*–guppy co-evolution. Significant contrasts at the $\alpha = 0.05$ level are indicated with an asterisk; data are modified from Palkovacs *et al.*, 2009).

scientists to predict where ecological and evolutionary effects are likely to be weak or strong. Moreover, attention to such effect sizes may be important from a very practical standpoint, given the possibility that studies quantifying ecological effect sizes may at times be confounded by the contemporaneous ecological effects of evolution and co-evolution (Strauss *et al.*, 2008).

Conclusions and future directions

Population-level genetic differentiation in quantitative traits can lead to variation in genetically based species interactions that may feed back to affect the phenotype and fitness of the interacting species (i.e. the co-evolutionary process) (Thompson, 2005). While there are an abundance of plant systems and experimental approaches to examine such hypotheses, including provenance trials with plants (see Barbour *et al.*, 2009) and genotype-by-genotype interactions, the majority of studies to date have focused on predator–prey systems (Pelletier *et al.*, 2009), leaving the door open to many important questions in many diverse systems, including the following. (1) Are eco-evolutionary effects stabilizing or disruptive processes in ecology (Palkovacs *et al.*, 2009)? (2) How common is rapid evolution and can it influence biodiversity and ecosystem services on similar timescales? (3) How do phenotypic/genetic effects depend on density regulation? (4) Do evolutionary effects decrease from populations to ecosystems (Bailey *et al.*, 2009)?

(5) Under what conditions do ecological and evolutionary feedbacks take place, and when are they positive or negative (Post & Palkovacs, 2009)? These questions all represent important areas of research and synthesis in the growing field of ecological and evolutionary dynamics. As the discussion at the symposium demonstrated, eco-evolutionary dynamics are common on an ecological timescale in nature, which means that addressing these and other questions is important if we are to understand and predict the dynamic interplay of ecological and evolutionary processes that result from natural or human-driven environmental changes.

Joseph K. Bailey^{1,2*}, Andrew P. Hendry³, Michael T. Kinnison⁴, David M. Post⁵, Eric P. Palkovacs⁶, Fanie Pelletier⁷, Luke J. Harmon⁸ and Jennifer A. Schweitzer¹

¹Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA;

²Department of Plant Sciences, University of Tasmania, Hobart, TAS 7001, Australia; ³Redpath Museum & Department of Biology, McGill University, Montreal, QC, Canada, H3A 2K6; ⁴School of Biology and Ecology, University of Maine, Orono, ME 04469, USA; ⁵Department of Ecology & Evolutionary Biology, Yale University, New Haven, CT 06520, USA; ⁶Duke University Marine Laboratory, Nicholas School of the Environment and Earth Sciences, Beaufort, NC 28516-9721, USA; ⁷Department of

Biology, University of Sherbrooke, Sherbrooke, QC, Canada, J1K2R1; ⁸Department of Biological Sciences, University of Idaho, Moscow, ID 83844-3051, USA (*Author for correspondence: email jbaile29@utk.edu)

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* 364: 1607–1616.
- Barbour RC, De Little DW, O'Reilly-Wapstra JM, Jordan GJ, Steane DA, Humphreys JR, Bailey JK, Whitham TG, Potts BM. 2009. Genetic similarity and hierarchical structure within a foundation tree species drives dependent community variation. *Ecology* 90: 1762–1772.
- Carroll SP, Hendry AP, Reznick DN, Fox CW. 2007. Evolution on ecological timescales. *Functional Ecology* 21: 387–393.
- Cavender-Bares J, Kozak K, Fine P, Kembel S. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.
- Ezard TH, Co te' SD, Pelletier F. 2009. Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philosophical Transactions of the Royal Society B* 364: 1491–1498.
- Hairston NG Jr, Ellner SP, Geber MA, Yoshida T, Fox JA. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* 8: 1114–1127.
- Harmon LJ, Matthews B, DesRoches S, Chase J, Shurin J, Schluter D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458: 1167–1170.
- Johnson MTJ, Vellend M., Stinchcombe JR. 2009. Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philosophical Transactions of the Royal Society B* 364: 1593–1606.
- Jones LE, Becks L, Ellner SP, Hairston NG Jr, Yoshida T, Fussmann GF. 2009. Rapid contemporary evolution and clonal food web dynamics. *Philosophical Transactions of the Royal Society B* 364: 1579–1592.
- Lankau RA, Strauss SY. 2007. Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* 317: 1561–1563.
- Palkovacs EP, Marshall MC, Lamphere BA, Lynch BR, Weese DJ, Fraser DF, Reznick DN, Pringle CM, Kinnison MT. 2009. Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philosophical Transactions of the Royal Society B* 364: 1617–1628.
- Pelletier F, Garant D, Hendry AP. 2009. Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B* 364: 1483–1490.
- Post DM, Palkovacs EP. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society B* 364: 1629–1640.
- Post DM, Palkovacs EP, Schielke EG, Dodson SI. 2008. Intraspecific phenotypic variation in a predator affects zooplankton community structure and cascading trophic interactions. *Ecology* 89: 2019–2032.
- Shuster SM, Lonsdorf EV, Wimp GM, Bailey JK, Whitham TG. 2006. Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution* 60: 991–1003.
- Strauss SY, Lau JA, Schoener TW, Tiffin P. 2008. Evolution in ecological field experiments: implications for effect size. *Ecology Letters* 11: 199–207.
- Thompson JN. 2005. *The geographic mosaic theory of coevolution*. Chicago, IL, USA: University of Chicago Press.
- Wade MJ. 2007. The co-evolutionary genetics of ecological communities. *Nature Reviews Genetics* 8: 185–195.
- Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, LeRoy CJ, Lonsdorf E, Allan GJ, DiFazio SP, Potts BM *et al.* 2006. A framework for community and ecosystem genetics: From genes to ecosystems. *Nature Reviews Genetics* 7: 510–523.
- Zheng C, Ovaskainen O, Hanski I. 2009. Modelling single nucleotide effects in phosphoglucose isomerase on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Philosophical Transactions of the Royal Society B* 364: 11519–11532.

Key words: co-evolution, community genetics, eco-evolutionary dynamic, effect size, genes to ecosystems, intraspecific genetic variation.