

“All effects of a gene on the world”: Extended phenotypes, feedbacks, and multi-level selection¹

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Biernaskie and Tyerman (2005) suggest that Whitham *et al.* (2003) misuse the concept of the extended phenotype (Dawkins, 1982), in which a behavioural trait such as nest construction by birds or dam building by beavers is an adaptive genetic trait of the individual. Dawkins recognizes that for extended phenotypes such as dam building to have evolutionary consequences for beavers, the dam building trait must have fitness consequences for the individuals expressing the trait. However, because there are ecological and evolutionary consequences of extended phenotypes such as beaver dams on other species, it is also important to consider those impacts that do not necessarily

involve feedbacks. Even Dawkins recognizes these other effects. For example, he says that a mutation that alters the shape of an oystercatcher’s foot (p. 206-207, 1999, 2nd Edition) has obvious implications for the oystercatcher’s fitness, and would also alter the shape of the bird’s footprints in the mud. Dawkins states that this “is of no interest to the student of natural selection, and there is no point in bothering to discuss it under the heading of the extended phenotype, though it would be formally correct to do so.” While the footprint may be an incidental side effect for an oystercatcher and have no effect on other species, the same cannot be said of a beaver dam, which both affects the beaver and has major effects on many other species. Furthermore, in the glossary of both editions, Dawkins (1982; 1999) defines the extended phenotype as “all effects of a gene upon the world”, which must also include effects without feed-

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backs. This issue is important as it affects the conceptual development of community and ecosystem genetics.

In their development of community and ecosystem genetics, Whitham *et al.* (2003) specifically adopted Dawkins' broader definition of the extended phenotype, *i.e.*, "the effects of genes at levels higher than the population; *sensu* Dawkins, 1982." This definition intentionally did not include the more limiting requirement of a feedback of fitness consequences on the individual. The restriction of a feedback on fitness also is not included in the definitions of the "traditional" phenotype in modern quantitative genetics. For example, Lynch and Walsh (1998) refer to the pioneering work of Wilhelm Johannsen, who coined phenotype as "the observed value [of a continuous character] for an individual – a compounding of genetic and environmental effects" (p. 11).

So why don't geneticists include a feedback in their definition of the traditional phenotype? There are two likely reasons. First, geneticists recognize that the phenotypes of genes can have positive, negative, or neutral selection impacts on the individual. Second, gene x environment interactions can result in a phenotype having positive selective value on the individual in one environment, but in another environment the same phenotype could have neutral or negative fitness consequences for the individual. By considering the phenotype and selection separately, confusion is avoided and ecological geneticists can deal with a much wider range of possibilities, as we illustrate below.

EXTENDED PHENOTYPES WITH AND WITHOUT FEEDBACKS

The same phenotype can have extended effects that may or may not feed back on the individual expressing the trait. For example, the concentration of condensed tannins (a trait that has been mapped on the *Populus* genome) represents a traditional phenotype. The extended phenotype of condensed tannin concentrations in leaf litter acts through a diverse soil microbial community to strongly affect rates of leaf litter decomposition and nutrient release and decomposition (Schweitzer *et al.*, 2004, in review). Because most leaf litter falls beneath the tree that produced it, there are likely to be fitness consequences for the individual trees that express different levels of condensed tannins (Schimel *et al.*, 1998; Northup *et al.*, 1998; Fischer *et al.*, in review).

It is easy to understand that genetic control over plant nutrient availability likely involves a feedback that affects the fitness of the individual expressing the genes for condensed tannins; however, the same phenotype can have community and ecosystem consequences that may not involve feedbacks. In streams, genetically based differences in condensed tannins of *Populus* also affect the rate of leaf litter decomposition, which is a major source of nutrients for aquatic organisms (Driebe & Whitham, 2000). In contrast to terrestrial ecosystems, leaf litter falling into streams may end up far from the tree that produced the litter, with little opportunity for feedbacks to the original trees. Nevertheless, the effects of condensed tannins extend into the adjacent stream, affecting macroinvertebrate and microbial communities (Wallace *et al.*,

1997). We consider aquatic communities to be extended phenotypes because they fall within the broader definition of the term: there are evolutionary implications for the aquatic ecosystem even though no apparent feedback on the tree is involved.

The fact that the same phenotype in the above example has multiple extended phenotypes, some with and some without feedbacks, illustrates the problem of combining phenotype and feedbacks (*i.e.*, selection) into one definition. These problems will only increase in community and ecosystem contexts, which are likely to involve many complex and unapparent feedbacks. The broader definition of Dawkins' (1982; 1999) and Whitham *et al.* (2003) avoids these problems by dealing with the phenotype and selection separately.

COMMUNITY-LEVEL SELECTION

Because Biernaskie and Tyerman (2005) misinterpret what we mean by community-level selection, we wish to clarify our position. Community-level selection simply means that the relationship between the value of an individual's phenotype and that individual's fitness (selection) depends on the interaction with one or more individuals of a different species. Given this definition, it is important to recognize that phenotypes can have fitness consequences for both the individual expressing the trait and for individuals of other species that may be living in association with the individual expressing the trait (Wade, 2003).

As we stated in Whitham *et al.* (2003), an individual's fitness is contextual and may depend on population, community, and ecosystem contributions to an individual's fitness. In other words, populations, communities, and ecosystems affect the fitness of individuals, but populations, communities, and ecosystems do not have fitness (Kerr & Godfrey-Smith, 2002). For example, the particular community (*e.g.*, extended phenotype) that arises in the context of genetic interactions between a dominant tree (*e.g.*, cottonwood) and a keystone herbivore (*e.g.*, beavers) can result from community-level selection. This community may or may not feed back to affect the fitness of beavers and trees. For example, the microbial decomposer community beneath a tree will affect the ability of a tree to take up nitrogen, but the aquatic decomposer community is much less likely to do so. In the case of our riparian community studies, the abundance of dependent species (*e.g.*, arthropods) will covary with tree genetics (*e.g.*, McIntyre & Whitham, 2003), but may not affect tree fitness. In each example, fitness of individual community members (*e.g.*, microbes and arthropods) is likely to depend on tree genes causing extended community phenotypes to develop from community-level selection. Considering the implications of extended phenotypes in a larger context (*i.e.*, with and without feedbacks) facilitates our placing community and ecosystem ecology within a genetic and evolutionary framework.

A broader definition of an extended phenotype that does not require feedbacks advances the theory of community genetics because it recognizes that genes can have predictable and cascading effects on the community and ecosystem. Importantly, just as "traditional" phenotypes can be heritable, so can extended phenotypes be heritable.

Two recent studies (Johnson & Agrawal, 2005; Shuster *et al.*, 2005) have demonstrated heritability of the arthropod community associated with individual plant genotypes. Whether or not these arthropod communities are adaptive for their host plants is unknown. Some extended phenotypes may feed back to affect the fitness of the individual expressing the trait, while others may not. However, just because many may not affect the fitness of the individual does not mean that they are unimportant or cannot affect the community and species' evolution in different genetic and community contexts. In fact, as the importance of species interactions increases, we expect that these indirect effects may become more important than the direct effects (Wolf *et al.*, 1998). In our view, restricting the concept and consequences of the extended phenotype to just those that affect the fitness of the individual ignores the expression of genes at the population, community, and ecosystem levels, and is inconsistent with the broader definition as originally proposed.

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Literature cited

- Biernaskie, J. M. & J. G. Tyerman, 2005. The overextended phenotype. *Écoscience*, 12: 3-4.
- Dawkins, R., 1982. *The Extended Phenotype*. Oxford University Press, New York, New York.
- Dawkins, R., 1999. *The Extended Phenotype* (2nd Edition). Oxford University Press, New York, New York.
- Driebe, E. & T. G. Whitham, 2000. Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. *Oecologia*, 123: 99-107.
- Fischer, D. G., S. C. Hart, T. G. Whitham, B. J. Rehill, R. L. Lindroth & P. Keim.** Hidden belowground responses to defense: Do highly defended leaves require more roots? *Proceedings of National Academy of Sciences* (in review).

- Johnson, M. T. J. & A. Agrawal, 2005.** Plant genotype and the environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology* (in press).
- Kerr, B. & P. Godfrey-Smith, 2002. Individualist and multi-level selection perspectives on selection in structured populations. *Biology and Philosophy*, 17: 477-512.
- Lynch, M. & B. Walsh, 1998. *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Sunderland, Massachusetts.
- McIntyre, P. J. & T. G. Whitham, 2003. Plant genotype affects long-term herbivore population dynamics and extinction: Conservation implications. *Ecology*, 84: 311-322.
- Northup, R. R., R. A. Dahlgren & J. G. McColl, 1998. Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: A positive feedback? *Biogeochemistry*, 42: 189-220.
- Schimel, J. P., R. G. Cates & R. Ruess, 1998. The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan taiga. *Biogeochemistry*, 42: 221-234.
- Schweitzer, J. A., J. K. Bailey, B. J. Rehill, G. D. Martinsen, S. C. Hart, R. L. Lindroth, P. Keim & T. G. Whitham, 2004. Genetically based trait in a dominant tree affects ecosystem processes. *Ecology Letters*, 7: 127-134.
- Schweitzer, J. A., S. C. Hart & T. G. Whitham.** Consequences of genetic-based plant traits on ecosystem nutrient dynamics: Condensed tannins and nutrient transformations. *Ecosystems* (in review).
- Shuster, S. M., E. V. Lonsdorf, G. M. Wimp, J. K. Bailey & T. G. Whitham.** Community heritability: The genetic basis of multilevel selection and community structure. *Proceedings of National Academy of Sciences* (in review).
- Wade, M. J., 2003. Community genetics and species interactions. *Ecology*, 84: 583-585.
- Wallace J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, 277: 102-104.
- Whitham, T. G., W. P. Young, G. D. Martinsen, C. A. Gehring, J. A. Schweitzer, S. M. Shuster, G. M. Wimp, D. G. Fischer, J. K. Bailey, R. L. Lindroth, S. Woolbright & C. R. Kuske, 2003. Community and ecosystem genetics: A consequence of the extended phenotype. *Ecology*, 84: 559-573.
- Wolf, J. B., E. D. Brodie III, J. M. Cheverud, A. J. Moore & M. J. Wade, 1998. Evolutionary consequences of indirect genetic effects. *Trends in Ecology and Evolution*, 13: 64-69.

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