

FORUM

The overextended phenotype¹

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In a potentially influential article, Whitham *et al.* (2003) adopted the concept of the extended phenotype (Dawkins, 1982) to suggest a novel perspective on community genetics and evolution. Their purpose was to examine “how the extended phenotypes of genes have important consequences at community and ecosystem levels”, keeping in mind “the ultimate consequence of heritable extended phenotypes” (p. 560): community evolution by natural selection. We take issue with two aspects of the interpretation of extended phenotypes (EPs) given by Whitham *et al.* (2003) and adopted elsewhere in the emerging literature of community and ecosystem genetics (references below). First, we clarify that the functional concept of the EP (*sensu* Dawkins, 1982) is, in an important sense, more precise than employed by recent authors. Second, natural selection of so-called ‘extended phenotypes’ involves an unlikely mechanism of selection and instead implies the existence of adaptive ‘community phenotypes’.

As part of a special feature on community genetics (Ecology, volume 84, March 2003), Whitham *et al.*’s (2003) perspective was followed by a number of critical reviews. Critics ranged from optimistic (Cavender-Bares & Wilczek, 2003; Wade, 2003; Wilson & Swenson, 2003; and see Mitton, 2003) to highly skeptical of the concept of community evolution by natural selection (Collins, 2003; Morin, 2003; Ricklefs, 2003). Unfortunately, however, none of these critics revisited Dawkins’ (1982) original concept of the extended phenotype to adequately question its relevance to community genetics. Consequently, no critic fully explored the causal link between community-level genetic effects and the survival of the genes involved.

The extended phenotype is an aid for understanding genetic effects as adaptations. Specifically, Dawkins (1982, p. 207) considered phenotypes to be “devices by which genes lever themselves into the next generation, or barriers to their doing so”, and demonstrated that adaptive phenotypes need not be restricted to the boundaries of discrete ‘vehicles’ (*e.g.*, organisms or groups). (Hence, beaver dams and bird nests are phenotypes designed by natural selection even though they exist outside of the bodies of beavers and birds, respectively, that construct them). Of course, not all genetic effects on the

world at large are adaptive; many will be the side effects of other adaptations, and have no influence on the survival of the genes involved. For those incidental consequences, Dawkins (1982, p. 207) concluded, “we do not bother to regard them as phenotypic expressions of genes, either at the conventional or the extended phenotypic level”. Whitham *et al.* (2003, p. 560) do precisely this; they used a broad-sense concept of the extended phenotype as “the effects of genes at levels higher than the population”—which presumably include incidental side effects that act as neither tools nor barriers to gene survival.

Many of the proposed ‘extended phenotypes’ from Whitham *et al.* (2003) stand out as incidental side effects. They suggested, for example, that genes for the timing of salmon migration and spawning have the extended phenotypic effect of enhanced riparian plant growth. In the logic of the EP, their example suggests that *enhanced riparian plant growth is the phenotypic effect of a gene ‘for’ plant growth, sitting in the bodies of salmon but acting via behavioural modification of the animals that transfer salmon-derived nutrients to the forest. We see the effects of this gene today because it has outlasted rival alleles that do not have the effect of enhancing riparian plant growth.* Of course, it is difficult to conceive of any immediate effects that could possibly benefit the next generation of salmon that carry the enhanced plant growth allele. Hence, it seems implausible that enhanced plant growth actually represents a device by which salmon genes ‘lever themselves into the next generation’.

Similarly, recent investigations in community genetics that allude to ‘extended phenotypes’ (see Bailey *et al.*, 2004; Fischer *et al.*, 2004; Schweitzer *et al.*, 2004) describe higher-order genetic effects that can be understood as incidental consequences. In most cases, the authors demonstrate 1) that genetic variation exists for some trait in a given species, and 2) that variation in that trait correlates with a community- or ecosystem-level effect. In no case, however, is the intention to determine whether the higher-order effect serves to increase the frequency of alleles ‘for’ that effect, at the expense of alternative alleles. Without addressing this final criterion, there is no justification for invoking the concept of the extended phenotype.

Given that most community-level effects seem implausible as true extended phenotypes, how might they be considered adaptive? Whitham *et al.* (2003) adopted a multi-level selection approach as their model for the evolution of ‘extended phenotypes’, in which higher-order

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groups (*e.g.*, riparian communities) might act as unitary, 'reproducing' vehicles for gene survival. Note the difference with our approach above, where we presumed that the effect of enhanced plant growth, for example, would have to influence the reproductive success of individual salmon bodies. Also notice that if the whole group is considered as a functional unit, then Whitham *et al.*'s community-level effects are not actually meant to extend beyond the boundary of the relevant unit (the group) at all. They could more simply be understood as 'community phenotypes' upon which, in theory, group selection may act. In reality, however, most communities seem to lack the high rates of reproduction and replacement that would be necessary for effective selection at the community level (Williams, 1992).

Community-level selection is far from an obvious consequence of the extended phenotype *sensu* Dawkins (1982). In fact, the gene-centric viewpoint that is central to extended phenotypes can do without the notion of 'vehicles' altogether. Instead, seemingly harmonious higher-order units arise by a form of frequency-dependent selection, in which "each gene [is] selected because it prospered in its environment, and its environment necessarily included the other genes which were simultaneously prospering in the gene pool" (Dawkins, 1982, p. 240). And for many extended phenotypic interactions, a gene's environment will necessarily include the effects of genes in other gene pools, potentially across phyla, and even across kingdoms. Thus, even 'harmonious' multi-species units may be adequately explained by frequency-dependent selection acting at the gene level. The association of extended phenotypes and higher-order group selection is an added source of imminent confusion.

Genetic effects at the community and ecosystem level may certainly have important ecological consequences; whether these effects are adaptive or not does not alter the conclusion (see also Hochwender & Fritz, 2004). Whitham *et al.*'s suggestion, however - that many community-level phenotypes are in fact adaptive - must be considered carefully. We have suggested that many of the higher-order effects from the community genetics literature are irrelevant for the survival prospects of the genes involved, unless some plausible mechanism exists for group selection to act at the whole-community level. It would be a shame to confuse the plausibility of extended phenotypes (*sensu* Dawkins, 1982) with the plausibility of

adaptive 'community phenotypes'. Future debate should be focused squarely on the latter.

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NOTE ADDED IN PROOF

In a recent essay, Richard Dawkins similarly appealed for a "disciplined extension" of his extended phenotype concept, though he did not treat 'community genetics' explicitly (Dawkins, 2004). We discovered Dawkins' article while our own essay was in the press.

Dawkins, R., 2004. Extended phenotype--but not *too* extended. A reply to Laland, Turner, and Jablonka. *Biology and Philosophy*, 19: 337-396.

“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 nec-

essarily 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, a nutrient release and decomposition (Schweitzer *et al.*, 2004, unpubl. data). 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.*, unpubl. data).

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.*, unpubl. data) 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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Extended phenotypes and community genetics: Semantics and mechanics¹

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In this issue of *Écoscience*, Biernaskie and Tyerman (2005) openly criticize a recent paper on community genetics and extended phenotypes (EPs) by Whitham *et al.* (2003). Their critique is articulated around two main themes: the scope of the original EP concept in Dawkins (1982) *versus* Whitham *et al.* (2003), and the nature and plausibility of the selective mechanisms that can operate on Whitham *et al.*'s EPs.

Biernaskie and Tyerman (2005) first argue that Whitham *et al.* (2003) have unduly expanded the original scope of Dawkins' EP concept, hence their title, by including incidental effects of gene expression that do not affect this particular gene's survival. In so doing, they are in line with Dawkins' original purpose for developing the EP concept. Indeed, Dawkins' central argument is that genes (or rather, replicators) survive and lever themselves into the next generation by virtue of their phenotypic effects upon the world. It seems that the term 'extended phenotype' was coined to signify that these effects are not necessarily limited to the vehicle harbouring that particular gene or replicator unit. Biernaskie and Tyerman (2005), therefore, are legitimately concerned with the use of the EP concept in contexts that omit to consider if and how phenotypic effects are favouring or hindering the unit being transmitted.

In their answer to Biernaskie and Tyerman (2005), Whitham *et al.* (2005; 17 co-authors!) clarify their notion of EPs in the context of community genetics and evolution. Far from reducing the applicable scope of this concept, they explicitly extend it to genetic effects that do not feedback to the individual carrying the gene responsible for these effects. They resort to the second edition of Dawkins' book (1999) to justify that it is formally correct to discuss all effects of any gene expression as extended phenotypes. I believe they may be right in doing so because effects of individual gene expression can indeed be of the utmost importance in determining community composition and richness. These authors have themselves presented much fascinating and detailed empirical evidence that species assemblages can be strongly influenced by the expression of genes in other species (Whitham *et al.*, 2003 and references therein).

The main issue, however, is on the mechanisms that link EPs to community evolution. Here, I stand with Biernaskie and Tyerman (2005), and probably with Dawkins (1982; 1999), in considering that extended phenotypes without feedback effects on the fitness of the individual expressing an EP are not pertinent to discussion about natural selection, whatever level it is acting at. According to Whitham *et al.* (2005), Biernaskie and Tyerman (2005) misunderstood their notion of community-level selection. However, that an individual fitness is contingent upon biotic interactions within a given community context is nothing new and cannot serve as a definition of community-level selection. Certainly, empirical data show that the EPs of a given gene, as conceived by Whitham *et al.* (2003; 2005), can have "predictable and cascading effects on community and ecosystems". It is also plausible that some sort of determinant (but poorly supported as of now) high-order selective mechanisms can operate within that community as a result of the critical influence of such EPs. However, can these EPs have any predictable effects on community evolution if the frequency change of the gene responsible for the EP is totally independent from the community it engendered? This is unlikely, unless the fate of that particular gene is governed by some other form of selection (*e.g.*, from direct fitness effect of the individual phenotype resulting from that gene). Otherwise, if the gene in question does not have fitness effect on the individual expressing it [note here that the individual phenotype is still worthy of interest in Whitham *et al.*'s (2005) logic], its frequency will vary haphazardly and so will its EP, *i.e.*, the community resulting from it. This type of implicit assumption certainly needs to be addressed by proponents of community evolution as a consequence of EPs.

The work of Whitham, his collaborators, and supporters is certainly of importance. Demonstrating that genetically determined phenotypes have major effects on community structure is a major contribution that empirically anchors community ecology within evolutionary genetics. The resistance and/or incomprehension expressed by population geneticists/molecular ecologists such as Biernaskie, Tyerman, and myself is probably normal, for we tend to be strongly attached to explicit mechanistic explanations. I can only wish that they use this and other opportunities to further scrutinize the "nuts and bolts" of the emerging discipline of community genetics. In so doing, they would also positively respond to the advice of Antonovics (2003), who questioned the relative intellectual rigour of applying genetic terms to a community context.

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