

Extended phenotype redux

How far can the reach of genes extend in manipulating the environment of an organism?

The idea of the extended phenotype (EP), which was first proposed by the British evolutionary biologist Richard Dawkins to explain how and why organisms—or, more fundamentally, their genes—are able to manipulate their environment (Dawkins, 1982), has been the focus of intense debate and much research for more than 20 years. In his book, *The Extended Phenotype: The Long Reach of the Gene*, Dawkins observed that, “[the extended phenotype] so far changes the way we see animals and plants that it may cause us to think of testable hypotheses that we would otherwise never have dreamed of.” The EP has certainly been the stimulus for a great deal of research activity recently, as the tools of genomics and proteomics provide fresh evidence of its importance. The concept of the EP helps, for example, to explain how parasites modify the behaviour of their hosts to their advantage, or nest-building behaviour in birds. In particular, the relationship between the bacterial flora of the gut and their mammalian hosts has been a hot topic of late; one that has yielded new examples of the EP to support the themes Dawkins originally outlined.

The [extended phenotype] has certainly been the stimulus for a great deal of research activity recently, as the tools of genomics and proteomics provide fresh evidence of its importance

At the same time there has been an ongoing debate among proponents of neo-Darwinism—of which the EP is an important component—between those who advocate the EP and those who advocate theories such as niche construction, which propose that other factors—in addition to genes—have a crucial role in the way that organisms manipulate their environment, so that their descendents inherit both their genetic legacy and their environmental legacy. These different strands of the EP debate were finally pulled together at a

conference on the subject, organized by the European Science Foundation (ESF; Strasbourg, France) in late 2008. The main conclusion of the meeting was that the EP concept has become even more relevant in the light of recent research, but that its role will ultimately be restricted to an explanatory one, rather than as a tool for designing meaningful experiments.

In detail, the EP states that the genes of an organism can be expressed beyond their immediate biological boundaries, such as skin, shells or leaves. The EP can embrace nest-building or the manipulation of host behaviour by parasites. The main point is that the EP embraces entities such as nests or the dams built by beavers, the quality or functionality of which is correlated with certain alleles of the organism, on which natural selection can then act. This is the distinction between the EP and niche construction; for example, the EP is subject to a reproductive bottleneck as the benefit of the EP is passed on solely through the genes of an organism, rather than as an altered environmental niche for its progeny. In this manner, an allele that leads to better dams, for example, will increase the fitness of the beaver in which the allele is expressed. Similarly, an allele in a parasite that makes the parasite more effective at weakening the resistance of its host, or that is in some way able to modify its host’s behaviour to make it more likely that the parasite’s progeny will find a new host, will similarly be selected for by natural selection.

As Dawkins wrote, “Replicators are not, of course, selected directly, but by proxy; they are judged by their phenotypic effects. Although for some purposes it is convenient to think of these phenotypic effects as being packaged together in discrete ‘vehicles’ such as individual organisms, this is not fundamentally necessary. Rather, the replicator should be thought of as having extended phenotypic effects, consisting of all its effects on the world at large, not just its effects on the individual body in which it happens to be sitting” (Dawkins, 1982).

The point is that the EP is not the phenotype of the organism whose genes it encodes; it is the phenotype of a nest, a dam or, in the case of parasite–host interaction, changes in the host’s behaviour or appearance. This can be best demonstrated by one of the more dramatic examples of the EP: nematodes that infect ants and make them resemble ripe fruits (Hughes *et al*, 2008). Frugivorous birds that normally avoid ants now eat them—as their abdomens look similar to berries—and thus disperse the nematode eggs in their droppings, which are collected by ants looking for seeds and fed to their larvae, thus completing the cycle. In this case, as in others, the nematode does not, in any direct way, change the ant’s own genes; rather, it modifies the ant’s behaviour and appearance through its own genes. The ant’s new ‘fruit phenotype’ is actually the EP of the nematode.

The point is that the EP is not the phenotype of the organism whose genes it encodes; it is the phenotype of a nest, a dam or [...] changes in the host’s behaviour or appearance

In addition to constructions—such as bird nests or beaver dams—and modified host behaviour, there is a third category of EP that is described as genetic action at a distance, as noted by David Hughes, convenor of the ESF workshop, who is now at Harvard University (Cambridge, MA, USA). “The parasite and its host are in close contact, but genes can also cause EPs even if the two organisms are physically separated,” he said. “An example would be orchid genes causing a bee to pollinate it by tricking the bee into ‘thinking’ the orchid was another bee.” In this example, the orchid induces a phenomenon known as pseudocopulation: it mimics a female bee through appropriate chemical and tactile signals, and, if male



© Image Source/Corbis

bees attempt to mate with it, they pollinate the flower. In this case, the EP is the modified behaviour of the bee, and the alleles of relevant flower genes that mimic female bees most effectively will be favoured by natural selection.

Of these three categories, it is the EP of constructions that has been most widely known and studied so far. As Dawkins has pointed out, this has led to confusion over how far the EP extends, with some people asking whether a building would constitute the EP of an architect. The answer is no, as an architect's specific alleles are neither more nor less likely to be selected based on the design of his or her latest building. Yet, this idea leads to the consideration of a more interesting situation that involves constructions built or modified by a number of animals and that are not the product of a single organism. This is where niche construction theory comes into play, and it is the topic that has led to debates between proponents of the EP and proponents of niche construction.

Niche construction theory goes further than the EP by suggesting that many organisms within an ecosystem can alter the selective pressures on all of them by modifying their environment in various ways—not necessarily to their own immediate advantage. Dawkins has argued that niche construction is really a special case of the EP (Dawkins, 2004), which relates, in fact, to the genes of those organisms that participate in the relevant environmental components of the niche. But, he has dismissed the idea that evolution can act in a broader sense across a whole ecosystem and extend to organisms that are not directly involved in the niche construction. He has also reiterated the point, which runs throughout his books, that selection can only operate against variations of replicators, which are almost always alleles.

Yet, some advocates of niche construction insist that evolution can operate at a longer range: beaver dams might benefit other animals not directly involved in their construction, for example, increasing the

fitness of those organisms. Although this might be the case, Dawkins has pointed out that this still would not constitute any type of selection operating on beaver alleles. Only the selection of those organisms whose response to better dams is of direct benefit to beavers will subsequently influence the selection of beaver genes. Indeed, as the debate over the EP was revived earlier this decade, Dawkins quickly reined in the genie that he had originally released with a 2004 paper titled, *Extended Phenotype—but not too extended. A Reply to Laland, Turner and Jablonka* (Dawkins, 2004). This was a direct response to papers by so-called 'niche constructionists' Scott Turner, at State University New York (Syracuse, NY, USA), Kevin Laland, at the University of St Andrews (Fife, UK), and Eva Jablonka, at Tel Aviv University in Israel. In his paper, Dawkins clarified that the EP concept was only valid in situations where there was a direct correspondence between variations in the EP and in the selection of the replicators. "Extended phenotypes are worthy of the name only if they

are candidate adaptations for the benefit of alleles responsible for variations in them," he wrote. The niche constructionists seemed to be arguing that selective pressures can be coupled together at a longer range and operate simultaneously on the genes of many organisms—an extension of phenotype too far in Dawkins' view.

Indeed, since the 2004 paper, the EP and niche construction have often been depicted as opposing views, at least until the recent ESF conference in which a consensus emerged that the two were more complementary than contradictory, according to Patrizia d'Ettorre, Associate Professor at the Centre for Social Evolution, University of Copenhagen, Denmark, who wrote a report of the meeting. "[W]e concluded that the EP is alive and well today and it is not in conflict with concepts like niche construction or interacting phenotypes," she confirmed, and added that one of the main achievements was persuading representatives of different viewpoints to communicate directly with each other.

In fact, the EP camp concedes that phenotypes interact on a large scale and affect the adaptive landscape in which they operate, creating feedback on the organisms that express them. In turn, niche constructionists agree that EPs can only exert direct selective pressure on genes, or any other replicators—such as memes—if there is variation in the EP associated with the replicator. Still, the debate at the ESF meeting shifted to discussing whether the EP or niche construction is more important as an evolutionary driving force.

...the EP and niche construction have often been depicted as opposing views, at least until the recent ESF conference in which a consensus emerged that the two were more complementary than contradictory...

Niche constructionists, such as Turner, who attended the ESF conference, argue that the neo-Darwinist view of the gene as the sole determinant of cellular processes and ultimately phenotypes, and as the predominant unit of the adaptive process, is seriously flawed. Turner argued at the conference that our growing knowledge of heritable epigenetic mechanisms that effectively change gene expression—and therefore

phenotype—without altering the underlying DNA, suggests that evolution operates at different levels above the gene. First principles of genetic inheritance alone, he said, cannot explain the physiological factors that shape evolution and adaptability.

Jablonka goes even further, as she proposes that Darwinian evolution has been driven as much by adaptation of ecosystems as it has by genetic sequences (Jablonka, 2004). "As to niche construction, it goes beyond Dawkins' EP idea, because it recognizes that variations in ecological legacies can be inherited, and that this can happen even when there is no genetic change—no change in DNA base sequence," she said. Jablonka also believes that epigenetic mechanisms have a crucial role in this adaptive dance between organisms and environment: "Ecological inheritance may be facilitated or dependent on epigenetic inheritance mechanisms. Clearly, co-developing partners may induce epigenetic variations in each other. For example, nutrition-based developmental programming by the mother during her pregnancy can lead to offspring with the same preferences, which aids the construction of the same food-related environment."

In such a scenario, the environment that conferred the greatest fitness on individuals would be favoured, in turn prolonging the underlying epigenetic changes through successive generations. But, as the EP proponents point out, although these epigenetic changes themselves provide part of the selective landscape, it is still the underlying genes that provide the ultimate source of variation. Epigenetic mechanisms, after all, rely on genes. "There is a little bit of a gap there that no one has quite managed to bridge," Turner commented. "I am suggesting that a comprehensive theory of evolution is not possible until the gap is bridged."

Turner defined this gap as a paradox in which, by creating their own environment, organisms are in effect adapting to themselves. "The way out of the conundrum, I think, is to treat evolution and natural selection as the physiological process it properly is, which includes the expression and selection of heritable memory in DNA. This is more in line with the emerging picture of the genotype as a dynamic and integrated part of the cell rather than a determiner of it," Turner concluded.

Within this picture, there is broad agreement now that the EP concept is helpful to explain some

adaptations that have occurred within all three categories, many of which differ in the rate of evolution of the associated genotypes. The first category—constructed EPs such as nests or dams—includes single organisms, usually multicellular eukaryotes, whose genomes evolve relatively slowly and therefore lead to stable long-term adaptations. The second category—host–parasite interactions—involves both the genomes of the host and of the parasite in the attempt to modify the host's behaviour. The parasite's genes almost always evolve faster and tend to call the shots, whereas the host is usually restricted to damage limitation.

Yet, as Sylvain Gandon, from the Centre of Evolutionary and Functional Ecology in Montpellier, France, pointed out, this does not mean that parasites inevitably evolve into a state of symbiosis with the host: "There are many ways a parasite can improve its habitat within the host. Symbiosis might be one way but, [by] contrast, extreme virulence—with more aggressive exploitation strategies—could be another. Thus, no, symbiosis is not the ultimate evolutionary outcome of host–parasite co-evolution," he said.

Jablonka [...] proposes that Darwinian evolution has been driven as much by adaptation of ecosystems as it has by genetic sequences...

Aside from dramatic examples such as rabies, in which the host nearly always dies, there are many examples of host–parasite homeostasis that exhibit varying levels of virulence. "The most classic example is perhaps the evolution of virulence of the myxoma virus in rabbits," noted Gandon (Fenner & Fantini, 1999). "The virus was introduced in 1950 in Australia to control the population of European rabbits [...]. Although the virulence of the virus rapidly decreased, it reached a plateau—average virulence was around 70% at the plateau—after a few years." In fact, there are many models showing that parasite virulence need not always evolve towards zero (Frank, 1996).

There are also well-known examples of the EP in the third category—genetic action at a distance—such as social parasites that manipulate the host from afar. In some cases the social parasite never encounters the host at all, as in the case of

the common European cuckoo, which lays its eggs in the nests of birds such as meadow pipits, dunnocks and reed warblers. The EP is the trickery involved in persuading the host birds to incubate the egg and raise the young. The relevant adaptation lies in making the eggs, and subsequent chicks, sufficiently similar to those of the host that they are not thrown out of the nest.

Insects can also be social parasites, even of their own kind, such as the 'slave-making' ant species *Polyergus rufescens*, which d'Ettorre studies. The *Polyergus* ant enters the nests of its 'host'—species of the *Formica* ant family—and emits chemical signals to disguise its presence. The *Polyergus* ant then kills the resident queen and dupes the host workers into obtaining food for its own kin. The EP in this case, similarly to the cuckoo, lies in fooling the host species into feeding the parasitic brood. Clearly, *Polyergus* alleles that made the ant more effective at disguising itself would be favoured by natural selection. As d'Ettorre noted, there are variations on this theme: "[t]here are other kinds of ant social parasites, so called 'inquilines' that do not kill the host queen but co-habit with her," she explained. "These inquilines are able to suppress the reproduction of the host queen—action at distance—so that she is only producing workers but not new males and reproductive females."

These examples highlight the power of the EP to explain the vast panoply of complex relationships and adaptations observed in nature. It remains to be seen, however, whether the idea of the EP itself can be extended to become an integral part of a unified theory of evolution, one that fully bridges the gap between genotypes and environments.

REFERENCES

- Dawkins R (1982) *The Extended Phenotype: The Long Reach of the Gene*. Oxford, UK: Oxford University Press
- Dawkins R (2004) Extended Phenotype—but not too extended. A reply to Laland, Turner and Jablonka. *Biology & Philosophy* **19**: 377–396
- Fenner F, Fantini B (1999) *Biological Control of Vertebrate Pests. The History of Myxomatosis: An Experiment in Evolution*. Wallingford, UK: CAB International
- Frank SA (1996) Models of parasite virulence. *Q Rev Biol* **71**: 37–78
- Hughes DP, Kronauer DJC, Boomsma JJ (2008) Extended Phenotype: nematodes turn ants into bird-dispersed fruits. *Curr Biol* **18**: R294–R295
- Jablonka E (2004) From replicators to heritably varying phenotypic traits. The Extended Phenotype revisited. *Biology & Philosophy* **19**: 353–375

Philip Hunter

doi:10.1038/embor.2009.18