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Personal effects

Living things from bacteria to humans change their environment, but the consequences for evolution and ecology are only now being understood, or so the 'niche constructivists' claim. Dan Jones investigates.

In the Negev Desert of Israel, small organisms can have a big impact. Take the cyanobacteria that live in the soil. Some species secrete sugary substances that form a crust of sand and soil, protecting the bacterial colonies from the effects of erosion. When the rains come, the crusty patches divert water into pools in which wind-borne seeds can germinate. These plants in turn make the soil more hospitable for other plants. Thanks in part to these bacteria, patches of vegetation can be found where they might not otherwise exist. The action of the bacteria, together with local climate change, could lead to the greening of large parts of the desert.

The Negev cyanobacteria, and organisms like them, are also having an impact on evolutionary biologists these days. Examples of creatures altering their environment abound — from beavers that dam streams and earthworms that enrich the soil to humans who irrigate deserts. But too little attention has been given to the consequences of this, say advocates of niche construction. This emerging view in biology stresses that organisms not only adapt to their environments, but also in part create them. The knock-on effects of this interplay between organism and environment, say niche constructivists, have generally been neglected in evolutionary models. Despite pointed criticism from some prominent biologists, niche construction has been winning converts.

"What we're saying is not only novel, but also slightly disturbing," says Kevin Laland, an evolutionary biologist at the University of St Andrews in Fife, UK, and one of the authors of the idea[1]. "If we're right, it requires rethinking evolution."

The conventional view of evolution sees natural selection as shaping organisms to fit their environment. Niche construction, by contrast, accords the organism a much stronger role in generating a fit by recognizing the innumerable ways in which living things alter their world to suit their needs. From this perspective, the road between organism and environment is very much a two-way street.

The intellectual stirrings of niche construction date back to the early 1980s, when Harvard University geneticist Richard Lewontin turned to differential equations — stock in trade for population biologists — to look at evolution from two different perspectives[2]. He created one set of equations to describe the conventional view of evolution, the one-way-street version. A second set of equations, which he felt better described real evolutionary processes, depicted evolution as a continual feedback loop, in which organisms both adapt to their environments and alter them in ways that generate new selective pressures. Although Lewontin's equations provided a broad perspective rather than a detailed model, he helped to kick-start the niche-constructivist approach, says Laland. "He really put the idea on the map."

"What we're saying is not only novel, but also slightly disturbing. If we're right, it requires rethinking evolution." — Kevin Laland

Sons of soil

But it has taken years for biologists to begin to incorporate niche construction into more detailed models of evolution and ecology, in part because organism–environment interactions can be so complex. Earthworms, for instance, not only aerate the soil by tunnelling, as any gardener knows, but they also alter its chemical composition by removing calcium carbonate, adding their mucus and excrement, and pulling leaves down into the soil to decay. All of this produces a more favourable environment for worms to live in. Yet classical evolutionary models have typically failed to consider how this transformation alters the selective pressures on the worms and other soil inhabitants, say niche-construction advocates.

Back in the Negev Desert there are further examples of dramatic niche construction. At least three species of snail feed on lichens that live just below the surface of porous rocks. To

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From dissolving desert rocks to building dams, all organisms mould their environment to a certain extent.

get at the lichens, the snails have to literally eat through the rock, which they then excrete, creating soil around the rock in the process. This might sound insignificant, but it has been calculated that the combined action of these snails could generate enough soil to affect the whole desert ecosystem[3]. By transferring nitrogen in rocks to the soil, where plants use it for growth, the snails contribute substantially to sustaining local biodiversity.

Bigger picture

In extreme cases, niche-constructing activities can affect the whole world. The classic example from early evolutionary history is that of oxygen-producing cyanobacteria, which helped to set the stage for the evolution of animals and plants. Today, niche construction by human threatens to affect practically all life, as we pump large amounts of carbon dioxide into the atmosphere.

Critics are quick to point out that such cases have been well known to biologists for some time. "Darwin realized that organisms can change their environments in ways that affect their own evolution," says Laurent Keller, an evolutionary biologist at the University of Lausanne in Switzerland. "There are already many cases of niche construction by animals and especially humans," he says.

But advocates of niche construction counter that previous attempts to include these effects in evolutionary models have not gone nearly far enough. "People hadn't thought through the consequences of these effects, either for evolution or ecology," says John Odling-Smee, a biological anthropologist at the University of Oxford, UK.

To encourage people to consider the issue, Odling-Smee and Laland have taken a two-pronged approach. First, they have catalogued hundreds of examples, involving thousands of species such as the Negev Desert organisms, to drive home the point that niche construction is a widespread phenomenon. In addition, they have developed mathematical models that capture the bidirectional nature of the niche-constructivist view, to show how these processes can actually be modelled.

Traditional ecological models typically distinguish between living things and their physical environment, but it is hard to model both elements at the same time. To find a way around this, Laland and Odling-Smee teamed up with Marcus Feldman, an evolutionary biologist and mathematical modeller at Stanford University in California. They found that they could look at niche construction by treating both living and non-living components of a niche as environmental factors that are both affected by, and feed back to, all the organisms in the ecosystem. They presented their results in a 2003 book[1], whose purpose, they say, was in part to convince other scientists to take niche construction into account in their research.

Perhaps the most direct way an organism can alter the challenges it must face is by selecting where it lives, says Robert Holt, an ecologist at the University of Florida in Gainesville. Such habitat selection defines the future context for the evolution of the new residents and their progeny. By choosing to live in places to which they are already adapted, organisms can short-circuit the selective forces that ordinarily lead to evolutionary change. In this way, habitat selection can lead to niche conservatism, which is the tendency not to adapt to new environments, and may explain the evolutionary stasis often seen in the fossil record.

> "Even Darwin realized that organisms can change their environments in ways that affect their evolution." — Laurent Keller

Organisms can also shape their interaction with the world in more subtle ways. Developmental biologists know, for instance, that the mature form of many organisms varies depending on the environment in which they grow up. This is known as phenotypic plasticity. Although some creatures, such as beavers and cyanobacteria, alter their environment directly, others niche construct by modifying themselves, says Sonia Sultan, a botanist at Wesleyan University in Middletown, Connecticut. Sultan defines a niche according to the way an organism experiences the world — its niche is the sum of its experiences, rather than its immediate physical surroundings. Some plants, for example, can grow smaller or larger leaves, depending on whether they happen to be growing in a sunny or shady spot. So this is a form of niche construction, claims Sultan, because the plant is altering its own experience of sunlight.

Although phenotypic plasticity has been well studied by a number of researchers, it has yet to be incorporated into the core of evolutionary theory. "Niche construction weaves together a number of themes in ecology and evolution that have typically been studied in isolation," Sultan says. Rethinking evolution in light of plasticity and other issues raised by niche construction could contribute to an updating of evolutionary theory, Sultan suggests.

An update is precisely what Laland and his colleagues have proposed in what they have dubbed extended evolutionary theory. In classical theory, genetic inheritance is the only link through time between generations. Niche construction requires that a second form of inheritance, termed ecological inheritance, be taken into account.

Inherit the earth

According to this view, many of the physical features that a creature encounters, and the kinds of problem it has to solve, are inherited from the activities of the previous generation. Forest fires, for example, which help to distribute the seeds of some plant species, might be thought to rely solely on the chance of a lightning strike. But the plants in the forest can themselves increase the odds of a fire by secreting flammable oils and retaining dry dead wood in the canopy[4]. Similarly, every earthworm inherits an environment more suited to its lifestyle thanks to the activities of its forebears. Ecological inheritance means that the effects of genes on the environment are, a little like the genes, passed down through the generations.

The notion that genes reach beyond the bounds of the organism is often referred to as the 'extended phenotype', a term coined by

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Construction workers: humans create towns from deserts, but how do we and our niches interact?

J. MARSHALL/CORBIS

Richard Dawkins, an evolutionary biologist at the University of Oxford, in his 1982 book of the same name. So it might come as something of a surprise that Dawkins has written a highly critical commentary accusing niche constructivists of a serious conceptual blunder[5].

Dam fools

Dawkins's classic example of an extended phenotype is the beaver dam. These remarkable structures dramatically alter the surrounding ecosystem. Trees are felled to make the dam, which in turn floods the area, providing a new environment for species from frogs to fish. If the beaver's footprint on its environment is viewed as an example of ecological inheritance, it would seem that the extended phenotype and niche construction should make natural bedfellows.

But guess again. Although Dawkins says he recognizes the importance of organism-induced effects on the world, he believes that niche construction conflates two distinct kinds of effects. Dam-building certainly counts as an organism engineering its environment, he says, but other effects, such as the oxygenation of the atmosphere by cyanobacteria, are mere co-incidental by-products of life. These types of effects, which Dawkins calls niche changing, are too loosely connected to the success of the organisms that cause them to count as genuine niche construction.

Dawkins is not alone in this view. Kim Sterelny, a philosopher of biology at the Victoria University of Wellington, New Zealand, says that niche construction "lumps too many things together". This matters, because the two kinds of effects, construction versus mere changing, generate different feedback loops between the organism and the environment, which can lead to different evolutionary dynamics, Sterelny says.

Laland says he is sympathetic to the distinction, but is concerned that the term 'mere' associated with 'niche changing' downplays its evolutionary importance. For Laland, niche changing is as important to evolution as beaver-like niche construction. When you get down to doing the models it often doesn't help much to make the distinction, says Laland. The effects of organisms can have evolutionary consequences regardless of whether they are produced by adaptations.

Although the philosophical debates continue, other researchers are busily incorporating the ideas of niche construction into their work. Sultan, for instance, finds the concept useful in thinking about invasive species, whose potentially destructive power is a key issue in conservation biology.

Kevin Laland (left) thinks the power of niche construction is being underestimated, but Laurent Keller is not convinced.

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Invasive species, such as weeds, often experience a time lag between arriving in a new niche and colonizing it. It may take a while for successful genetic variants of the invader to arise and spread, for instance. But if a species arrives that has sufficient phenotypic plasticity to thrive in the new environment, the take-over might be much more rapid. Sultan believes that explicitly adopting niche-constructivist views on phenotypic plasticity could help scientists to devise appropriate strategies for combating conservation problems: it could give them, for example, more accurate tools for projecting the rate of spread of an invasive plant.

Others are pioneering ways to study perhaps the ultimate niche constructors — us. In many obvious ways, humans have utterly transformed otherwise inhospitable parts of the world to suit our needs, from ranks of houses in the desert to skyscrapers. Perhaps a less obvious example of niche construction is human culture. Culture itself can be seen as a niche that we inhabit, and just as we shape our culture, our culture shapes us. One example of this is the emergence over several thousand years of lactose tolerance in European adults, which has followed the cultural practice of drinking cow's milk[6].

Culture club

Now a number of anthropologists are scrutinizing how culture can put selective pressure on our genetic make-up. In the past, many have been reluctant to tackle such questions, in part because of fears of being associated with genetic determinism, but also because of the daunting mathematics of modelling gene–culture interactions. But that seems to be changing, says Joe Henrich, an anthropologist at Emory University in Atlanta, Georgia. "The study of cultural evolution is expanding rapidly within scientific anthropology," he says.

One of the hottest areas at the moment is the puzzle of human sociality — why we are so often willing to cooperate with unrelated people, even when it is not in our immediate self-interest[7]. Whether or not genes promoting sociality flourish depends in part on the social environment in which they find themselves, which in turn is affected by culture. "We have shown that culture can evolve to change the selective environment faced by genes favouring cooperation. This opens up a whole evolutionary vista unavailable to non-cultural species," says Henrich.

Niche-construction advocates are passionate about their new view of ecological and evolutionary processes, whether they study bacteria or humans, but it is too soon to say whether the approach will yield insights that might otherwise have been missed. Still, Laland fully accepts the challenge. "The onus is on us to show that this is going to be useful," he says. ■

Dan Jones is a copy editor for *Nature Reviews Drug Discovery*.

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